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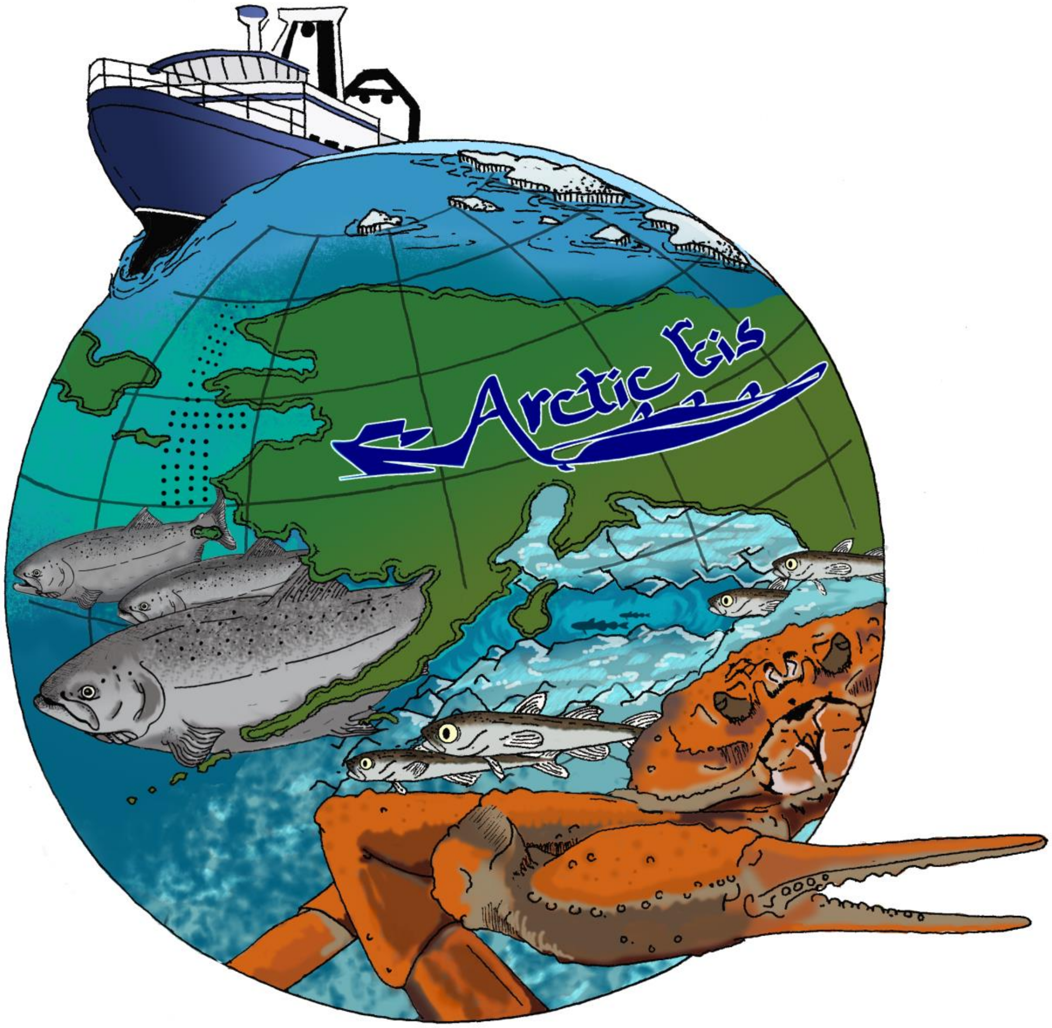
Arctic Ecosystem Integrated Survey Final Report on Distribution of Fish, Crab, and Lower Trophic Communities in the Northeastern Bering Sea and Chukchi Sea



US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region

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Arctic Ecosystem Integrated Survey Final Report on Distribution of Fish, Crab, and Lower Trophic Communities in the Northeastern Bering Sea and Chukchi Sea

May 4, 2018

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Prepared under BOEM Awards
M12AC00009 (University of Alaska Fairbanks), M12PG00018 (Alaska Fisheries Science Center) and M10PG00050 (U.S. Fish & Wildlife Service)
Prepared under Alaska Coastal Impact Assistance Program Award Number
F12AF00188 (University of Alaska Fairbanks)

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US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

OCS Study
BOEM 2017-077

DISCLAIMER

Study concept, oversight, and funding were provided by the US Department of Interior, Bureau of Ocean Energy Management (BOEM), Environmental Studies Program, Washington, DC, under Contract Numbers: M12AC00009 (University of Alaska Fairbanks, UAF), M12PG00018 (NOAA Alaska Fisheries Science Center, NOAA-AFSC), and M10PG00050 (US Fish and Wildlife Service, USFWS). This report has been technically reviewed by BOEM and it has been approved for publication. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions of policies of the US Government, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

Majority funding was provided with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program (CIAP-USFWS), U.S. Department of the Interior under Agreement Number F12AF00188 with UAF. Gap funding for the 2013 Northern Bering Sea portion of the surface and midwater trawl cruise was provided by the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative through NOAA-AFSC. Additional support was provided by AFSC, UAF, USFWS, and the Alaska Department of Fish & Game (ADFG).

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CITATION

Mueter, FJ, Weems, J, Farley, EV, Kuletz, K, Lauth, RR, Sigler, MF. 2017. Arctic Ecosystem Integrated Survey Final Report on Distribution of Fish, Crab, and Lower Trophic Communities in the Northeastern Bering Sea and Chukchi Sea. US Dept. of the Interior, Bureau of Ocean Energy Management, Alaska OCS Region. OCS Study BOEM 2017-077. 1558 p.

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List of Abbreviations and Symbols

ADFG	Alaska Department of Fish and Game
AFSC	Alaska Fisheries Science Center
Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CFOS	College of Fisheries and Ocean Sciences
CIAP	Coastal Impact Assistance Program
NOAA	National Oceanic and Atmospheric Administration
PMEL	Pacific Marine Environmental Laboratory
UAF	University of Alaska Fairbanks
USFWS	US Fish and Wildlife Service

1. Abstract

This study on the *Distribution of Fish, Crab, and Lower Trophic Communities in the Northeastern Bering Sea and Chukchi Sea* formed a large part of the broader Arctic Ecosystem Integrated Survey, the first comprehensive fisheries ecosystem assessment of the northern Bering Sea and Chukchi Sea. Surveys were conducted in the summers of 2012 and 2013 from several platforms to sample demersal as well as pelagic fish communities. Oceanographic and biological samples collected during these surveys provided a trove of new information on the distribution, abundance, biology and population dynamics of pelagic and demersal fish and invertebrate populations in the northern Bering Sea and Chukchi Sea, in addition to new insights into the physical forcing and plankton dynamics of the system.

Among the scientific highlights were: (1) Large differences in oceanographic conditions between 2012 and 2013, associated with differences in local winds and in the flow of water through Bering Strait and its advection in the Chukchi Sea, reverberated throughout the ecosystem and apparently affected the distribution and abundance of biota at all trophic levels; (2) High densities of larval and young-of-year Arctic cod (*Boreogadus saida*) were, for the first time, observed in the northeast Chukchi Sea in both survey years, suggesting that the northeast portion of the Chukchi Sea is an important nursery area for the early life history stages of Arctic cod in the Pacific Arctic; (3) Plankton, fish and invertebrate species of Pacific origin dominate demersal and pelagic communities throughout the region, but distinct Arctic populations of some species were associated with Arctic water masses on the northeast Chukchi Sea shelf; (4) Juvenile salmon of western Alaska origin, in particular chum (*Oncorhynchus keta*), pink (*O. gorbuscha*), and Chinook salmon (*O. tshawytscha*), were widespread and abundant in the northern Bering Sea, extending into the Chukchi Sea and mixing with local populations from Kotzebue Sound; (5) Arctic cod and snow crab (*Chionoecetes opilio*), two of the most abundant species by weight in Chukchi Sea catches, are continuous with and directly connected to populations in the Bering Sea. To what extent the Chukchi Sea populations of these species originate from spawning areas to the South or to the North of Bering Strait remains an area of active investigation.

Major results from these studies were published in a special issue in Deep-Sea Research (Mueter et al. 2017), but data collected during these surveys will continue to contribute to new and ongoing studies. A major legacy of the project will be the databases and maps available through the Alaska Ocean Observing System's Arctic Portal (http://portal.aoos.org/arctic), as well as through national archives. In addition to the databases and published studies, a major benefit of the project was the training that was provided for a number of students and post-docs. Both from a scientific and educational standpoint, the project has met its goals and has exceeded our expectations in terms of scientific output. This is in no small part due to our success in leveraging external resources and forging productive collaborations with investigators at multiple universities and agencies.

2. Introduction

Arctic marine ecosystems are undergoing rapid changes associated with ice loss and surface warming resulting from human activities (IPCC 2013). The most dramatic changes include an earlier ice retreat and a longer ice-free season, particularly on Arctic inflow shelves such as the Barents Sea in the Atlantic Arctic and the northern Bering Sea and Chukchi Sea in the Pacific Arctic, the two major gateways into the Arctic (Serreze et al. 2007, Frey et al. 2015, Wood et al. 2015, Danielson et al. 2017). The retreat of Arctic sea ice has opened access to the Arctic marine environment and its resources, particularly during summer, and among other changes has brought with it increased research activities. For the Pacific Arctic region, these activities have led to a number of recent compendiums examining physical, biogeochemical, and biological patterns and trends in this rapidly changing environment (Bluhm et al. 2010, Hopcroft and

Day 2013, Arrigo et al. 2014, Dunton et al. 2014, Grebmeier and Maslowski 2014, Arrigo 2015, Moore and Stabeno 2015, Arrigo 2016).

Changes in ice and thermal conditions in the Pacific Arctic impact all components of the ecosystem including benthic infauna and epifauna (Grebmeier et al. 2006a, Nelson et al. 2014), microbes and zooplankton (Nelson et al. 2014, Ershova et al. 2015), as well as fishes, seabirds, and marine mammals that provide important subsistence resources for communities in the Pacific Arctic (Moore et al. 2014). In spite of recent advances, significant gaps remain not only in our understanding of these impacts, but also in describing basic life history characteristics of key fish and invertebrate species in the Pacific Arctic, such as Arctic cod (*Boregadus saida*), saffron cod (*Eleginus gracilis*) and snow crab (*Chionoecetes opilio*), which have been identified as potential target species for a fishery (NPFMC 2009). Other fish species that currently occur in low abundances north of Bering Strait, including salmon (*Oncorhynchus* spp.), yellowfin sole (*Limanda aspera*), Bering flounder (*Hippoglossoides robustus*), and walleye pollock (*Gadus chalcogrammus*), have the potential to expand into the Arctic, with unknown consequences for the ecosystem (Moss et al. 2009b, Nielsen et al. 2012, Hollowed et al. 2013, Logerwell et al. 2015).

The Pacific Arctic Gateway, encompassing the broad shelf regions of the northern Bering Sea and Chukchi Sea (Fig. 1), has a strong influence on the Arctic Ocean through the transport of freshwater, heat, nutrients and plankton from the Subarctic to the Arctic (Roach et al. 1995). As a transition zone between Subarctic and Arctic communities, this region is characterized by strong gradients in species composition, diversity, and abundance of fish and invertebrates (Stevenson and Lauth 2012, Mueter et al. 2013). These strong gradients imply that small shifts in the distribution of water masses and biological assemblages can be associated with large changes at a given location such as a seabird colony or a coastal community. Therefore, broad-scale surveys are essential to linking biological assemblages to biophysical gradients in the environment in order to understand the consequences of a changing environment or human impacts on these assemblages.

3. The Arctic Ecosystem Integrated Survey

The Arctic Ecosystem integrated survey (Arctic Eis)[1], supported by the Bureau of Ocean Energy Management (BOEM), the Coastal Impact Assistance Program (CIAP), and the National Oceanic and Atmospheric Administration (NOAA), conducted comprehensive ecosystem surveys over two years (2012 and 2013) on the US portions of the Northern Bering Sea and Chukchi Sea shelves. Recognizing the relative lack of information on fish populations in the region, the primary goals of the Arctic Eis project were to (1) collect baseline fisheries and oceanographic data to enable resource managers to better predict effects of climate and human impacts on ocean productivity and on the ecology of marine and anadromous fish species and seabirds within the northeastern Bering Sea and Chukchi Sea, (2) assess the distribution, relative abundance, diet, energy density, size, and potential predators of juvenile salmon and other commercially or ecologically important marine fishes (e.g. forage fishes) within the region, and (3) evaluate the effect of climate change on the health and status of pelagic fishes within the region.

Ecosystem surveys focused on assessing biological resources on the seafloor and throughout the water column (zooplankton, fish, invertebrates) and included oceanographic sampling to assess water mass characteristics (temperature, salinity), nutrient concentrations, and phytoplankton biomass. To assess biological resources, surveys used (1) bottom trawls to sample fish and invertebrates on the seafloor, (2) surface trawls to sample fish in the surface layer, including juvenile salmon, forage fish and juvenile life stages of bottom fishes, (3) plankton nets to sample zooplankton and larval fish, and (4) acoustic surveys in combination with mid-water trawls to sample fishes throughout the water column and to assess the

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[1] https://web.cfos.uaf.edu/wordpress/arcticeis/

abundance and biomass of selected species (Arctic cod; saffron cod; Pacific herring, *Clupea pallasi*; and capelin, *Mallotus villosus*). In addition, seabirds were surveyed along the ship's track to assess their species composition, distribution and abundance throughout the region. Sampling was conducted on an extensive grid of sampling stations spanning the US portions of the northern Bering Sea and Chukchi Sea shelves (Fig. 2) and along east-west transects connecting these stations (acoustics, seabird observations). Subsamples of fish were returned to the laboratory for analysis, including (1) genetic analyses to determine the population structure of Arctic cod, saffron cod, capelin and salmon across the survey region and throughout the Pacific Arctic, (2) otolith analyses to determine ages and growth rates of Arctic cod, saffron cod and chum salmon (*Oncorhynchus keta*), (3) diet analyses to determine the food habits of selected species, (4) stable isotope analyses to determine the trophic position of, and dietary sources for, selected species, and (5) energetic and hormonal analyses to assess the physiological condition of fishes in the study region.

This overview synthesizes some of the major findings of the project that highlight the breadth and diversity of the science conducted as part of the Arctic Eis project. Detailed methods and findings are presented in 26 individual component reports (Appendix A-Z). In combination, these reports provide a significant step forward in our understanding of the northeastern Bering Sea and Chukchi Sea ecosystems, in particular with respect to ecologically important fish, crab and seabird species. A major legacy of the project will be the databases that will be accessible through the Alaska Ocean Observing System's Arctic Portal (http://portal.aoos.org/arctic). In addition to these databases and published studies, a major benefit of the project was that it provided training for a number of graduate students, all of whom contributed as first authors or contributing authors to the component reports. In combination, these contributions mark an important milestone towards improving our capacity to adequately monitor and predict the impacts of climate variability and of anthropogenic activities, including oil & gas development, fishing and climate change on marine ecosystems in the Pacific Arctic and throughout the wider Arctic.

4. Major findings

4.1 A tale of two contrasting years: wind-induced changes in oceanographic conditions and associated ecosystem changes

Oceanographic conditions differed greatly between the two sampling years (2012 and 2013) due to differences in local winds and in the flow of Pacific waters through Bering Strait (Danielson et al. 2017). Water mass structure differed primarily because of differernces in the August regional wind field, which was more energetic in 2012 but more persistently from the northeast in 2013. Persistent wind forcing from the northeast in 2013 was associated with flow reversals in the Alaska Coastal Current and with the advection of Arctic waters onto the Chukchi Shelf via Barrow Canyon, as evident in surface and bottom layer characteristics (Fig. 3). These contrasting conditions were associated with differences in nutrient concentrations and abundances of biota in the Chukchi Sea at all trophic levels (Pham and Kuletz 2016, Danielson et al. 2017, De Robertis et al. 2017b, Pinchuk and Eisner 2017). The influence of Pacific waters in the eastern Chukchi Sea was more limited spatially in 2012, but concentrations of nutrients and chlorophyll *a* (Danielson et al. 2017), the density of zooplankton such as the copepods *Neocalanus* spp. and *Eucalanus bungii* (Pinchuk and Eisner 2017) and the density of midwater fishes (De Robertis et al. 2017b) in waters originating on the Bering Sea shelf were all higher in 2012 compared to 2013. While the reasons for these differences remain uncertain, Danielson et al. (2017) hypothesize that differences in salinity and nutrients may be a consequence of diminishing net transport through Bering Strait from 2011 to 2012. Although a link between the zooplankton community and chlorophyll *a* or nutrients has not been established, moderate to strong coupling between zooplankton, pelagic fish, benthic, and seabird communities (Pham and Kuletz 2016, Sigler et al. 2017) suggest that differences at the lower trophic levels, whether linked to inflow through Bering Strait or local processes, reverberate throughout the food web.

The intrusion of Arctic waters onto the northeastern part of the shelf in 2013 (Danielson et al. 2017) was most apparent in differences in the zooplankton (Fig. 4) and fish communities (Fig. 5). An Arctic community of zooplankton characterized by *Calanus hyperboreus, Metridia longa*, *Paraeuchaeta glacialis,* and *Themisto abyssorum* was much more widespread over the shelf in 2013, while species of Pacific origin were more widespread and more abundant on the shelf in 2012 (Pinchuk and Eisner 2017, Fig. 4). The Arctic and Pacific zooplankton communities also show differences in age structure, as stage prevalence in the water column of the dominant copepod *Calanus glacialis* was comprised of a distinctly younger cohort (primarily stage CIII) in the Arctic water mass as compared to the Pacific-origin waters, which was dominated by Stages CIV and CVs (Fig. 4). Similar to these Arctic zooplankton species, young-of-year Arctic cod were much more widespread and abundant in 2013 compared to 2012 in the northeastern Chukchi Sea (De Robertis et al. 2017b), perhaps suggesting an Arctic origin (Fig. 5).

The observed differences between 2012 and 2013 are consistent with the observation that in 2012 the distribution of biological communities from plankton through seabirds, including epibenthic fish and invertebrates, largely reflected the distribution of water masses (Sigler et al. 2017). The observed spatial gradients in 2012 are consistent with the response of these communities to hydrographic differences between 2012 and 2013, which imply an expansion of the Arctic community (sensu Sigler et al. 2017) in 2013, reflecting the increased extent of Arctic water masses, and a contraction of the Chirikof Basin / southern Chukchi Sea community, reflecting a reduced extent of Pacific waters on the shelf.

4.2 Assessing demersal fish biomass in the Arctic: Methodological advances and broad-scale patterns in biomass and community composition

The current study contributed to advancing fisheries research in Alaska's Arctic by improving estimates of both demersal and midwater fish biomass and species composition. Demersal fishes have been sampled in the Chukchi Sea using a variety of sampling gears, but two primary bottom trawls have been used in recent decades as described below. The comprehensive Arctic Eis survey provided the first opportunity for direct comparisons of these gear types to estimate their relative selectivity at different sizes and to inform future sampling efforts. Gear selectivity is an important issue when estimating the size and species composition of fishes in the environment from trawl catches, and when using these catches in conjunction with acoustic backscatter to estimate the midwater biomass of fishes or plankton. One specific objectives of the Arctic Eis project was to compare the size selectivity of two different bottom trawls that have commonly been used to assess fish populations in the U.S. Arctic: 1) the 3-m plumb-staff beam trawl (PSBT; after Gunderson and Ellis, 1986; Abookire and Rose, 2005, Norcross et al., 2010), and 2) the Alaska Fisheries Science Center (AFSC) 83-112 Eastern bottom trawl (EBT; Stauffer, 2004).

A paired comparison study was conducted in 2012 to compare catch composition and sampling characteristics of the two trawl gears. Because the areas swept by the two trawls are vastly different in size (by orders of magnitude), the trawls have very different mesh sizes and vertical openings, and the gear is towed at different speeds, a direct comparison of fish density between the two trawls is challenging as each trawl samples a different size range of fish while missing a large fraction of either the small fishes (83-112) or the larger, faster swimming fishes (PSBT). However, side-by-side comparisons allowed the development of a ratio statistic to estimate the relative selectivity (probability of retention) at a given size for the EBT and PSBT (Kotwicki et al. 2017). In general, the selectivity of the EBS increased relative to the PSBT as the size of fishes or invertebrates increased. The finer mesh and harder bottom-tending characteristics of the PSBT retained juvenile fishes and other smaller macroinvertebrates and it was also more efficient at catching benthic infauna that were just below the surface. The EBT was more efficient at capturing larger and more mobile organisms, and likely captured more organisms that were further off bottom due to its larger net opening. Estimates of relative selectivity at present do not allow us to estimate absolute abundance or biomass using the swept-area method. However, if selectivity of one of the trawls for a given species is known, or under certain simplifying assumptions, absolute selectivity and therefore densities can be estimated (see Appendix F for snow crab and Appendix M for Arctic cod).

While neither trawl is sufficient by itself to fully assess demersal fish biomass, catch-per-unit-effort (CPUE) in the large-mesh trawl survey (Goddard et al. 2016) can be directly compared to results from similar surveys conducted in the eastern Bering Sea using the same gear configuration. Annual surveys have been conducted in the Southeast Bering Sea since 1982 and a single comprehensive survey was conducted in the northern Bering Sea in 2010 (Lauth et al. 2011). The combined survey results suggest an exponential decline in demersal fish biomass from the south to the north, decreasing by two orders of magnitude (Fig. 6). The decrease in biomass is accompanied by a strong North-South gradient in species composition from a subarctic community dominated by a number of commercially important species to an Arctic community dominated by Arctic cod, eelpouts, and snailfish (Fig. 7).

4.3 First comprehensive assessment of midwater-fishes

The Arctic Eis surveys included, to our knowledge, the first-ever acoustic trawl surveys of the US portions of the northern Bering Sea and Chukchi Sea, providing abundance estimates of pelagic age-0 Arctic cod (*Boreogadus saida*), age-0 saffron cod (*Eleginus gracilis*), capelin (*Mallotus villosus*), and Pacific herring (*Clupea pallasii*). In order to estimate abundances, several methodological challenges related to the presence of large numbers of jellyfish and to the small size of fishes had to be overcome. First, large jellyfish in the study region, in particular the scyphomedusa *Chrysaora melanaster*, can dominate biomass in the water column and impede the partitioning of backscatter among different organisms. The Arctic Eis survey provided ideal conditions to estimate the target strength of *C. melanaster* in order to improve estimates of target species abundances in mixed-species assemblages (De Robertis and Taylor 2014). Second, acoustic-trawl surveys require reliable estimates of the size and species composition from midwater trawls in order to convert acoustic backscatter to abundances. However, the mid-water fish assemblage in the Chukchi Sea is dominated by very small and/or juvenile fishes (often < 40 mm), which are inadequately sampled by the sampling gear used for the survey (De Robertis et al. 2017a). The authors developed a novel experimental and statistical approach to estimate trawl selectivity for the species of interest in order to correct abundance estimates for the biases associated with trawl sampling.

Results from the acoustic trawl survey revealed dense aggregations of young-of-year Arctic cod in the Northeast Chukchi Sea in both years (De Robertis et al. 2017b). Moreover, results suggest that juvenile gadids and forage fish partition the study region spatially with juvenile Arctic cod dominating in the Northeast Chukchi Sea north of 69.5 °N, saffron cod occupying Alaska Coastal Waters of the Chukchi Sea from 66.5 to 69.5 °N and Pacific herring distributed largely south of 67 °N. These three species also serve as indicators for three major cross-assemblage communities (Fig. 8) identified by Sigler et al. (2017). In contrast, capelin in both years were distributed throughout much of the study area, but were much more widespread and abundant in 2012.

Although early stages of Arctic cod in the study region have been reported previously (Fechhelm et al. 1984, Wyllie-Echeverria et al. 1997, Norcross et al. 2009, Kono et al. 2016), this is the first documentation of a dense and spatially extensive aggregation of age-0 Arctic cod, extending from Arctic waters (melt water over winter water) into adjacent Pacific water masses (Fig. 5). While spawning has been documented to occur under the ice during winter in other regions of the Arctic, the spawning locations that give rise to these dense aggregations are unknown and are the subject of ongoing field and modeling studies.

4.4 Spatial gradients in Arctic marine communities, connectivity, and population structure

The comprehensive surveys conducted in the northern Bering Sea and Chukchi Sea in 2012 and 2013, combined with other data sources, have contributed to our understanding of large-scale spatial gradients across the Subarctic-Arctic ecotone in the Pacific Arctic Gateway (e.g. Sigler et al. 2017, Figs. 7, 8). Understanding these gradients, how they are maintained, and how they vary is critical to understanding how these marine ecosystems may respond to human impacts including climate change. The distributions of many terrestrial and marine populations throughout the world, including fish populations, have been observed to shift in response to changing temperatures (Pecl et al. 2017), including northward shifts in the distribution of subarctic species in the Pacific and Atlantic Arctic gateways during recent periods of warming (Mueter and Litzow 2008, Fossheim et al. 2015). The northward shift in distribution and associated changes in community structure suggest increasing borealization of areas formerly characterized by Arctic species. However, the shallow shelf in the Pacific Arctic gateway implies that temperatures throughout the water column will remain cold for much of the year, in spite of a longer ice-free season and warmer summer temperatures, thereby restricting the northward expansion of boreal species (Stabeno et al. 2012a, Hollowed et al. 2013).

Many populations of plankton, fish, crab, seabirds and mammals have a continuous distribution between the Bering Sea and the Chukchi Sea as Bering Sea shelf waters and Alaska Coastal Current waters enter the Chukchi Sea through Bering Strait. For most planktonic organisms, such as calanoid copepods and krill, this northward advection is a one-way street to certain death as they are consumed by upper trophic level consumers in the Chukchi Sea including juvenile and adult fishes (Gray et al. 2017, Whitehouse et al. 2017), seabirds (Pham and Kuletz 2016), and mammals (Berline et al. 2008). While krill in the Arctic are generally believed to be expatriates (Wassmann et al. 2015), Pinchuk and Eisner (2017) show that the major calanoid copepod in the Chukchi Sea, *Calanus glacialis*, has two distinct populations originating in the Bering Sea and in the Arctic, respectively. Unlike plankton, southern populations of highly migratory seabirds and mammals travel to the Chukchi Sea on a seasonal basis to take advantage of the large advected biomass and local production (Hunt et al. 2013, Pham and Kuletz 2016), thereby returning some of the advected carbon to more southern latitudes. Seabirds like the least auklet (*Aethia pusilla*), a small planktivorous pursuit diver that requires high densities of suitable prey, are widely distributed throughout the northern Bering Sea and Chukchi Sea where they appear to be associated with areas of high zooplankton biomass in offshore, high salinity waters (Fig. 9).

The connectivity and population structure of fish and large invertebrates such as flatfish and snow crab is largely unknown. Analysis of ichthyoplankton and trawl samples, as well as genetic analyses, provide evidence both for connectivity between the Bering and Chukchi seas, as well as evidence for distinct Arctic populations of some species. For example, collections of pelagic eggs (Busby et al. 2016) suggests potential spawning areas for *Limanda* spp. (likely yellowfin sole) and Bering flounder (*Hippoglossoides robustus*) off the Seward Peninsula and off Point Barrow, respectively. In contrast, the high density of larval and early juvenile Arctic cod collected in the northeast Chukchi Sea likely originate far to the south of the observed aggregations, possibly south of Bering Strait, based on initial results from a biophysical transport model (Cathleen Vestfals, UAF, pers. comm.). This initial result, combined with estimates that the spawning biomass required to produce the observed age-0 Arctic cod in 2012 and 2013 is likely far larger than the biomass of Arctic cod present in the survey region during summer (section 4.7), leads us to hypothesize that Arctic cod may undergo extensive spawning migrations during winter to spawn under the ice in the northern Bering Sea or southern Chukchi Sea.

The influence of Pacific waters on population structure of both pelagic and demersal fishes is evident in their continuous distribution throughout much of the northern Bering Sea and Chukchi Sea. For example, two of three major groupings, encompassing several trophic levels, that were identified by Sigler et al.

(2017) span waters to the South and North of Bering Strait, suggesting a southern origin of the associated fish and plankton species with a range extending well into the Chukchi Sea. The fish community throughout the northern Bering Sea and the southern Chukchi Sea appears to be an extension of a subset of the Bering shelf community, although biomass, species diversity, and mean size of fishes decline rapidly from south to north (Stevenson and Lauth 2012, Mueter et al. 2013). For most species, it is unclear at this time to what extent these fish species have established local populations in the Chukchi Sea or are expatriates. However, chum salmon from the Chukchi Sea were genotyped to determine their stock of origin and suggest a mixture of populations originating both to the south and to the north of Bering Strait (Fig. 10, Appendix L). In 2012, juvenile chum salmon collected in the Chukchi Sea were predominantly from the 'local' Kotzebue Sound stock group, while those collected in the northern Bering Sea were predominantly of Norton Sound origin. Similarly, juvenile chum salmon collected in 2013 were a mixture of western Alaska populations, with about 25% originating from Kotzebue Sound and the remainder from Norton Sound, Kuskokwim River and northeastern Bristol Bay (Kondzela et al. 2016). The presence of a mixture of stocks within samples and regions was also evident in otolith elemental compositions associated with the early freshwater phase (Sutton and Pangle 2015).

While the Chukchi Sea fish community within waters of recent Bering Sea origin may predominantly originate in the Bering Sea, a relatively distinct community of 'high' Arctic zooplankton and fish populations occupies Chukchi Sea winter waters on the Northeast Bering Sea shelf. This community includes species originating in the Arctic basin (e.g. zooplankton: *Calanus hyperboreus*, *Themisto abyssorum*) or distinct Arctic populations of more widely distributed species, such as *C. glacialis* (Pinchuk and Eisner 2017), Bering Flounder (Busby et al. 2016), or Canadian eelpout *Lycodes polaris* (Goddard et al. 2016). However, it is notable that few of the pelagic or demersal fish species on the Chukchi Sea shelf appear to originate from the Arctic basin, highlighting the dominance of Pacific fauna throughout much of the Chukchi Sea.

Weak population structure of fish species in Alaska's Arctic is supported by genetic analyses of Arctic cod, saffron cod, and capelin. Both saffron cod and capelin in the study region were genetically distinct from conspecifics in the Gulf of Alaska, but showed weak or no apparent population structure within the study region (Appendix Y). While there was some evidence for more than one spawning population of capelin in the Arctic, the genetic evidence suggests that they disperse after spawning to forage throughout the Arctic and Bering Sea. Genetic analysis of Arctic cod in the study region suggests low genetic diversity and did not detect population structure in this species (Appendix Z), suggesting a single panmictic population. Genetic analyses also showed that some small individuals identified as saffron cod in the field were in fact Arctic cod (Tony Gharrett, UAF, pers. comm.), while some walleye pollock were misidentified as Arctic cod (Appendix Z). On the other hand, another closely related species that has sometimes been confused with Arctic cod, the polar cod *Arctogadus glacialis*, was not detected in any of the genetic samples (Appendix Z).

4.5 Trophic dynamics of Arctic marine fish communities

Understanding food web interactions is essential to predicting the impacts of climate change, fishing and other anthropogenic impacts on marine ecosystems. For example, it has been hypothesized that shallow continental shelf ecosystems in the Arctic may switch from benthic dominated systems to pelagic dominated systems with potentially profound changes for species composition at all trophic levels (Grebmeier et al. 2006b, Wassmann 2011). Any changes that affect the pathways of energy from primary producers to upper trophic levels are mediated through trophic interactions, therefore changes in upper trophic levels can only be predicted if we understand key trophic connections. Earlier studies have described fish food habits of selected fishes in Alaska's Arctic marine ecosystems (e.g. Frost and Lowry 1983, Craig 1984, Coyle et al. 1997, Cui et al. 2012) and trophic studies have become a major focus of

BOEM's Environmental Studies Program in Alaska[2] in recent years. Several components of the Arctic Eis project contributed towards a better understanding of trophic dynamics in the region.

Fishes and crab consume a large variety of pelagic and benthic prey in the northern Bering Sea and Chukchi Sea and diets typically differ among species, water masses and with predator size. For example, smaller-mouthed Arctic Staghorn sculpin (*Gymnocanthus tricuspis*) and larger-mouthed shorthorn sculpin (*Myoxocephalus scorpius*), while both generalist feeders that share a similar prey base, partition prey by taxa or size with little apparent overlap in prey use (Gray et al. 2017). However, diets differ spatially and both species have similarly diverse diets with a high proportion of benthic amphipods in the northern Chukchi Sea, likely reflecting the high benthic productivity in the area (Grebmeier et al. 2006a). Snow crab, a major component of epibenthic biomass across the northern Bering Sea and Chukchi Sea (Bluhm et al. 2009, Kolts et al. 2015), are omnivorous predators in the region, consuming polychaetes, decapod crustaceans (crabs, amphipods), echinoderms (e.g. ophiuroids), and mollusks (bivalves, gastropods), with evidence for substantial cannibalism in the Chukchi Sea (Divine et al. 2017).

Stable isotope analyses (Marsh et al. 2017) and multivariate analyses of prey composition across multiple predators (Whitehouse et al. 2017) confirm that trophic levels and diets of most species vary with predator size and among water masses. With the exception of pelagic forage fishes, most species in the Chukchi Sea rely increasingly on benthic prey as they increase in size (Marsh et al. 2017), reflecting a shift from early pelagic stages to a primarily benthic life style. Hypothesized changes in pelagic-benthic coupling may therefore increase food availability for forage fish, the early pelagic life stages of many fish species and semi-demersal fish, which have a more diverse prey base that includes both pelagic and benthic prey.

Classifying fishes into trophic feeding guilds can simplify the analysis of the complex Chukchi Sea food web (Fig. 11) and aid our understanding of climate-related changes to the structure and function of Arctic marine food webs. Whitehouse et al. (2017) identified four feeding guilds in the eastern Chukchi Sea, which reflect the dominant prey types in predator diets: gammarid amphipod consumers, benthic invertebrate generalists, fish and shrimp consumers, and zooplankton consumers (Fig. 12). These guilds can form the basis for monitoring and modeling food web dynamics. For example, the hypothesized increase in the flow of energy to the pelagic compartment would be expected to result in improved feeding conditions for zooplankton consumers. In addition to prey abundance, prey quality varies among different zooplankton and fish species, and data are now available for many Arctic fish species to consider not only variability in abundance but also in energy density (Appendix U, Fig. 13).

4.6 Winners and losers: Growth and condition in a changing climate

Fish communities in both the Pacific and Atlantic Arctic Gateways are changing. In the Atlantic Arctic, boreal fish species are increasingly replacing Arctic species in the Subarctic-Arctic transition zone (Renaud et al. 2012, Fossheim et al. 2015). Similarly, boreal fishes in the eastern Bering Sea expand northward during warm periods (Mueter and Litzow 2008) and there is a potential for at least some species to expand and become established in the Arctic north of Bering Strait, or for Arctic species to expand locally (Hollowed et al. 2013). While we cannot yet predict the impacts of a rapidly warming climate on fishes in the Pacific Arctic Gateway with any degree of certainty, results from Arctic Eis and other studies support hypotheses that cold-adapted species like Arctic cod may be replaced by competitors that are able to tolerate a wider range of temperatures, and that some boreal species, including salmon, may expand northward into the Chukchi Sea or beyond.

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[2] https://www.boem.gov/Alaska-Studies/

Arctic cod are a quintessential Arctic species: both juvenile (Laurel et al. 2016) and adult Arctic cod (Helser et al. 2017) are cold-adapted and their growth potential appears to be highest at low temperatures. Arctic cod partially overlap with and have similar diets to saffron cod, walleye pollock, capelin, and other forage fish (e.g. Hop and Gjøsæter 2013, Falardeau et al. 2014), implying a high potential for interspecific competition. The growth potential of some of these competitors, in particular walleye pollock and saffron cod, exceeds that of Arctic cod at temperatures above about 5 °C in the lab (Laurel et al. 2016), suggesting a competitive disadvantage of Arctic cod in warmer waters. Saffron cod collected across the northern Bering Sea and Chukchi Sea during the 2012 Arctic Eis surveys attained maximum sizes at a faster rate than Arctic cod (Helser et al. 2017). However, apparent growth rates of Arctic cod in the Chukchi Sea exceed those of saffron cod in the same year, while saffron cod grow at a faster rate than Arctic cod in the northern Bering Sea. It is unclear to what extent these differences reflect differences in environmental temperatures or other environmental conditions.

Salmon are an important subsistence and commercial resource in western Alaska and juvenile salmon of all five species of Pacific salmon were collected during the Arctic Eis surveys, although no chinook salmon (*Oncorhynchus tshawytscha*) and only 2 coho salmon (*O. kisutch*) were caught north of Bering Strait. Relatively few juveniles of any salmon species were caught in the Chukchi Sea in either 2012 or 2013, in contrast to the large numbers of pink (*O. gorbuscha*) and chum salmon (*O. keta*) observed during a survey in the southern portion of the Chukchi Sea in 2007 (Eisner et al. 2012), when water temperatures were considerably warmer (in part as a result of later sampling). These observations confirm the potential for juvenile salmon to expand northward into the Chukchi Sea during warm years to take advantage of feeding opportunities in this productive shelf area and possibly establish new runs in the Arctic (Irvine and Fukuwaka 2011, Nielsen et al. 2012, Logerwell et al. 2015).

Juvenile chum, pink, and Chinook salmon are widespread and abundant in the northern Bering Sea, largely originating from the Yukon River and Norton Sound (Kondzela et al. 2014). The origin of salmon is of great interest to managers, who are tasked with ensuring that sufficient numbers of salmon return to their natal streams to spawn. Stock identification is a particular challenge for chum salmon due to low genetic diversity. Otolith elemental analysis may provide a useful method for differentiating stocks of origin for salmon collected in the marine environment. A pilot study examining salmon collected during surveys in the eastern Bering Sea and Chukchi Sea showed clear differences in the chemical signature corresponding to the freshwater phase among four regions (Chukchi Sea, North and South Bering Sea, and Bristol Bay), but limited spatial differentiation within these regions (Sutton and Pangle, 2015). This suggests that the method has potential for differentiating among stocks, but validation with fish of know origin is required to accurately assign fish sampled in the marine environment to their stocks of origin.

Juvenile salmon utilize the Bering Sea shelf ecosystem during their early marine life to take advantage of high seasonal production (Farley et al. 2009a), gaining size and condition as they move offshore (Wechter et al. 2017). Chum salmon in the northern Bering Sea and Chukchi Sea during 2007, 2012 and 2013 entered the ocean environment from mid-June to mid-July and grew at similar rates in both areas and all years based on otolith growth increments (Vega et al. 2017). However, faster growth was observed in the Chukchi Sea in 2013 (Vega et al. 2017) and growth and energy allocation strategies of juvenile pink and chum salmon vary between warm and cold years in the northern Bering Sea (Andrews et al. 2009a, Wechter et al. 2017). Both species show coherent differences in length and condition among years and are longer but have lower energy density in years with warm spring temperatures. While warm spring conditions and larger size is typically associated with enhance survival of Alaska pink and chum salmon stocks (Mueter et al. 2002), it has been hypothesized that a lack of large, lipid-rich zooplankton prey during warm years could reduce survival of salmon in the Bering Sea (Farley et al. 2011a). However, trends in the abundances of small and large zooplankton differ between the southern and northern portions of the eastern Bering Sea shelf (Eisner et al. 2014), therefore the consequences of changing thermal conditions for pink and chum salmon survival in the northern Bering Sea remain uncertain.

In contrast to pink and chum salmon, Chinook salmon enter the marine environment at a larger size and the year class strength of Canadian origin Yukon River Chinook salmon appears to be established during the early marine period, prior to sampling in late summer surveys (Murphy et al. 2017). The abundance of juvenile Chinook salmon of Canadian origin on the northeast Bering Sea shelf is highly correlated with adult returns over the last ten years and appears to provide a useful early predictor for future returns (Fig. 14). Survival and abundance of juvenile Chinook salmon increased greatly in 2013 and 2014 after more than a decade of very poor survival, raising the possibility of restoring fishing opportunities on the upper Yukon River (Murphy et al. 2017), although the reasons for recent declines and the apparent recovery remain elusive.

4.7 Population dynamics of potential fishery targets: Arctic cod and snow crab

The Arctic Fisheries Management Plan (NPFMC 2009) identifies three potential target species in Alaska's Arctic waters: Arctic cod, saffron cod, and snow crab. However, the plan proactively prohibits "commercial harvests of all fish resources of the Arctic Management Area until sufficient information is available to support the sustainable management of a commercial fishery". To meet these information needs, the plan promotes research to increase knowledge of the marine environment and of the life history and biology of these species in particular. Closing significant gaps in our understanding of the population structure, trophic role, life history, and population dynamics of these key fish and crab species is also of primary importance to BOEM as it provides some of the information required to assess the impacts on these and other fish and shellfish populations from potential oil and gas development. Finally, monitoring these populations in a time of rapid changes in the Arctic is critical to understanding the combined impacts and risks from climate change and other anthropogenic factors.

The Arctic Eis project, in combination with other completed and ongoing research, has greatly expanded our understanding of the biology and dynamics of Arctic cod and snow crab populations in the Chukchi Sea, as well as our understanding of saffron cod biology. While the reproductive biology of Arctic cod in Alaska's Arctic remains poorly understood, much progress has been made in understanding aspects of their early life history, trophic dynamics (section 4.5) and general distribution and abundance. A large, previously undocumented aggregation of pelagic young-of-year Arctic cod was present over the Northeast Chukchi Sea shelf in both 2012 and 2013 (De Robertis et al. 2017b). In contrast, densities of age 1+ Arctic cod on the eastern Chukchi Sea shelf were low with a total biomass within the survey area estimated at 44,500 mt (95% confidence interval: 26,583 – 66,970 mt). Using estimates of growth (Helser et al. 2017) and reproductive parameters (fecundity, maturity-at-length) from the Atlantic (Nahrgang et al. 2016), combined with literature derived ranges for egg stage duration and egg and larval mortality, strongly suggest that mature females in the survey area cannot produce enough eggs to produce the estimated number of age-0s observed during acoustic surveys in late summer (Appendix M). This suggests that either mature fish are migrating into the northern Bering Sea or Chukchi Sea to spawn in the winter, that age-0 fish originate from a much larger spawning population outside the study area, or that we are underestimating the abundance of mature Arctic cod in the study area. Most likely, Arctic cod in the US portion of the Chukchi Sea are part of a larger stock with a much broader geographic distribution, with the Northeast Chukchi Sea serving as an important nursery area for Arctic cod in the Pacific Arctic. Exploratory acoustic surveys across the Chukchi Sea slope into the basin were conducted during the 2013 Arctic Eis survey but failed to find concentrations of older Arctic cod in deeper waters, which have been observed off the Beaufort Sea slope in the western Beaufort Sea (Parker-Stetter et al. 2011) and in the Canadian Beaufort Sea (Benoit et al. 2008, Geoffroy et al. 2016). However, a thin scattering layer of age-1 Arctic cod, as confirmed by a midwater trawl sample, was observed in Barrow Canyon between approximately 230 to 260 m depth, just within a slightly warmer, more saline Atlantic water mass (Fig. 15).

The abundance of snow crab in the Chukchi Sea is surprisingly high (Table 1) with an estimated biomass that exceeds the biomass of all demersal fish combined (Goddard et al. 2016), reflecting high benthic productivity. The snow crab population is dominated by small individuals that are generally well below the legal size (100mm) established for male snow crab in the Southeast Bering Sea. The size of snow crab is likely smaller in the northern Bering Sea and Chukchi Sea because growth is limited by cold bottom temperatures (Kolts et al. 2015). In spite of their small size, a sizable fraction of female crab in the northeast Chukchi Sea is mature (Goddard et al. 2016, Divine 2016) due to a relatively small size at maturity (50% mature at 46 mm, Fig. 16). Male snow crab mature at a larger size (50% mature at 62 mm, Fig. 16) and a relatively small proportion of male snow crab collected in the Chukchi Sea were sexually mature (Divine 2016, Fig. 16). In spite of low male abundances, mature females in the Chukchi Sea did not appear to be sperm-limited as they stored sperm in low to moderate amounts, comparable to the Bering Sea and Canadian waters (Sainte-Marie et al. 2002, Stichert et al. 2013). This suggests a reproductively active population in the northeast Chukchi Sea, which is also supported by the presence of early zoea stages of snow crab on the northeast Chukchi Sea shelf (J. Weems, unpublished data).

Snow crab in the southern Chukchi Sea tend to be smaller than in the northern Chukchi Sea and may primarily consist of juveniles emigrating from the northern Bering Sea after settling to the bottom in Chirikov Basin (Kolts et al. 2015). Settlement of crab originating from the Southeast Bering Sea in Chirikov Basin is supported by large abundances of late stage megalopae in plankton samples collected in the area (A. Pinchuk and J. Weems, unplublished data). Whether these snow crab contribute to the population in the northern Chukchi Sea through continued northward migration or by releasing larvae which are then transported to the north, or both, is currently unknown.

5. Conclusions

The Arctic Ecosystem Integrated Survey has provided a much more comprehensive assessment of the northern Bering Sea and Chukchi Sea ecosystem, with a focus on demersal and pelagic fishes and invertebrates, than was previously available. The assessment includes new information on the distribution, abundance, biology and population dynamics of plankton and fish populations in the northern Bering Sea and Chukchi Sea to address project objectives. While major results have been published in a special issue in Deep-Sea Research (Mueter et al. 2017), many laboratory studies are ongoing and data collected during Arctic Eis continues to contribute to much work that is still in progress. A major legacy of the project will be the databases and maps submitted to the Alaska Ocean Observing System's Arctic Portal (http://portal.aoos.org/arctic), as well as to national archives. In addition to the databases and published studies, a major benefit of the project was the training that was provided for a number of students and post-docs.

Some key scientific findings from the project include the surprising differences in oceanographic conditions between 2012 and 2013 due to differences in local winds and in the flow of Pacific waters through Bering Strait (Danielson et al., 2017). The observed differences between 2012 and 2013 are consistent with the observation that in 2012 the distribution of biological communities from plankton through seabirds, including epibenthic fish and invertebrates, was largely shaped by the distribution of water masses. These relationships foretell potential effects of climate change on these communities, which will be driven by changes in physical conditions that determine the thermal environment as well as advection through Bering Strait and the resulting distribution of water masses in the Chukchi Sea. However, understanding food web interactions is essential to predicting the ultimate consequences of climate change, oil and gas development, fishing and other anthropogenic impacts on these marine ecosystems as was vividly demonstrated in the Southeast Bering Sea when walleye pollock populations declined substantially as a result of unexpected changes in the food web (Hunt et al. 2011). In the northern Bering Sea and Chukchi Sea, ocean temperatures and food conditions likewise influence the community composition and may shift the balance between quintessential Arctic (e.g. Arctic cod) and subarctic (e.g. Pacific salmon) species in the future.

6. Acknowledgements

We thank the captains and crews of the FV Bristol Explorer and FV Alaska Knight, and all of the Arctic Eis investigators. Arctic Eis was funded in part with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior (Contract Agreement Numbers 10-CIAP-010 and F12AF00188), and by the U.S. Department of Interior, Bureau of Ocean Energy Management (BOEM), Environmental Studies Program, Washington, DC under Agreement numbers M12AC00009, M12PG00018, and M10PG00050.

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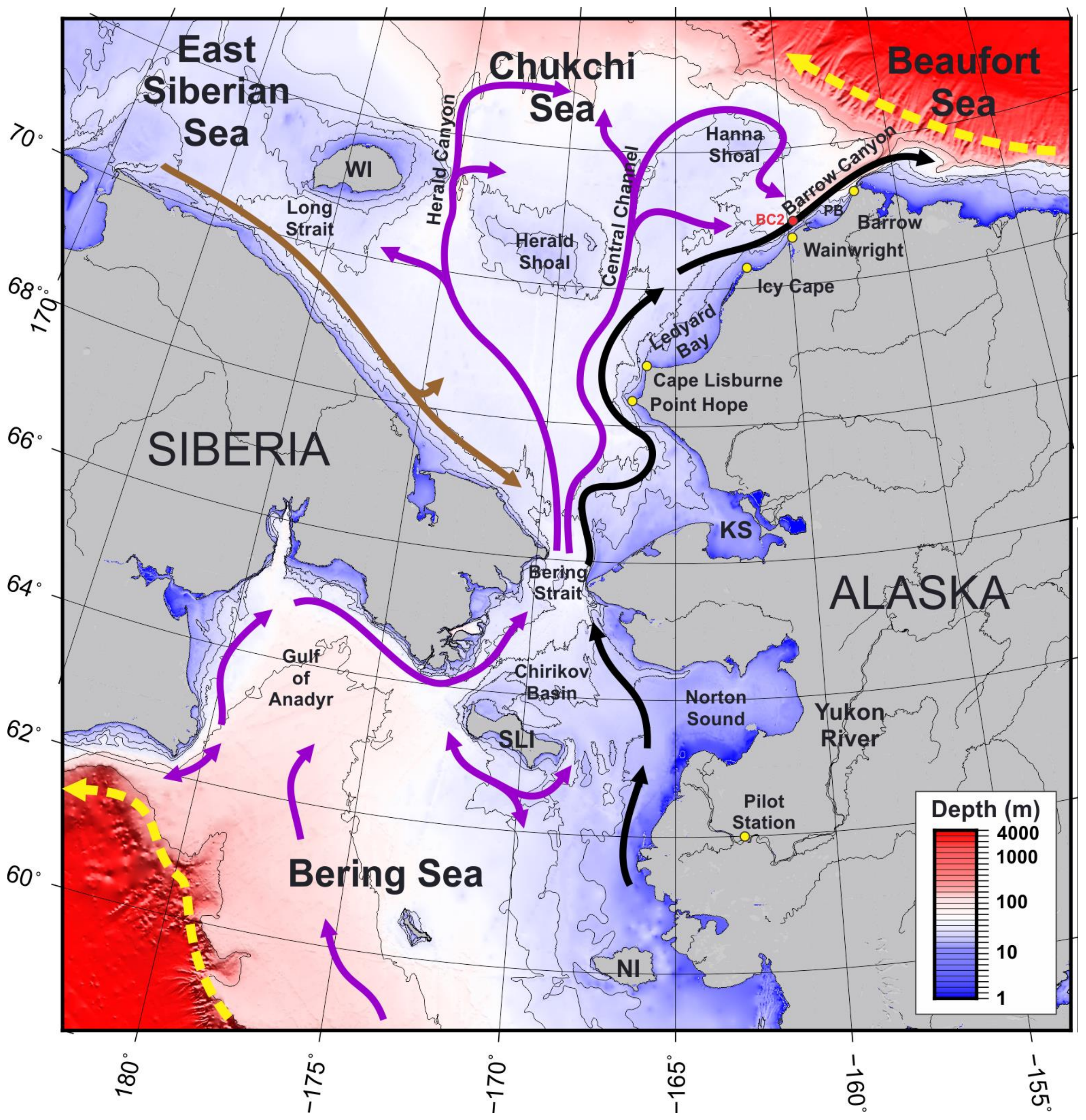
Figures



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Map of the Pacific Arctic with 200, 80, 45, 35, and 25 m isobaths, place names and inferred major current patterns. Abbreviations for major landmarks include NI = Nunivak Island, SLI = St. Lawrence Island, WI = Wrangel Island, KS = Kotzebue Sound, PB = Peard Bay. Mean flow pathways are color coded to denote current systems and/or typical water mass pathways: Yellow = Bering Slope Current and Beaufort Gyre; Black = Alaskan Coastal Current; Brown = Siberian Coastal Current; Purple = pathways of Bering shelf, Anadyr, and Chukchi shelf waters. Red circle denotes location of mooring BC2. Adapted from Danielson et al. (2017, Appendix C).

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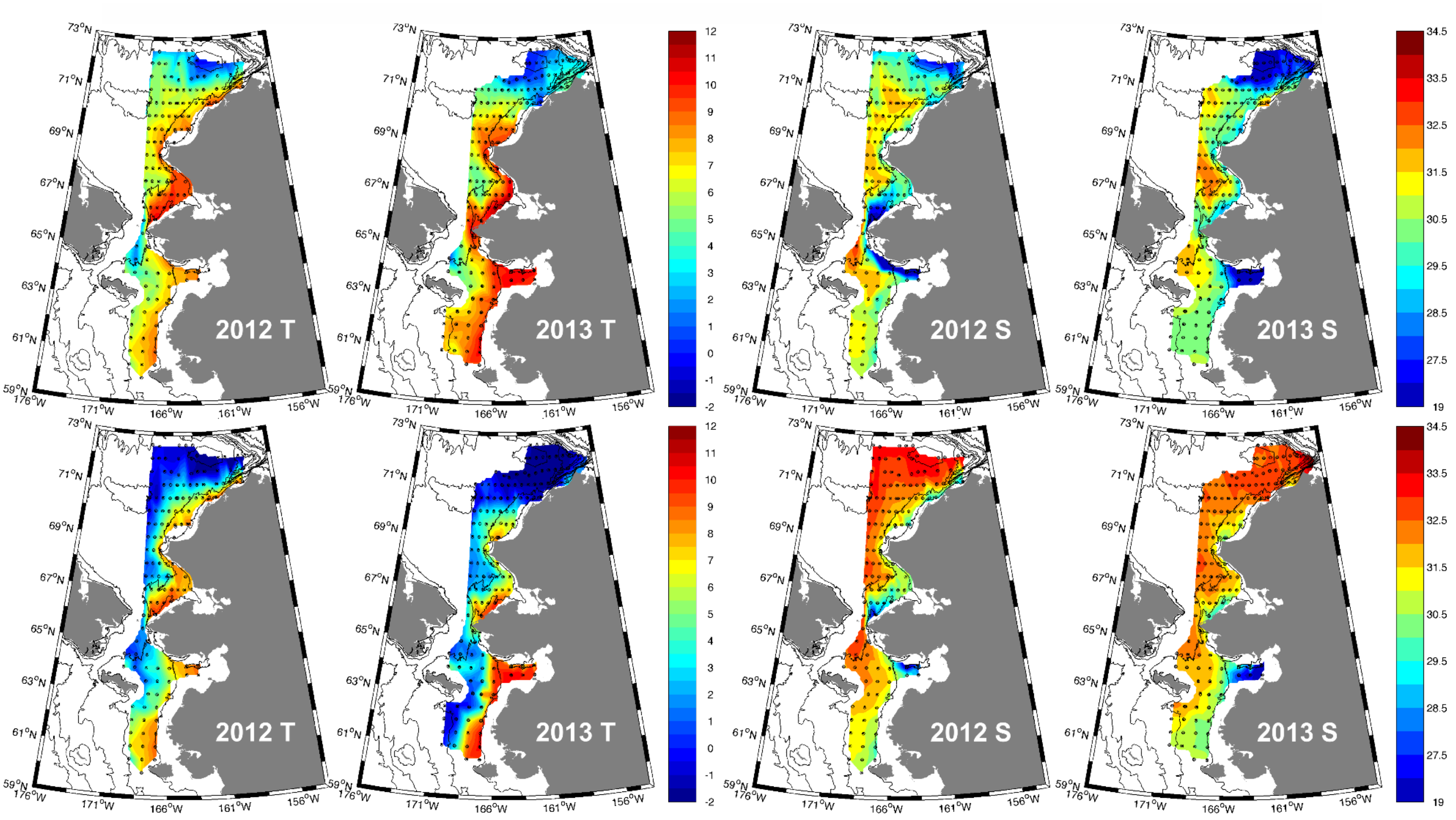
Stations sampled during the 2012 and 2013 Arctic Eis surveys. Not all stations could be sampled each year due to the presence of sea ice or inclement weather. All paired surface and bottom trawl stations (triangle, inset black circle) occurred in the Chukchi Sea north of Bering Strait. An acoustic survey was conducted along east-west transects between stations throughout the survey region. Midwater trawling (grey squares) was conducted to sample aggregations of midwater fishes identified by the acoustic survey. Oceanography stations (black crosses) denote stations where no fishing gear was deployed; however, oceanographic sampling (physics, chemistry, plankton) was conducted at all main stations as well as the additional 'Oceanography' stations in the Chukchi Sea. Adapted from Mueter et al. (2017).



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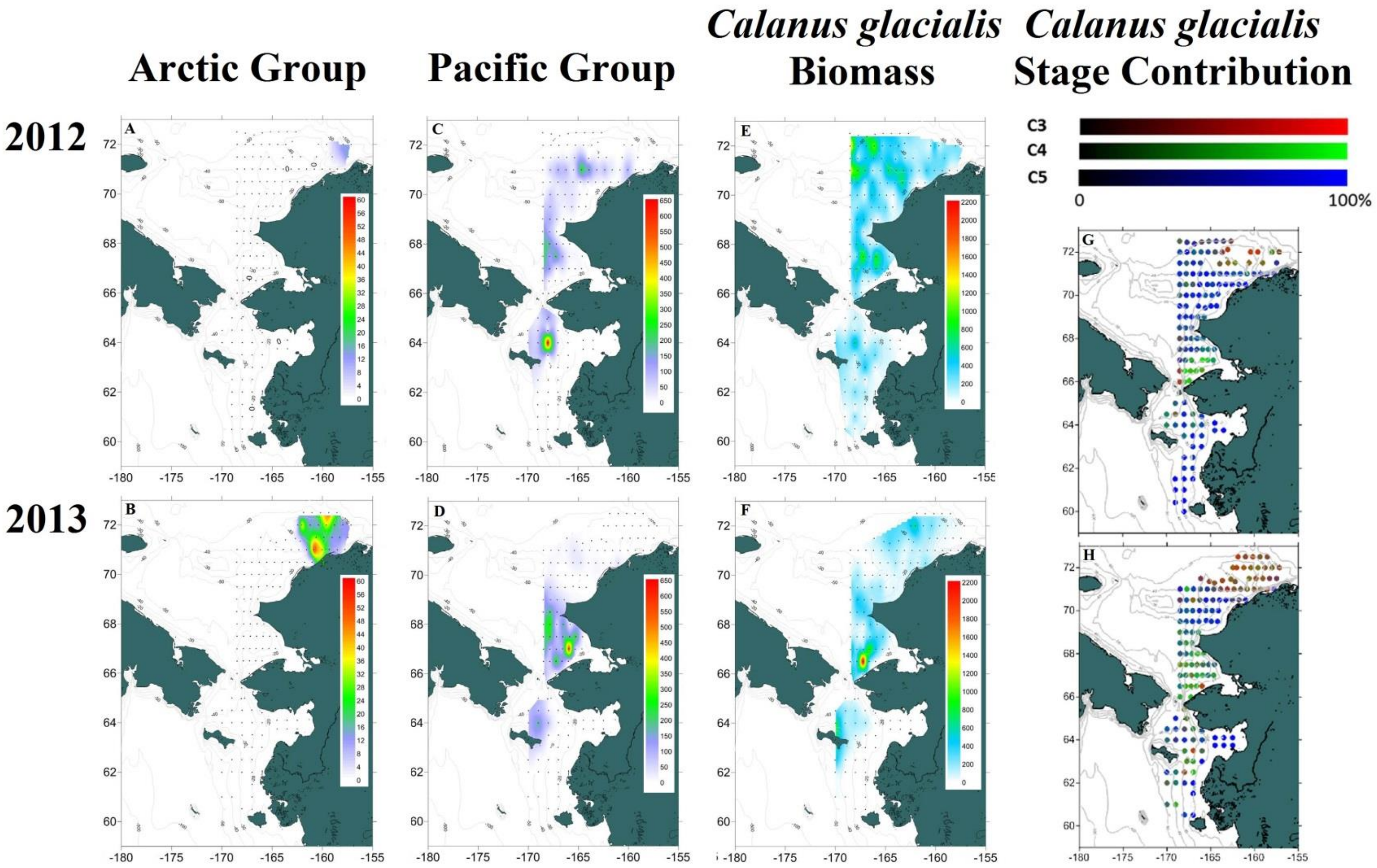

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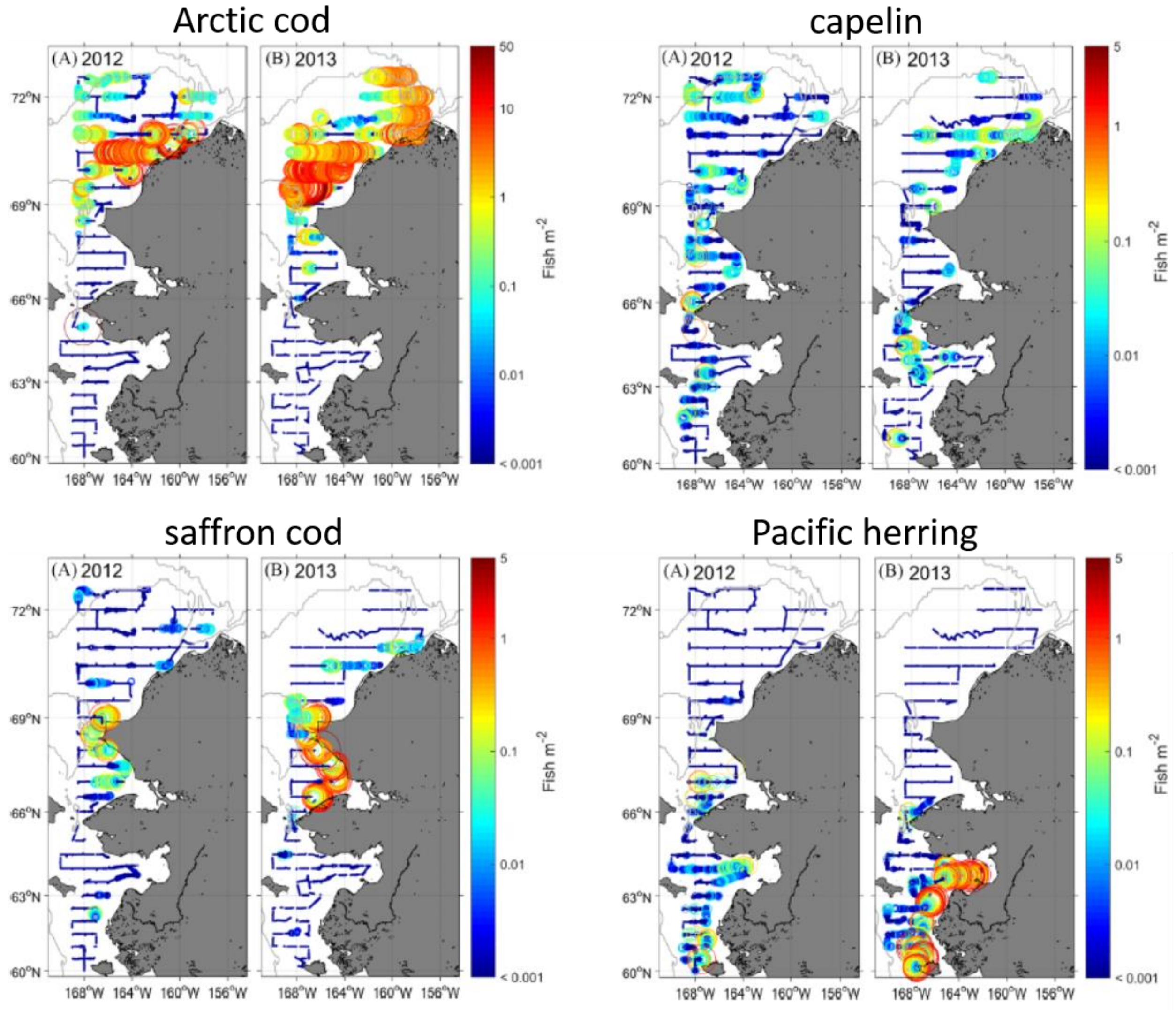

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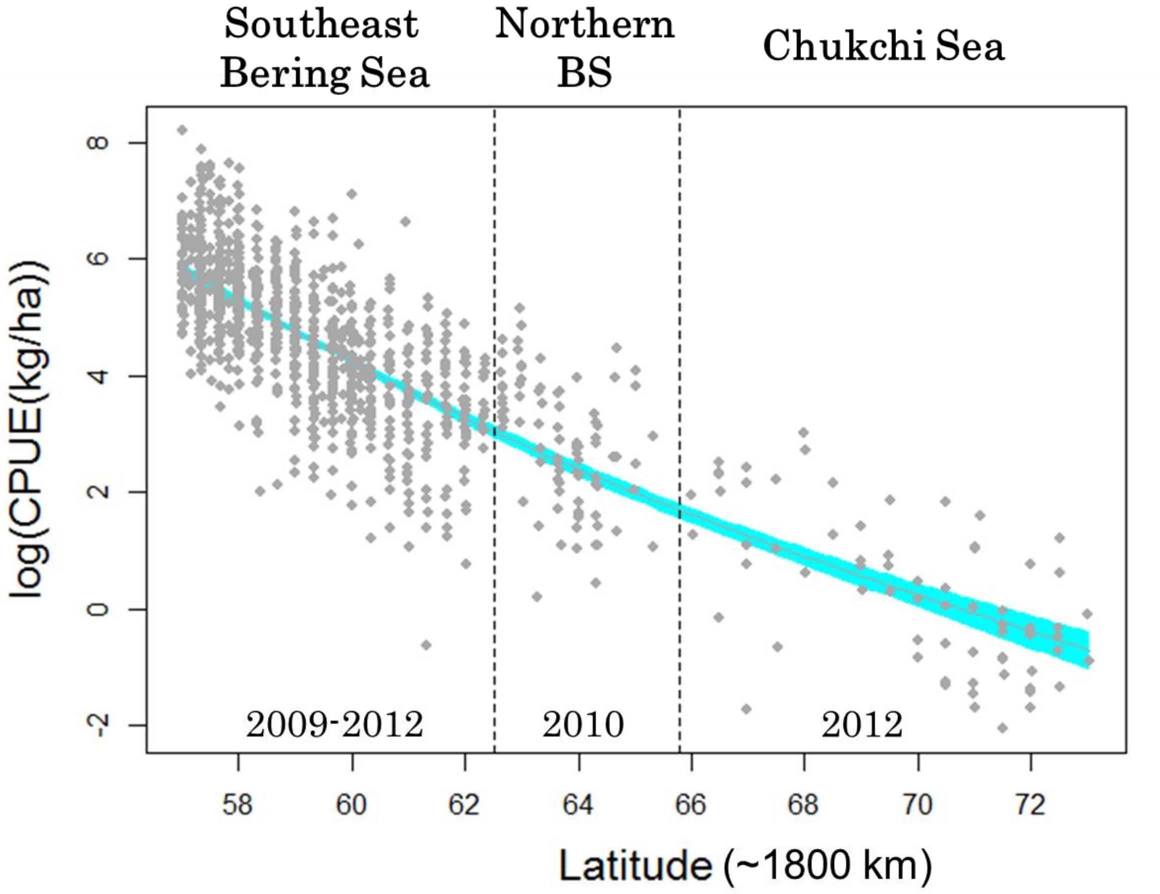

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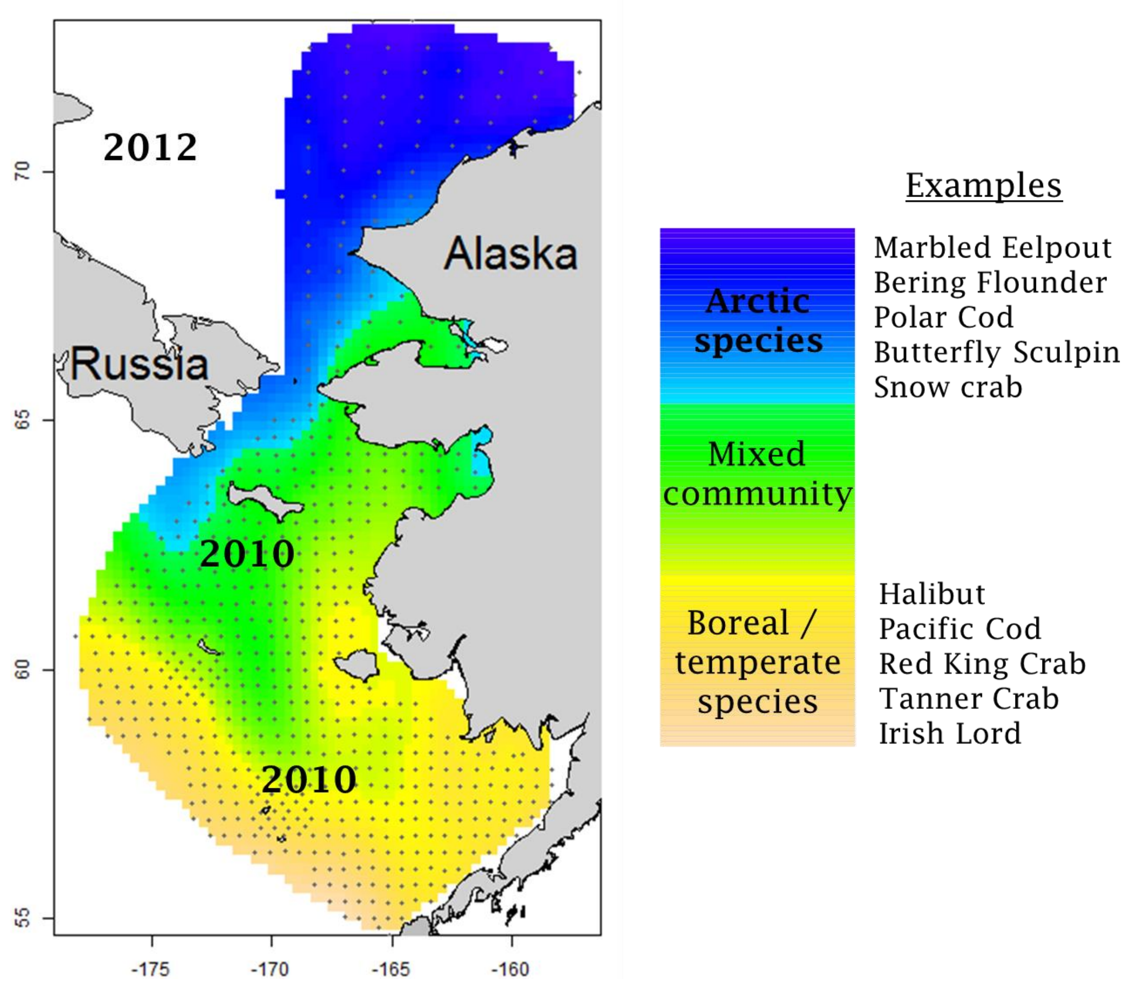

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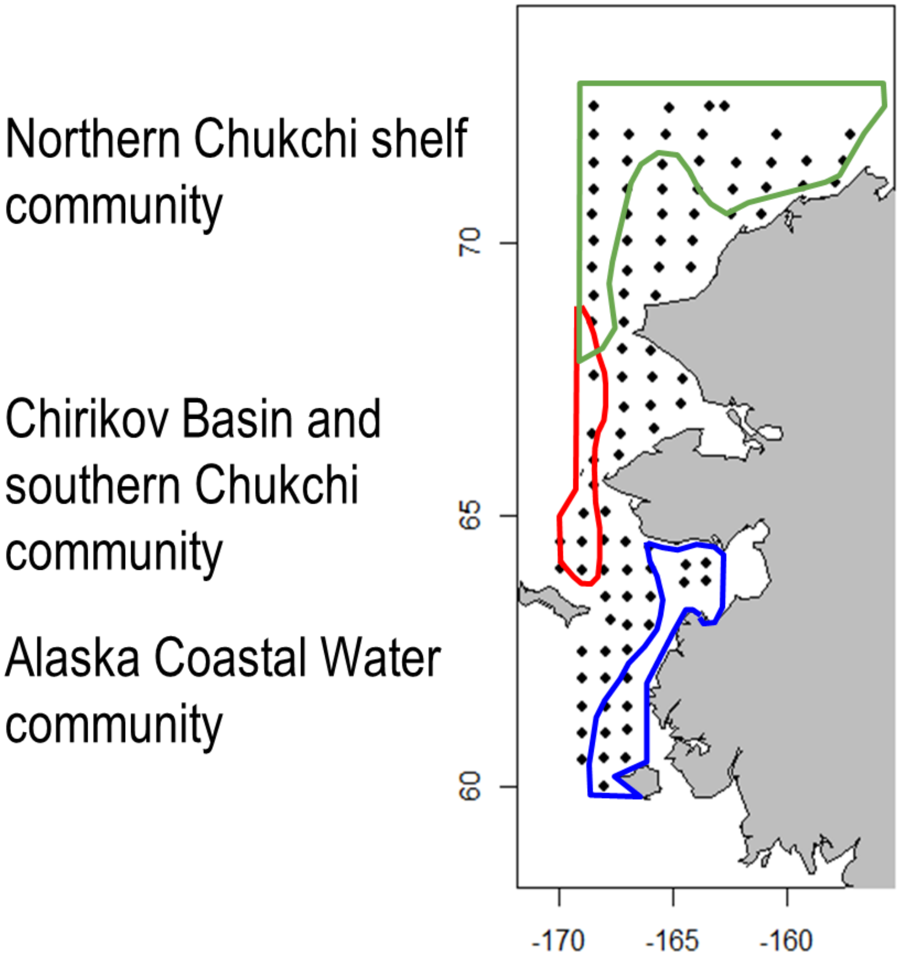

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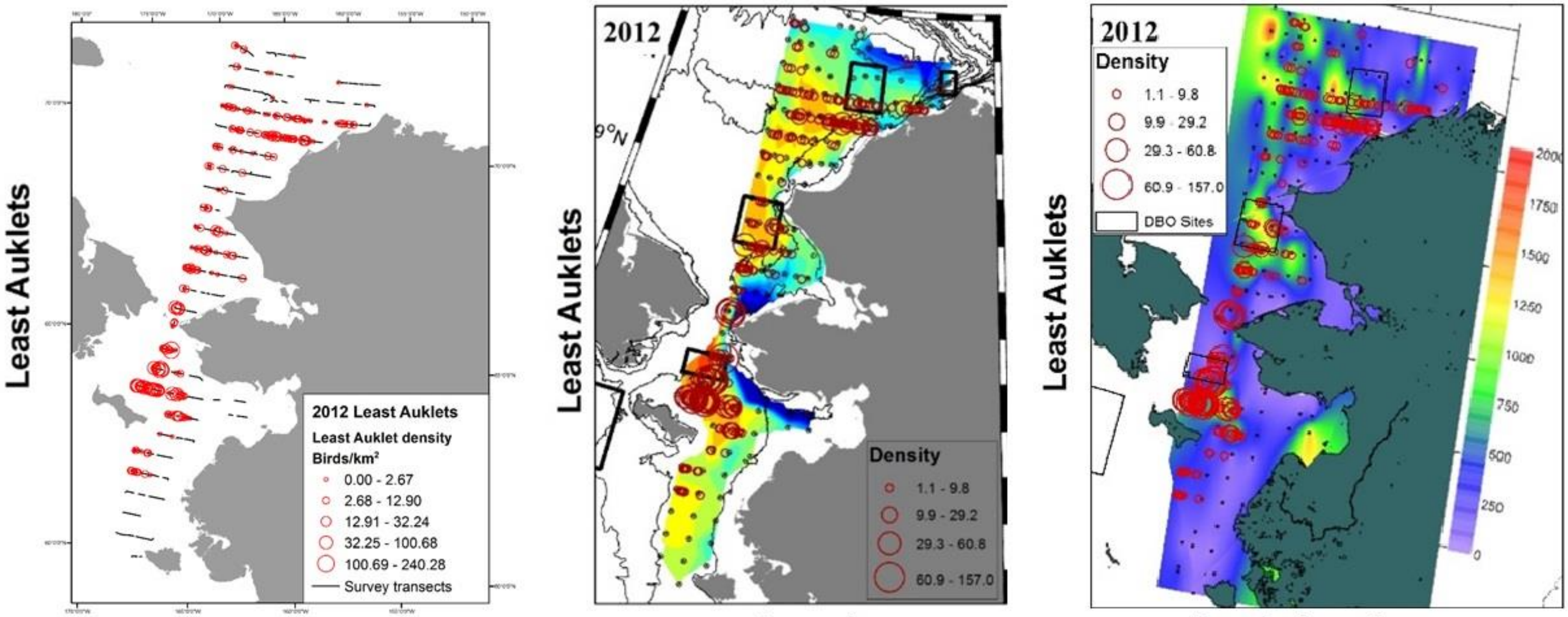

Sea Surface Salinity

Zooplankton Biomass

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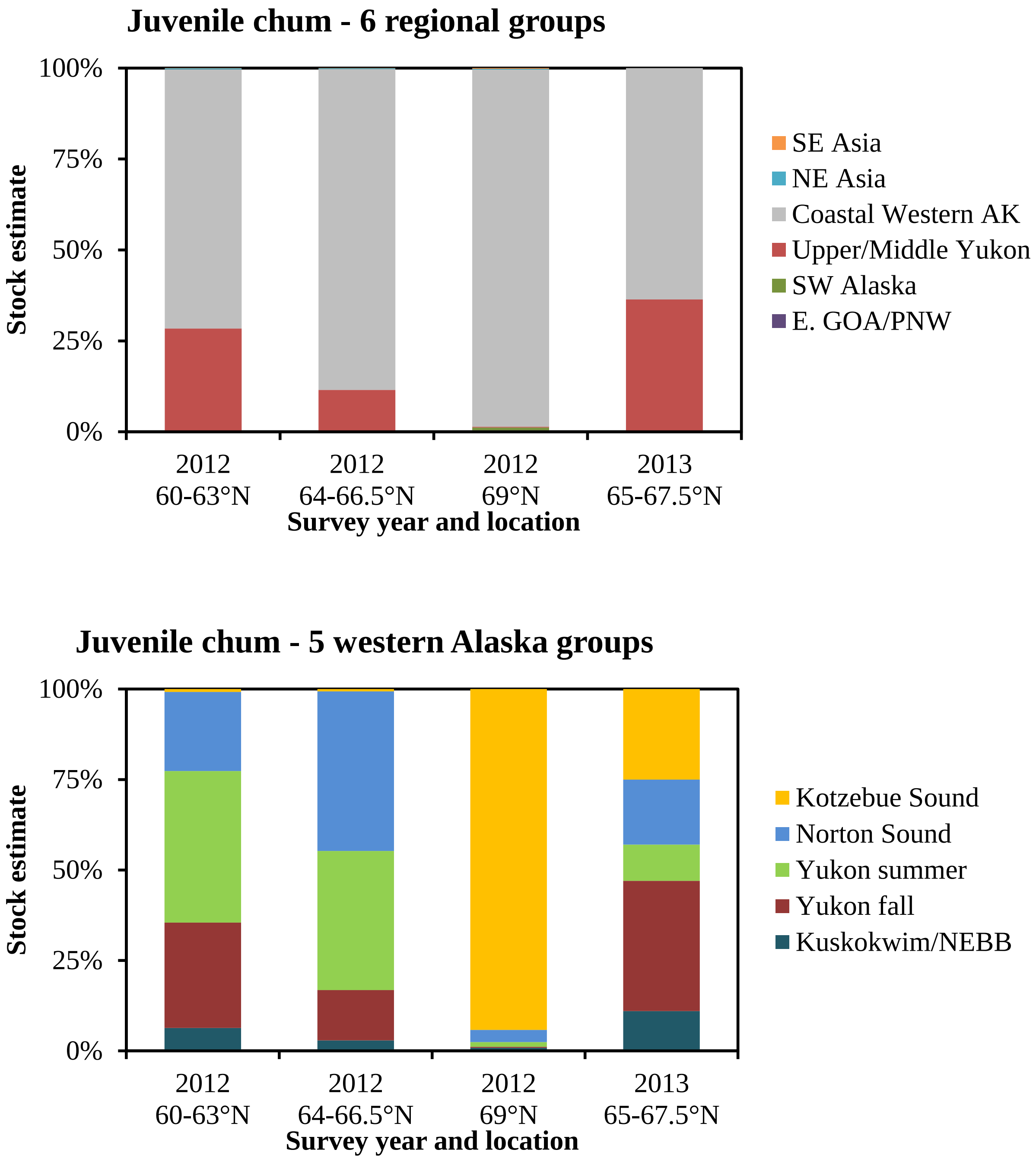

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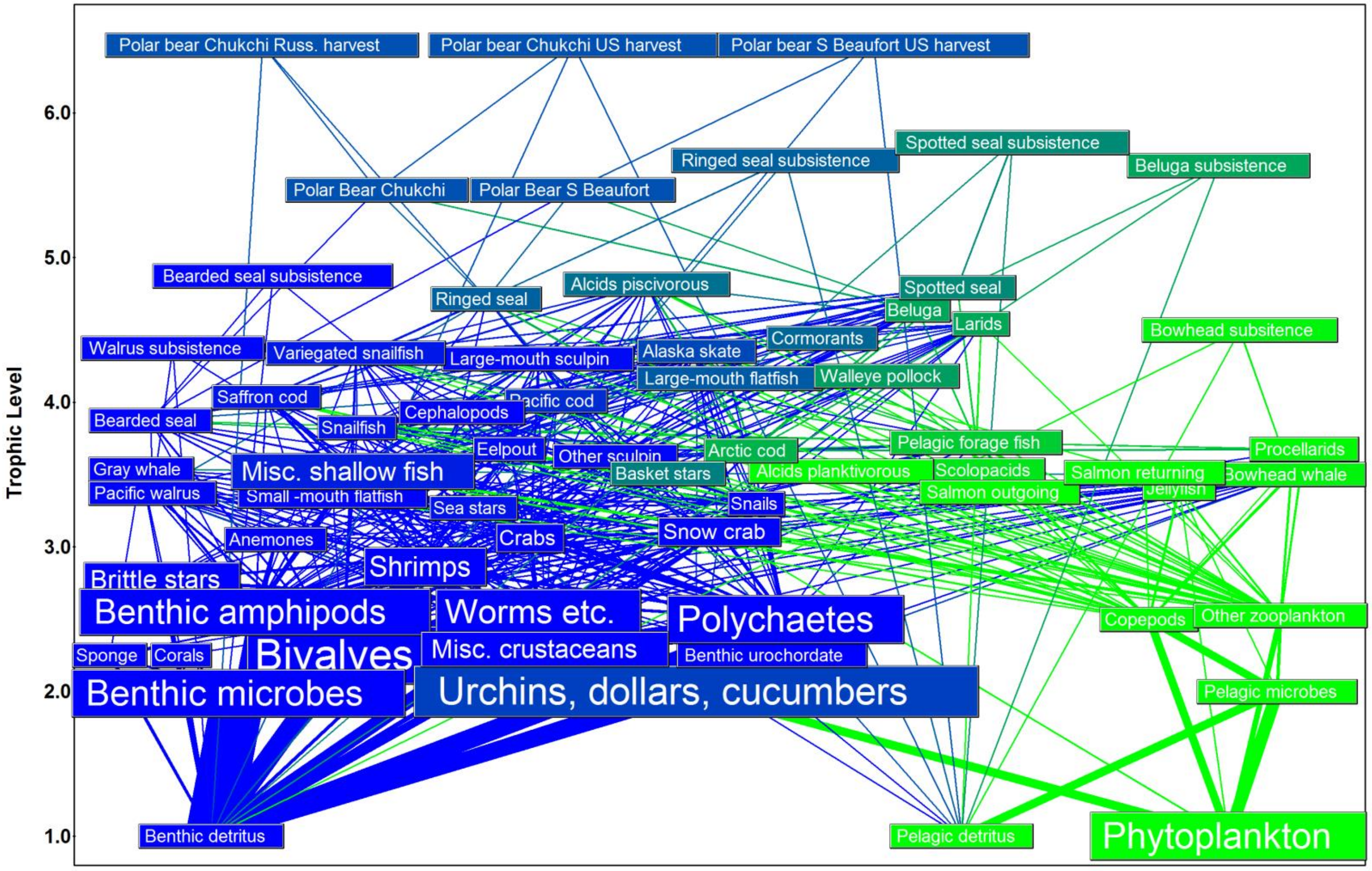

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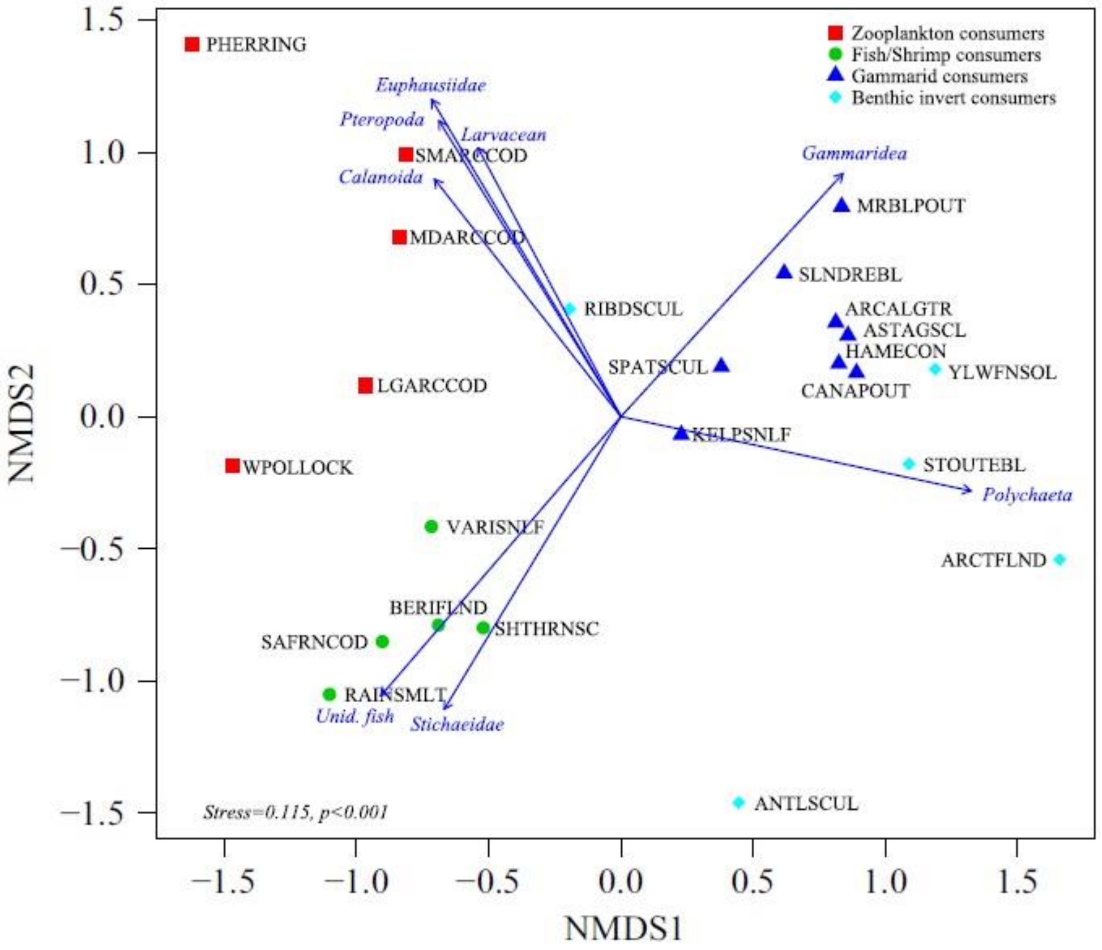
Functional groups (boxes) are arranged vertically by trophic level (a few groups moved up or down to improve readability). The height of the box is roughly proportional to the log biomass of the group. The width of the line between groups is proportional to the magnitude in mass flow. Blue boxes highlight benthic basal resource, and green boxes highlight pelagic sources, with varying shades in between. Adapted from Whitehouse and Aydin (Appendix W)



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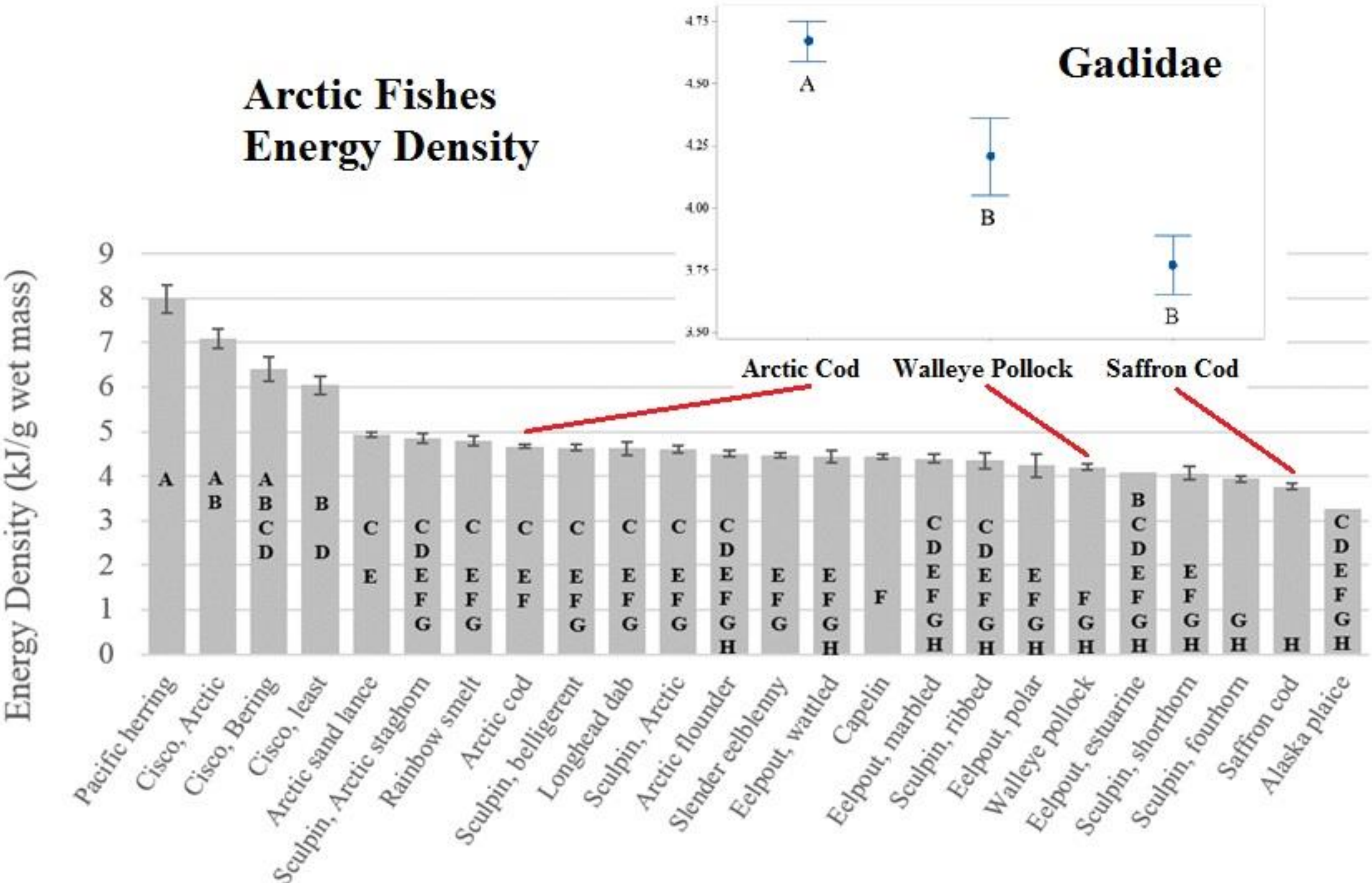
NMDS ordination constructed from the B–C matrix of diet dissimilarities. Four guilds identified by cluster analysis are highlighted. Loading vectors of significant prey types ($p < 0.01$) are included (blue vectors and prey names) to aid interpretation of ordination results. From Whitehouse et al. (Appendix X).



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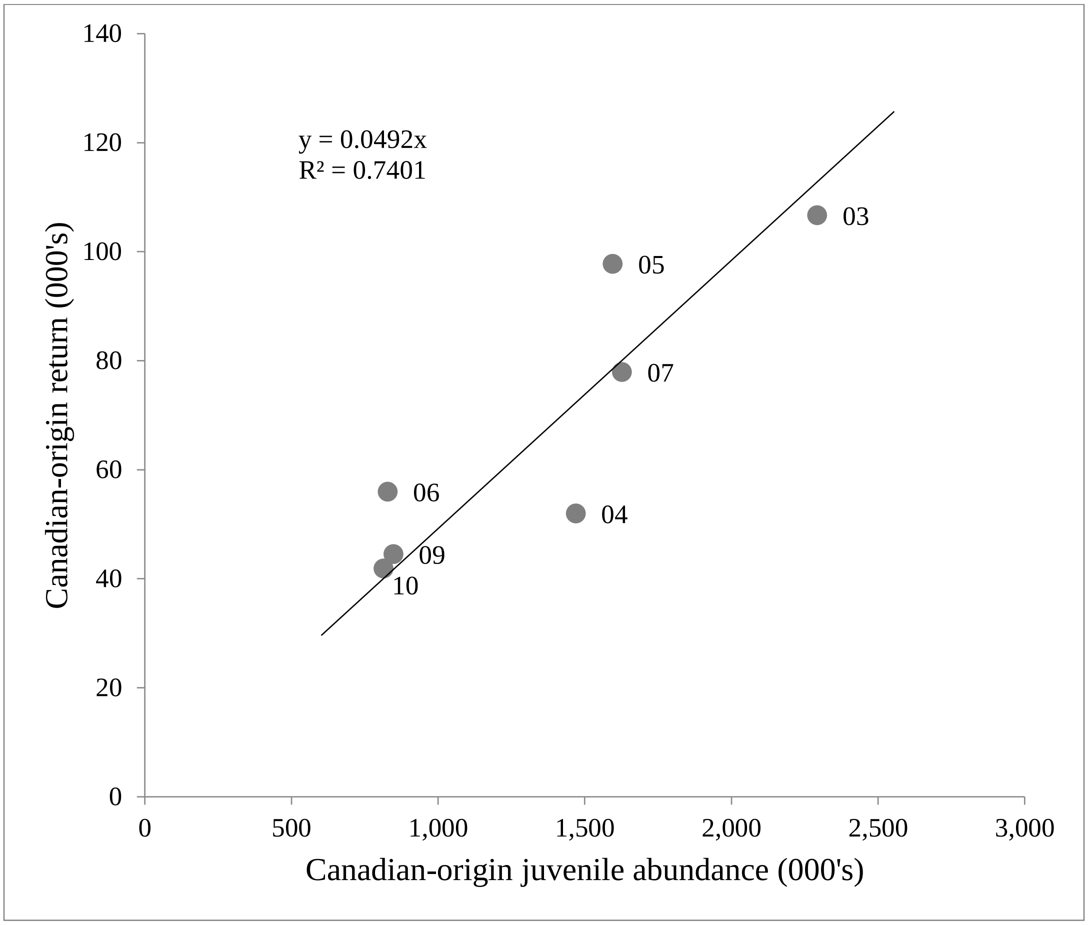
Average energy density (kJ/g wet mass) of all sampled Arctic fish species. Like letters indicate statistical similarity determined by ANOVA. Adapted from Vollenweider et al. (Appendix U).



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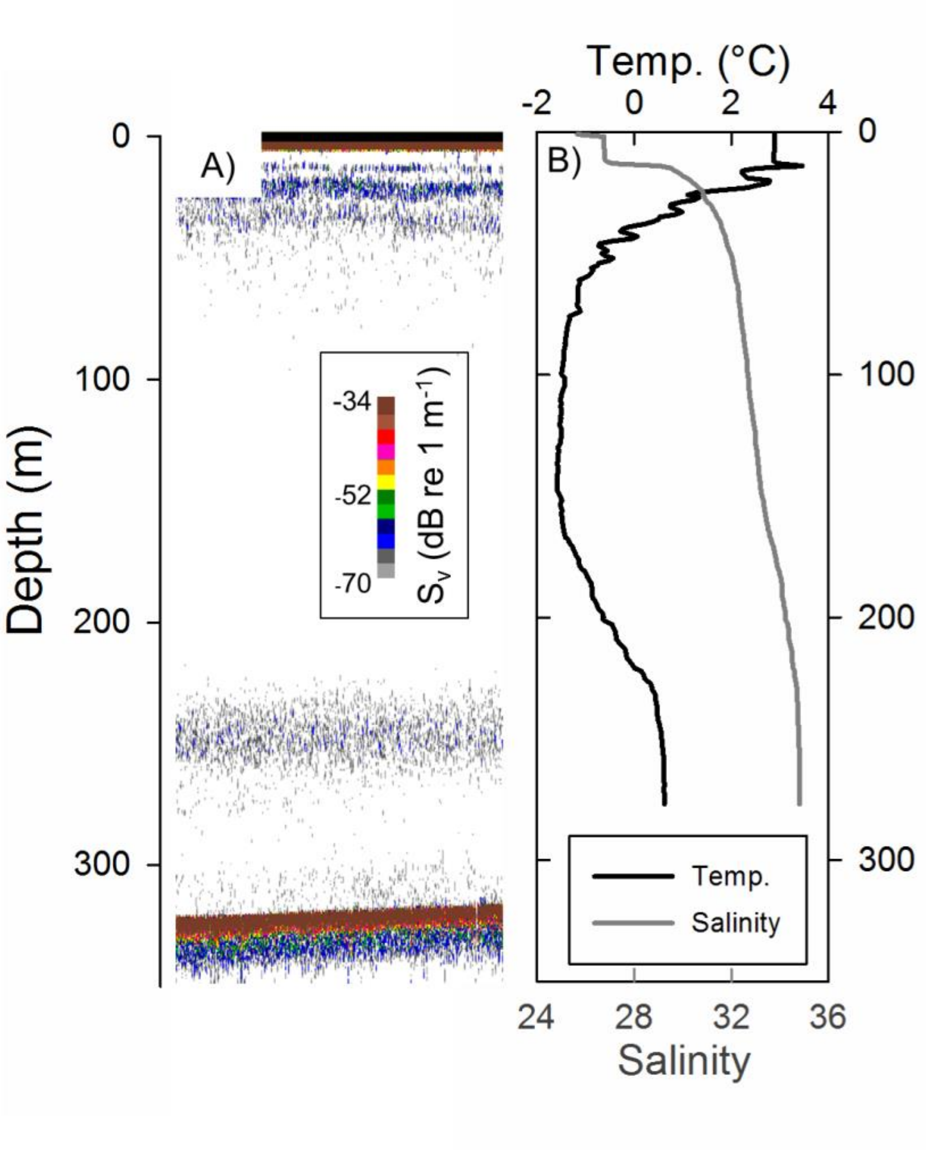

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Echogram showing the Arctic cod near-surface layer (age-0) and the deep layer (age-1+) observed during offshore exploratory survey near Barrow Canyon (left). The color scale is shown as an inset. Temperature and salinity profiles from this location show that the age-1+ fish layer coincides with warmer and more saline Atlantic water. From De Robertis et al. (2017b, Appendix E).

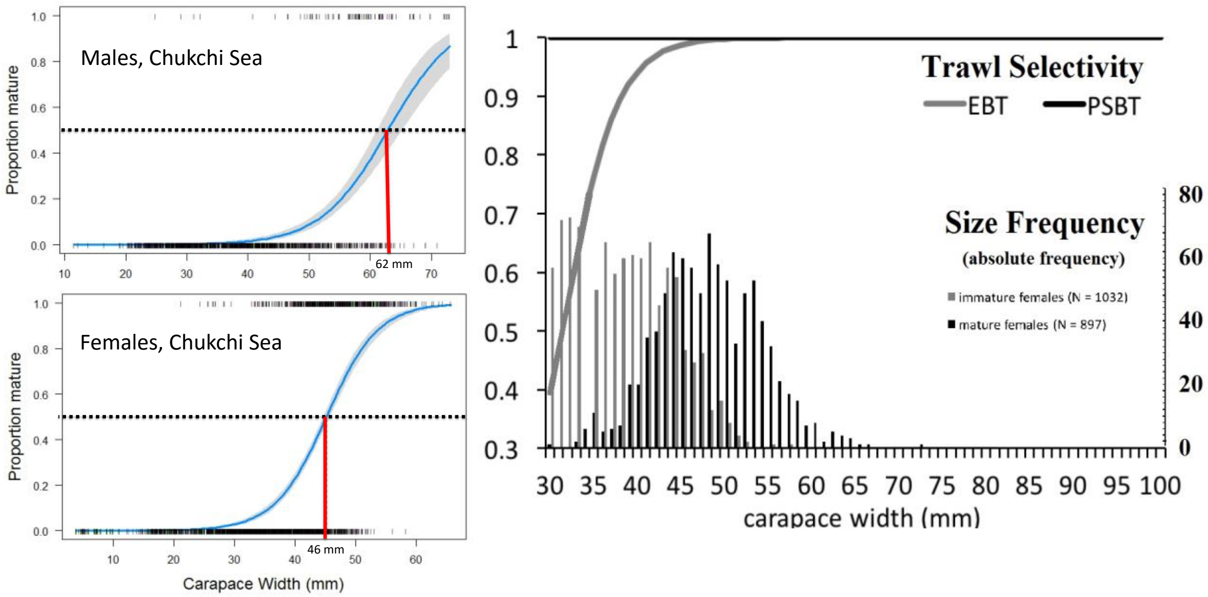

Figure 16. Snow crab maturity at size and selectivity at size
Estimated proportion of mature male and female snow crab in the Chukchi Sea with size at 50% maturity (left) and size frequency distributions of immature and mature female snow crab with estimated logistic selectivity at size of 83-112 Eastern Bottom Trawl (EBT) relative to Plumb Staff Beam Trawl (PSBT). Modified from Divine et al. (Appendix F).

Table 1. Estimated total abundances (N) of Arctic Cod (*Boreogadus saida*), Saffron Cod (*Eliginus gracilis*), Capelin (*Mallotus villosus*), Pacific Herring (*Clupea pallasi*), and snow crab (*Chionoecetes opilio*) from bottom trawl (BT, Britt et al. 2016, Divine et al. 2016), acoustic-trawl (AT, Robertis et al. 2016), and zooplankton tows (ZT, Busby et al. 2016, Weems unpubl.) in 2012 and 2013.

	Gear	Year	Region	N (millions)	Year	Region	N (millions)
Arctic Cod							
Adults	BT	2012	N. Chukchi Sea	1,487 ; 2,257	2013	N. Chukchi Sea	-
			S. Chukchi Sea	796 ; 541		S. Chukchi Sea	-
			N. Bering Sea	-		N. Bering Sea	-
Adults & Age-0	AT	2012	N. Chukchi Sea	80,000	2013	N. Chukchi Sea	240,000
			S. Chukchi Sea	190		S. Chukchi Sea	2,300
			N. Bering Sea	6,500		N. Bering Sea	0.00014
Larvae & Eggs	ZT	2012	N. Chukchi Sea	Present	2013	N. Chukchi Sea	Present
			S. Chukchi Sea	-		S. Chukchi Sea	Present
			N. Bering Sea	-		N. Bering Sea	-
Saffron Cod							
Adults	BT	2012	N. Chukchi Sea	11 ; 192	2013	N. Chukchi Sea	-
			S. Chukchi Sea	194 ; 511		S. Chukchi Sea	-
			N. Bering Sea	-		N. Bering Sea	-
Adults & Age-0	AT	2012	N. Chukchi Sea	690	2013	N. Chukchi Sea	1,600
			S. Chukchi Sea	780		S. Chukchi Sea	4,400
			N. Bering Sea	50		N. Bering Sea	15
Larvae & Eggs	ZT	2012	N. Chukchi Sea	Present	2013	N. Chukchi Sea	Present
			S. Chukchi Sea	-		S. Chukchi Sea	Present
			N. Bering Sea	-		N. Bering Sea	-
Capelin							
Adults & Age-0	AT	2012	N. Chukchi Sea	810	2013	N. Chukchi Sea	1,200
			S. Chukchi Sea	310		S. Chukchi Sea	27
			N. Bering Sea	330		N. Bering Sea	740
Larvae & Eggs	ZT	2012	N. Chukchi Sea	-	2013	N. Chukchi Sea	Present
			S. Chukchi Sea	Present		S. Chukchi Sea	Present
			N. Bering Sea	Present		N. Bering Sea	Present
Pacific Herring							
Adults & Age-0	AT	2012	N. Chukchi Sea	9.4	2013	N. Chukchi Sea	0.09
			S. Chukchi Sea	170		S. Chukchi Sea	40
			N. Bering Sea	1,300		N. Bering Sea	7,500
Larvae & Eggs	ZT	2012	N. Chukchi Sea	-	2013	N. Chukchi Sea	-
			S. Chukchi Sea	-		S. Chukchi Sea	-
			N. Bering Sea	Present		N. Bering Sea	-
Snow Crab							
Adults	BT	2012	N. Chukchi Sea	2,045 ; 72,631	2013	N. Chukchi Sea	-
			S. Chukchi Sea	1,904 ; 343,122		S. Chukchi Sea	-
			N. Bering Sea	-		N. Bering Sea	-
Larvae	ZT	2012	N. Chukchi Sea	1.05	2013	N. Chukchi Sea	-
			S. Chukchi Sea	0.44		S. Chukchi Sea	-
			N. Bering Sea	1.80		N. Bering Sea	-

* BT Gear Type: Adult Arctic Cod, Saffron Cod, and snow crab are demersal or benthically-oriented and caught best in bottom trawls. Adult catch-per-unit-effort (#/km2) estimates were taken from the 83-112 Otter Trawls and the

Plumb-Staff Beam Trawls in 2012 respectively, standardized by number of stations sampled per region, and multiplied by approximate survey area (N. Chukchi = 150,000 km2; S. Chukchi = 50,000 km2 or N. Bering = 150,000 km2).
* AT Gear Type: See De Robertis et al. 2016 for description.
* ZT Gear Type: Larval snow crab catch-per-unit-effort (#/m3xdepth) were taken from the 505um Bongo Net, standardized by number of stations sampled per region, and multiplied by approximate survey area (N. Chukchi = 150,000 km2; S. Chukchi = 50,000 km2 or N. Bering = 150,000 km2). Preliminary results, contact UAF-CFOS Ph.D. student Jared Weems.

Appendix A.

Paired catch comparisons from two standard bottom trawls used in Arctic surveys

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September 9, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

1. ABSTRACT

Long-term monitoring of the high-Arctic marine biota is needed to understand how the ecosystem is changing in response to climate change, diminishing sea-ice, and increasing anthropogenic activity. Since 1959, bottom trawls (BT) have been a primary research tool for investigating fishes, crabs and other demersal macrofauna in the high-Arctic. However, sampling gears, methodologies, and the overall survey designs used have generally lacked consistency and/or have had limited spatial coverage. This has restricted the ability of scientists and managers to effectively use existing BT survey data for investigating historical trends and zoogeographic changes in high-Arctic marine populations. Two different BTs currently being used for surveying the high-Arctic are: 1) a small-mesh 3-m plumb-staff beam trawl (PSBT), and 2) a large-mesh 83-112 Eastern bottom trawl (EBT). A paired comparison study was conducted in 2012 to compare catch composition and the sampling characteristics of the two different trawl gears, and a size selectivity ratio statistic was used to investigate how the probability of fish and crab retention differs between the EBT and PBST. Obvious contrasting characteristics of the PSBT and EBT were mesh size, area-swept, tow speed, and vertical opening. The finer mesh and harder bottom-tending characteristics of the PSBT retained juvenile fishes and other smaller macroinvertebrates and it was also more efficient catching benthic infauna that were just below the surface. The EBT had a larger net opening with greater tow duration at a higher speed that covered a potentially wider range of benthic habitats during a single tow, and it was more efficient at capturing larger and more mobile organisms, as well as organisms that were further off bottom.

2. INTRODUCTION

There are two primary research bottom trawl gears currently being used by U.S. researchers for long-term monitoring studies of the epibenthic macrofauna in Alaskan arctic seas: 1) the 3-m plumb-staff beam trawl (PSBT; after Gunderson and Ellis, 1986; Abookire and Rose, 2005, Norcross et al., 2010), and 2) the Alaska Fisheries Science Center (AFSC) 83-112 Eastern bottom trawl (EBT; Stauffer, 2004). Both are valuable research tools for understanding trends and temporal shifts in biota and for monitoring the health and status of the Arctic ecosystem (e.g., Norcross et al., 2010; Sigler et al., 2011; Stevenson and Lauth, 2011). However, the two standard survey gears are fundamentally different and there are no studies directly comparing standard samples of epibenthic macrofauna taken by each; these studies are necessary for assessing and interpreting the results from the respective surveys currently being done in the Arctic.

The PSBT has been used successfully since 2004 for research cruises in the Chukchi Sea, Beaufort Sea, and eastern Bering Sea shelf (Norcross et al., 2010; Norcross, pers. comm.). An average standard tow with the PSBT covers a bottom area of 300 m2 and the trawl net's small meshes (7 mm body; 4 mm cod end) are very effective at capturing juvenile and small adult bottom fish and other epibenthic macrofauna that are in contact with or immediately above the sea floor.

Since 1982, the EBT's primary use has been for assessing commercial bottom fish and crab stocks in annual surveys on the eastern Bering Sea shelf, and it has also been used episodically since 1976 to do fishery independent surveys in the northern Bering Sea (Lauth, 2011), Kotzebue Sound (Wolotira et al., 1977), northeastern Chukchi Sea (Barber et al., 1997), and Beaufort Sea (Rand and Logerwell, 2010). In contrast to the PSBT, the EBT covers an average bottom area of 22,000 m2 during a standard tow and the trawl net has relatively large meshes (102 mm body; 89 mm intermediate; 32 mm cod end) that allow escapement of small bottom fish, crabs and other small epibenthic macrofauna. For the commercially important bottom fish and crabs, there is considerable published research in fishery journals about the EBT trawl performance and catching efficiency (e.g., Somerton et al., 2007; Kotwicki et al., 2011), as well as published standard protocols for using the trawl in conducting bottom trawl surveys (Stauffer, 2004).

The objective of this experiment was to do standard paired tows with the small mesh PSBT and large mesh EBT for a general tow-by-tow comparison of catch and size composition of bottom fishes, crabs, and other epibenthic macrofauna. This report is limited to general comparisons for those paired trawl samples that were standardized to catch-per-area-swept. A more rigorous sampling design with replicate tows would be required for making statistically valid comparisons between the two trawl gear types.

3. METHODS

3.1 Vessel and Station Selection

The bottom trawl comparison study was integrated into the survey efforts that were conducted aboard the chartered F/V Alaska Knight as part of the 2012 Arctic Ecosystem Integrated Survey (Arctic EIS) supported by Bureau of Ocean Energy Management (BOEM), National Oceanic and Atmospheric Administration (NOAA) AFSC, University of Alaska Fairbanks (UAF), and U.S. Fish and Wildlife Service (USFWS). The F/V Alaska Knight is a 43.5 m long twin-engine house-forward commercial fishing trawler with a stern ramp and a Kort nozzle, allowing for suitable control of the vessel at the slow trawling speeds necessary for towing the PSBT (1.5 knots) and the EBT (3.0 knots) bottom trawls. During standard bottom trawling operations for the Arctic EIS survey, stations were opportunistically selected for gear comparison tows using the PSBT based on the amount of available survey time to switch trawls while at a selected station. Comparison tows were made along parallel tow tracks located less than 300 m apart following standard operating protocols for each trawl. The initial trawl net used at each station was randomly determined. When possible, the trawl was conducted near the center of the 30 x 30 nmi grid cell of the selected station and the vessel maintained a single heading during the tow.

3.2 83-112 Eastern Trawl (EBT) Design and Procedures

The EBT used for the study consisted of NOAA AFSC Resource Assessment and Conservation Engineering (RACE) Division standardized trawls, bridles, and trawl doors that had been certified for quantitative assessment work in the eastern Bering Sea. The EBT had a 25.3 m (83ft) headrope and a 34.1 m (112 ft) footrope (Figure 1). The footrope was fished without roller gear and consisted of a wrapped chain to maximize bottom contact and catchability. The body of the net was constructed from nylon mesh. Mesh sizes were 10.2 cm (4 in) in the wings and body and 8.9 cm (3.5 in) in the intermediate and codend. The codend also had a liner of 3.2 cm (1.25 in) mesh. They were towed behind 816 kg, 1.8 X 2.7 m, steel V-doors and paired with 54.9 m (180.1 ft) dandylines. Each lower dandyline had a 61cm chain extension connected to the lower wing edge to improve bottom tending characteristics.

A digital bathythermograph, CTD, and light meter were attached to the headrope and deployed with each trawl, resulting in oceanographic observations of the depth, temperature, salinity, and relative light intensity through the water column and at the targeted trawl depth. A bottom contact sensor (inclinometer/accelerometer) provided data used to assess the bottom tending performance of the net and to determine when the footrope was in contact with the seafloor. Net mensuration sensors were used to assess trawl performance and to provide net geometry data used to calculate the area swept by the trawl.

Operations were conducted in rigorous compliance with the national and regional protocols detailed in Stauffer (2004). Any hauls that sustained significant gear damage or contained debris were resurveyed immediately following the unsuccessful haul.

Comparison samples were collected by trawling at 1.54 m/sec (3.0 knots) for 15 minutes. Trawl warps (wire out) were determined using the standardized scope table used in the Eastern Bering Sea (Stauffer, 2004). Total catches weighing less than 1,150 kg (2,500 lb) were placed directly onto a sorting table and the catch was sorted and enumerated in its entirety. Larger catches were weighed in aggregate and subsampled before sorting. After sorting subsampled catches, individual species were weighed in aggregate and counted, and then these numbers were expanded to the total catch weight.

3.3 Plumb Staff Beam Trawl (PSBT) Design and Procedures

The PSBT used for the study consisted of a modified design from that originally described by Gunderson and Ellis (1986) and has been used extensively in recent years within the Chukchi and Beaufort seas (Norcross et al., 2010; Brenda Norcross pers. comm.). The PSBT consisted of a 4.1 m headrope and 5.1 m footrope that were held open by a reinforced 3.8 cm x 3.1 m steel beam that is attached to the headrope with a 1.0 cm x 1.8 m nylon bridle and to the footrope with a 1.3 cm x 1.4 m nylon bridle (Figure 2). A 19 kg tip weight was attached on each end of the footrope and one 20 cm plastic float was attached to each end of the reinforced beam. The footrope was lead-lined and had 15 cm lengths of hanging chain attached every 15 cm. Additionally, the trawl had a double tickler chain that sweeps the substrate in front of the footrope. The body of the trawl had 7 mm square knotless nylon mesh and the codend had a 4 mm nylon mesh liner. The steel beam created a fixed net opening with an effective net width when fished on the bottom of 2.257 m (Gunderson and Ellis, 1986).

A digital bathythermograph was attached to the center ring on the reinforced steel beam and deployed with each trawl, resulting in oceanographic observations of depth and temperature through the water column and at the targeted trawl depth. A bottom contact sensor (inclinometer/accelerometer) was attached to one of the hanging chain segments attached to the lead-lined footrope near the centerline of the trawl which provided data used to assess the bottom tending performance of the net and to determine when the footrope was in contact with the seafloor.

Comparison samples were collected by trawling at 0.77 m/sec (1.5 knots) for 2-5 minutes. The net was fished from a single 1.91 cm double-braided nylon tow line using the scope table designed by Norcross (Brenda Norcross, pers. comm.). All of the catches from the PSBT were placed directly onto a sorting table and the catch was sorted, weighed, and enumerated in its entirety.

3.4 Catch Analysis

For comparison purposes, catch rates were expressed as kilograms or numbers of individuals per hectare (1 hectare = 10,000 m2). These catch per unit effort (CPUE) values were estimated for both trawls using the area-swept method (Alverson and Pereyra, 1969). In the case of the EBT, area swept was estimated by multiplying the distance towed by the mean net spread, empirically derived from the net mensuration sensors attached to the wing tips of the trawl. For the PSBT, the effective fixed net width was determined to be 2.257 m, based on the direct measurements of effective net width made by Gunderson and Ellis (1986). The distance towed for both trawls was determined by computing the distance traveled over ground by the vessel between the time the footrope came into contact with the bottom and the time when the footrope came off the bottom, as determined by the attached bottom contact sensor. For each species, a CPUE was calculated for each tow by dividing the catch weight (kg) or number of individuals by the area swept by the trawl in hectares (ha).

Estimation of the size composition for each species was derived by expanding the length frequencies collected (to the nearest millimeter, mm) to the total catch at each station for each trawl. Fork length (FL) was the default measurement for fishes, and total length (TL) was used for fishes having a caudal fin with a straight or rounded posterior edge.

Only stations completed according to standard operating protocols for both trawls were used for comparison.

4. RESULTS & DISCUSSSION

A total of 39 of the 70 sampled stations sampled during the 2012 Arctic EIS bottom trawl survey were successfully sampled with both the 83-112 Eastern bottom trawl and the PSBT (Figure 3).

Of these, 35 stations were sampled along parallel trawl paths within a three hour period. The PSBT tows at the remaining four stations (A-01, B-01, C-02, and D-02) were separated by 30-35 days from the time of the EBT tow because there was additional survey time available during the return transit after completing the Arctic EIS bottom trawl sampling in the Chukchi Sea. Selected stations for paired tows were randomly spread throughout the study area, representing the full geographic range of available habitats to bottom trawls in terms of depth, temperature, and bottom type.

Direct comparisons of the catch and haul characteristics for the PSBT and EBT at each station can be found in Appendix A. Each comparison shows differences in the overall area sampled by each trawl (in hectares), bottom depth, temperature, total catch weight (in kg), and measures of species richness in terms of the number of fish and invertebrate taxa caught, as well as the number of taxa caught that were unique to a specific trawl gear type at each station. The CPUEs for weight and number of individuals for both trawl gear types are also summarized in tables by station in Appendix A. The top ten fish and top twelve invertebrate taxa were chosen for each paired towed based upon those with the highest CPUE weight (kg) for both trawls combined.

Overall, the mean area swept by the PSBT per haul was 2% of the mean area sampled by the EBT, or 0.045 ha compared to 1.945 ha. The area sampled by all 39 PSBT hauls combined was less than the average area sampled by a single EBT tow. Similarly, the mean total catch weight for the EBT was 94% greater than the PSBT, or 230.81 kg compared to 13.18 kg.

Species/taxa presence or absence was a good measure for determining general differences between trawl catches. Comparative size composition plots were also created for five different fish species and snow crab (Chionoecetes opilio) at each station. Fish species were selected based on whether they were part of the top ten list used in Table 2 catch comparisons for each station, or secondarily, if they represented a significant portion of the catch at a station. Some stations had less than five total species resulting in fewer than five comparative size composition plots.

In terms of catch, a total of 55 different species of fish and 288 different taxa of invertebrates were observed in the combined catches of both the PSBT and EBT. On average, the two trawls caught a similar number of taxa per haul, with the EBT catching 9.56 fish species and 39.41 invertebrate taxa compared to 9.41 fish species and 31.28 invertebrate taxa for the PSBT. However, as observed in the station-by-station comparisons in Appendix A, the catch composition between the PSBT and the EBT, as well as between each station, was very different. The EBT caught 12 fish species and 80 invertebrate taxa that were not observed in the PSBT catches while the PSBT caught 6 fish species and 54 invertebrate taxa that were unique. Combining these results, 33% of the fish species and 47% of the invertebrate taxa were gear-specific. A high abundance of clams from the genera Nucula or Nuculana or both were present in PSBT catches (e.g., Stations N-05, O-02, M-02, L-04) compared to very low abundance or absence from EBT catches suggesting that the PSBT tended the bottom harder than the EBT and was more efficient at capturing benthic infauna near the surface.

Gear-specific sampling was also observed in the size composition of fishes and snow crabs from paired tows, with the EBT catching larger fish overall while rarely sampling the earlier life stages that were very common in the PSBT catches. The mean fork length of Arctic cod (Boreogadus saida) collected in the EBT was 113 ± 20 mm (1 SD) and 93 ± 26 mm for the PSBT. Even greater differences were observed with saffron cod (Eleginus gracilis), where the mean fork length was 194 ± 77 mm for the EBT and 55 ± 15 mm for the PSBT. This was the general trend for all fish species caught and snow crab.

The PSBT and EBT were completely different sampling tools in terms of their design and use, and differences between the two were also clearly evident in the station-by-station comparisons of catch (Appendix A). Obvious contrasting characteristics of the PSBT and EBT were mesh size, area-swept, tow speed, and vertical opening. The finer mesh and harder bottom-tending characteristics of the PSBT retained juvenile fishes and other smaller macroinvertebrates and it was also more efficient catching benthic infauna that were just below the surface. The EBT had a larger net opening with greater tow duration at a higher speed that covered a potentially wider range of benthic habitats during a single tow, and it was more efficient at capturing larger and more mobile organisms, as well as organisms that were further off bottom.

Endeavoring to design and conduct a more rigorous experiment with sufficient power for making statistical comparisons between standardized catches of the PSBT and EBT is probably not practical or feasible given the large differences between the two trawl gears in terms of the area covered during a single tow, as well as the other inherent dissimilarities between the PSBT and EBT. The dissimilarities between gears and the resulting catches underscore the high variability in catching efficiency and selectivity between different kinds of bottom trawls. If used separately, each gear would provide differing interpretations and conclusions about the composition of the benthic community. However, if used as complementary sampling tools, the PSBT and EBT provide a more inclusive catalogue of the composition and size range of epibenthic macrofauna present at each sampling station or within a survey area.

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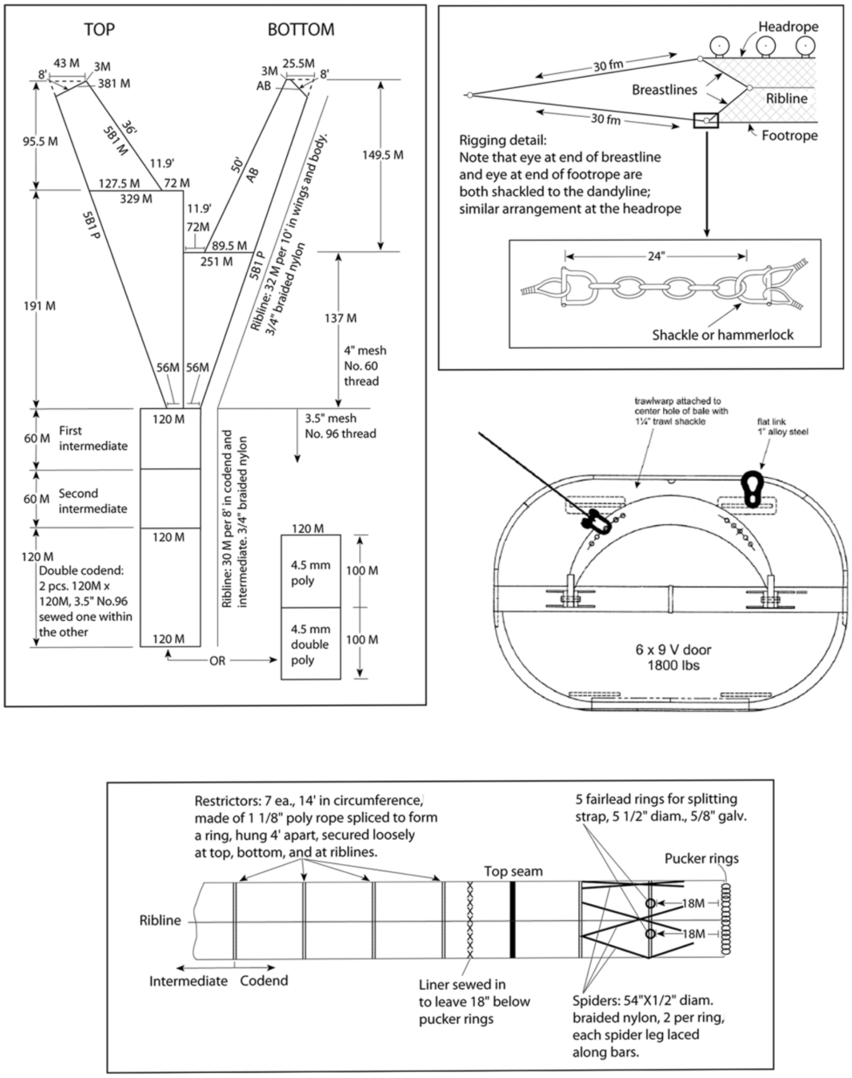


Figure 1. Schematic diagram of the standard Alaska Fisheries Science Center 83-112 Eastern bottom trawl (EBT) gear used for the gear comparison study during the 2012 Arctic EIS bottom trawl survey.

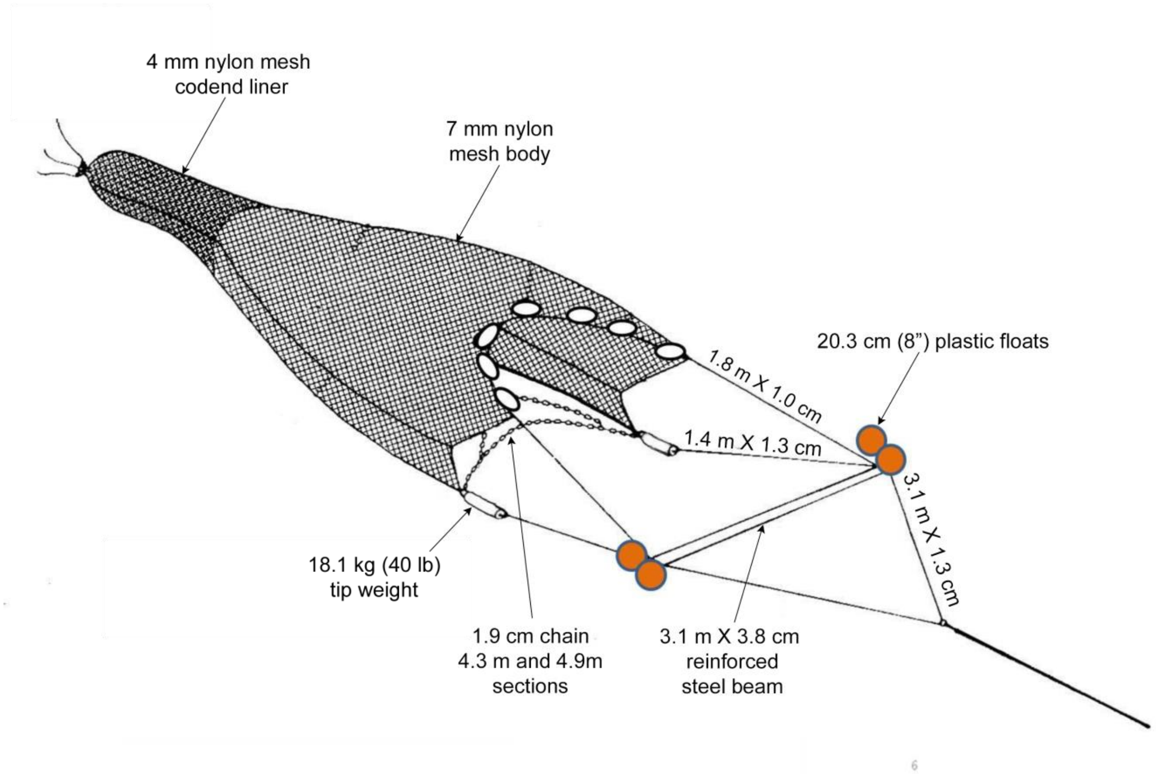


Figure 2. Schematic diagram of the plumb staff beam trawl gear used for the 2012 Chukchi Sea gear comparison study.

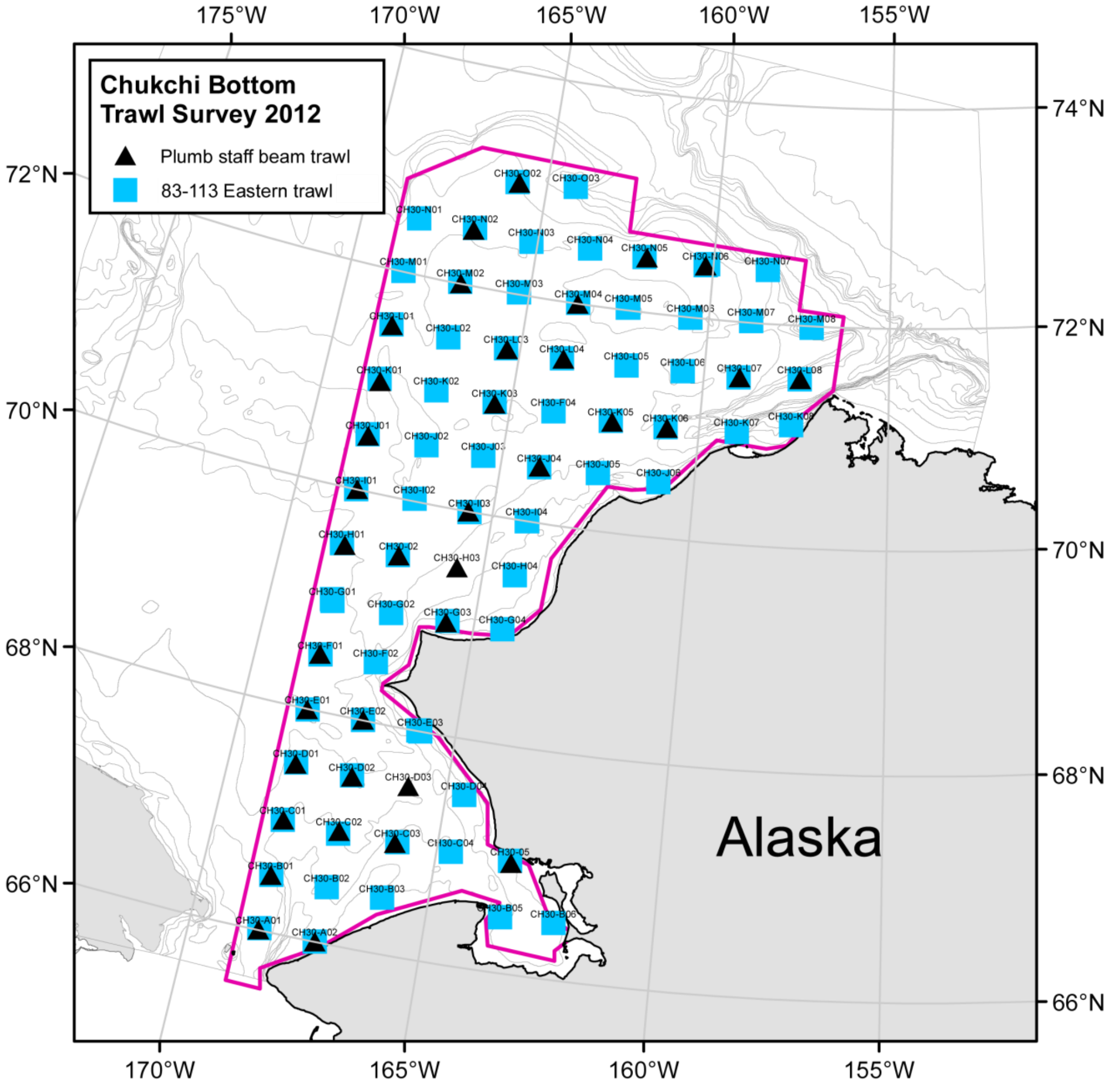


Figure 3. Map showing the location of stations sampled using the plumb staff beam trawl (black triangles) and the 83-112 Eastern bottom trawl (blue squares) during the 2012 Arctic EIS bottom trawl survey.

Station-by-station comparison of 39 paired Plumb Staff Beam Trawl (PSBT) and 83-112 Eastern Trawl (EBT) tows made during the 2012 Arctic EIS Bottom Trawl Survey. For each successfully completed pair of tows at a station, there is a single page with three tables and one figure with multiple plots. The three tables include: 1) differences in sample area and catch metrics, 2) catch per unit effort (per hectare) for the top ten fish species, and 3) catch per unit effort (per hectare) for the top twelve invertebrate taxa. Figures compare size compositions for the major species captured in number/hectare (ha). The size range on the abscissa varies between species and stations, and the range of catch values on the ordinate can vary between the PSBT (blue) and the EBT (red) within a species and station and between species and station.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.867	0.040	98%
Depth (m)	52	55	-6%
Bottom Temperature (°C)	1.6	1.1	31%
Total Catch Weight (kg)	1660	17.63	99%
Number Fish Species	11	9	18%
Unique Fish Species	4	2	50%
Number Invert Taxa	26	32	-23%
Unique Invert Taxa	16	22	-38%

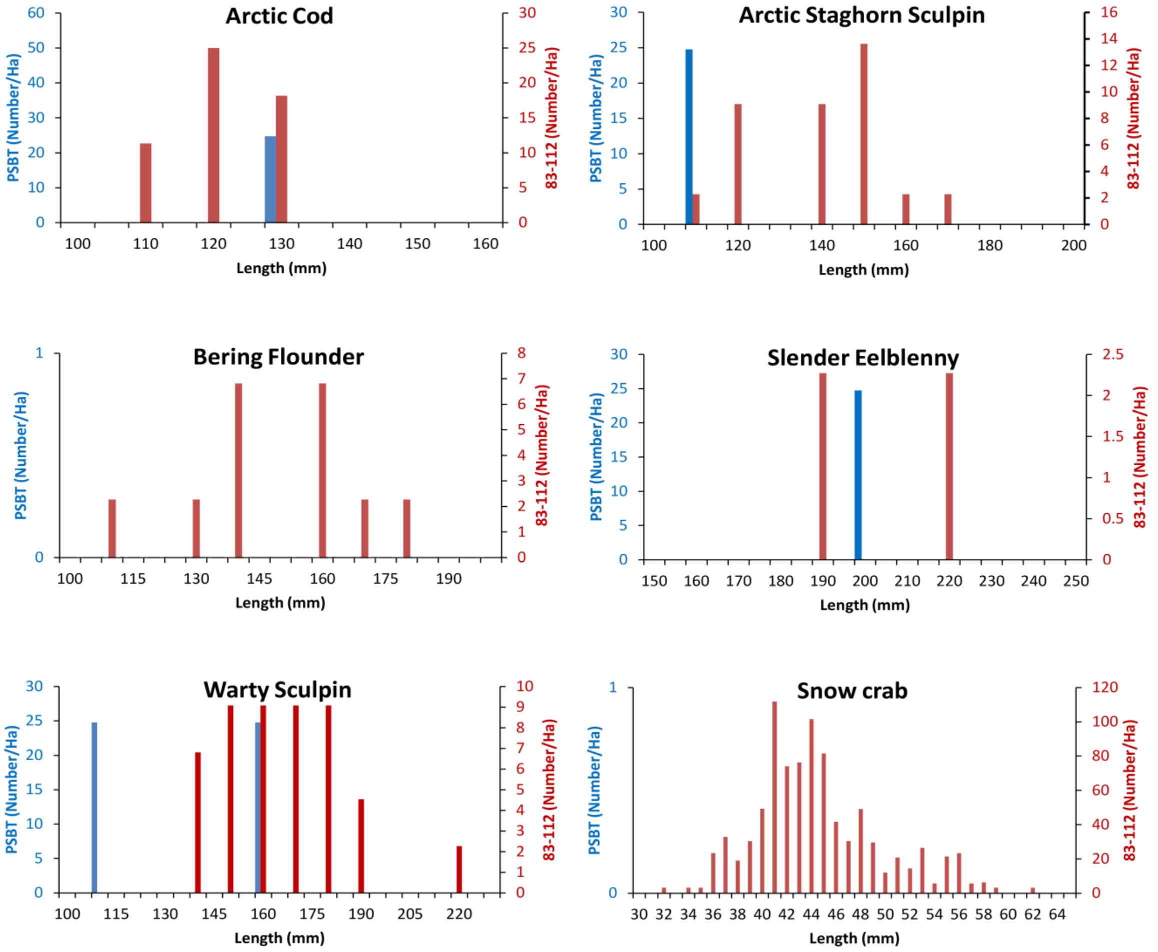
Table 2. Catch per unit effort (per hectare) comparison for station A-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	2.28	185.90	0.50	24.75
Arctic staghorn sculpin	0.41	9.11	1.04	24.75
Bering flounder	0.17	5.36	-	-
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	0.01	1.07	0.45	24.75
stout eelblenny	-	-	0.15	24.75
variegated snailfish	0.22	0.54	17.48	49.50
warty sculpin	0.77	11.79	1.88	49.50
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station A-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	14.79	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	23.59	902.73	-	-
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	19.67	83.04	-	-
Neptunea heros	-	-	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	36.29	526.10	-	-
Strongylocentrotus droebachiensis	378.09	14,171.52	-	238.96

Station A-01



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station A-01.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.003	0.028	99%
Depth (m)	15	16	-7%
Bottom Temperature (°C)	9.9	9.7	2%
Total Catch Weight (kg)	43.758	0.852	98%
Number Fish Species	12	6	50%
Unique Fish Species	8	2	75%
Number Invert Taxa	18	8	56%
Unique Invert Taxa	14	4	71%

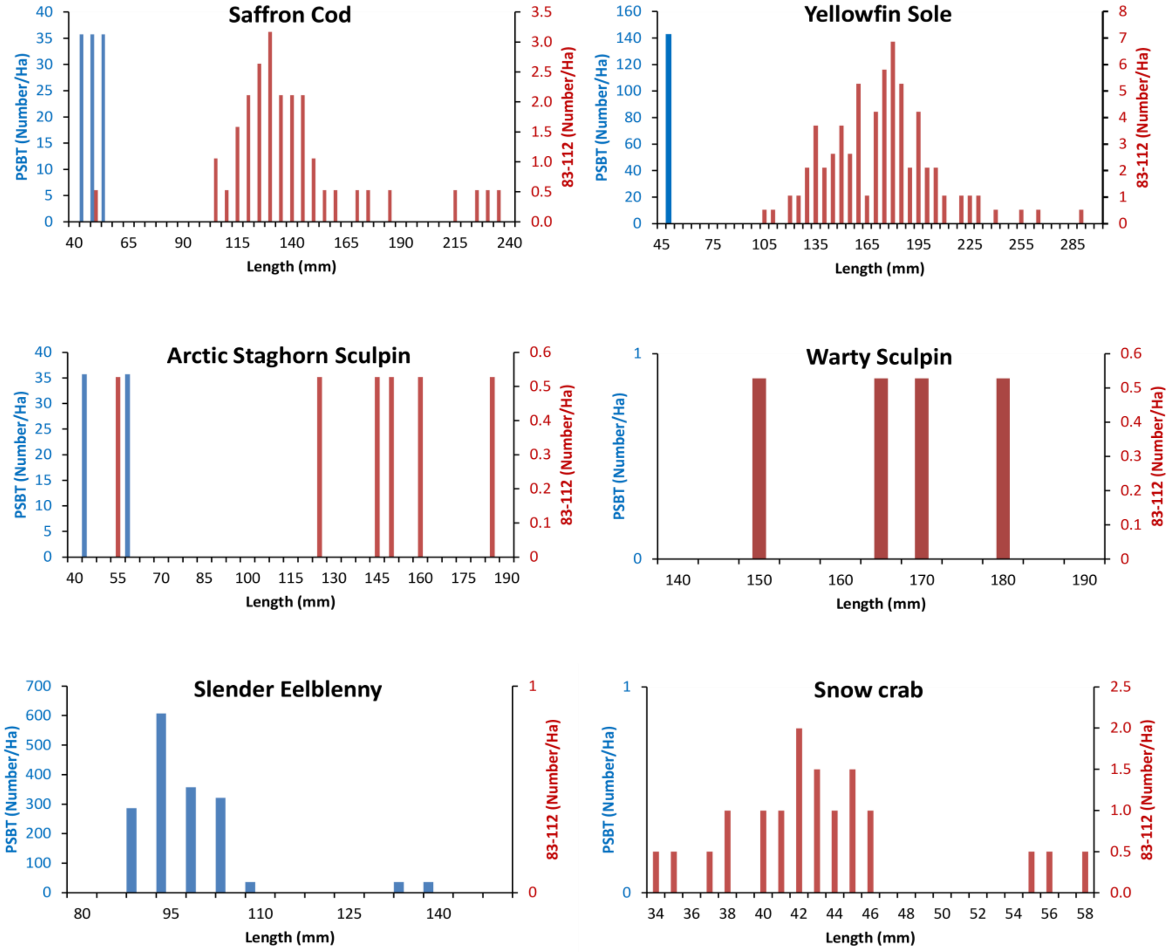
Table 2. Catch per unit effort (per hectare) comparison for station A-02 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.02	1.50	-	-
Arctic staghorn sculpin	0.14	2.99	0.07	71.46
Bering flounder	-	-	-	-
Pacific herring	0.54	6.49	-	-
saffron cod	0.56	22.46	0.07	107.19
slender eelblenny	-	-	4.43	1,679.36
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	4.38	61.90	1.86	142.92

Table 3. Catch per unit effort (per hectare) comparison for station A-02 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	6.65	108.32	14.79	214.39
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.47	12.98	-	-
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	0.50	2.99	-	-
Neptunea heros	0.25	2.00	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	-	-	-	-
Strongylocentrotus droebachiensis	0.01	0.50	-	-

Station A-02



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station A-02.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.817	0.067	96%
Depth (m)	52	53	-2%
Bottom Temperature (°C)	1.3	1.8	-38%
Total Catch Weight (kg)	841.952	16.43	98%
Number Fish Species	14	12	14%
Unique Fish Species	7	5	29%
Number Invert Taxa	31	38	-23%
Unique Invert Taxa	14	21	-50%

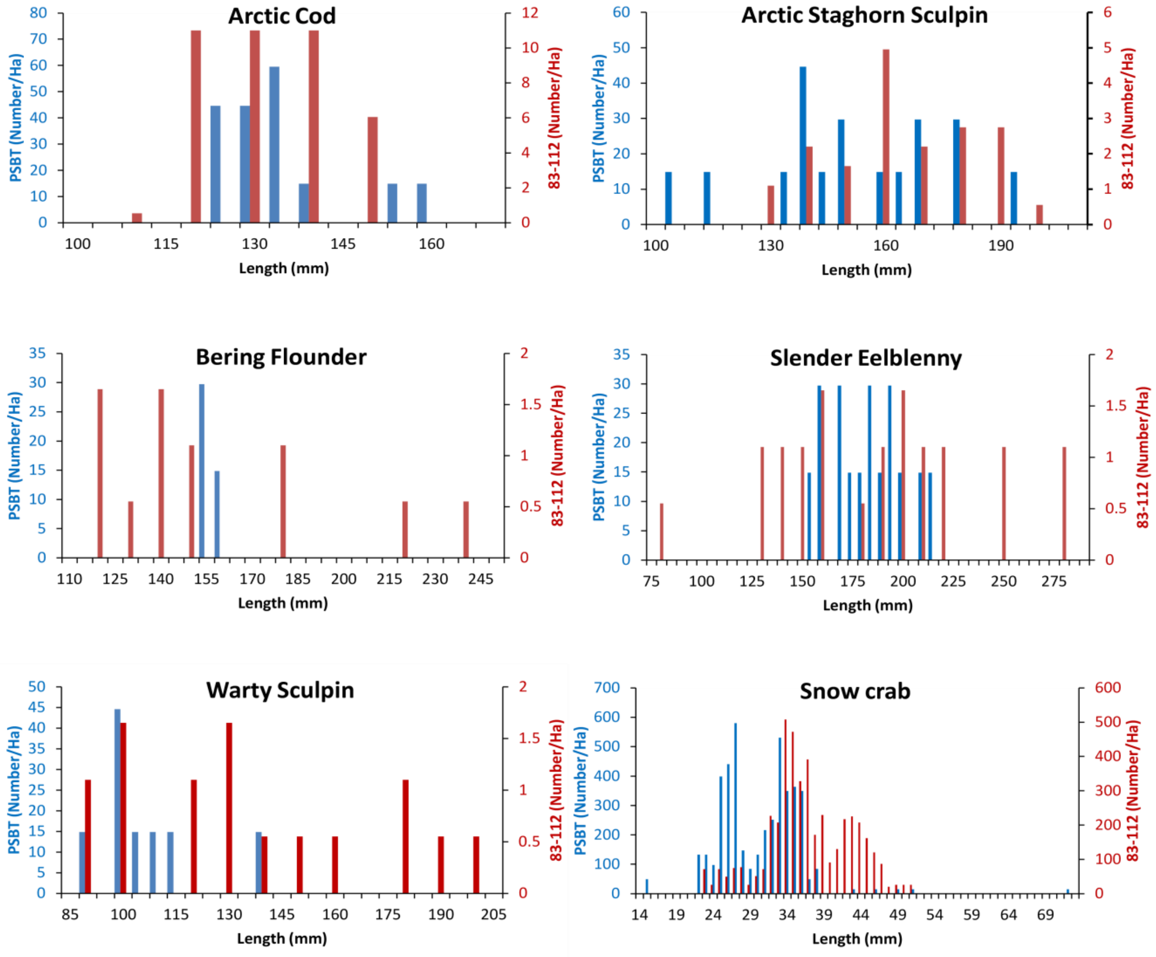
Table 2. Catch per unit effort (per hectare) comparison for station B-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.90	78.71	2.68	193.28
Arctic staghorn sculpin	0.55	18.16	5.62	237.89
Bering flounder	0.30	7.16	1.64	44.60
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	0.20	13.21	3.42	223.02
stout eelblenny	-	-	0.15	44.60
variegated snailfish	1.48	17.61	5.35	44.60
warty sculpin	0.40	9.36	1.96	118.94
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station B-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	93.89	4,386.86	52.66	4,460.40
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	35.70	354.47	17.25	148.68
Neptunea heros	47.80	453.55	5.06	44.60
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	32.45	858.11	34.05	341.96
Strongylocentrotus droebachiensis	106.26	1,995.83	36.60	609.59

Station B-01



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station B-01.

Station C-01

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

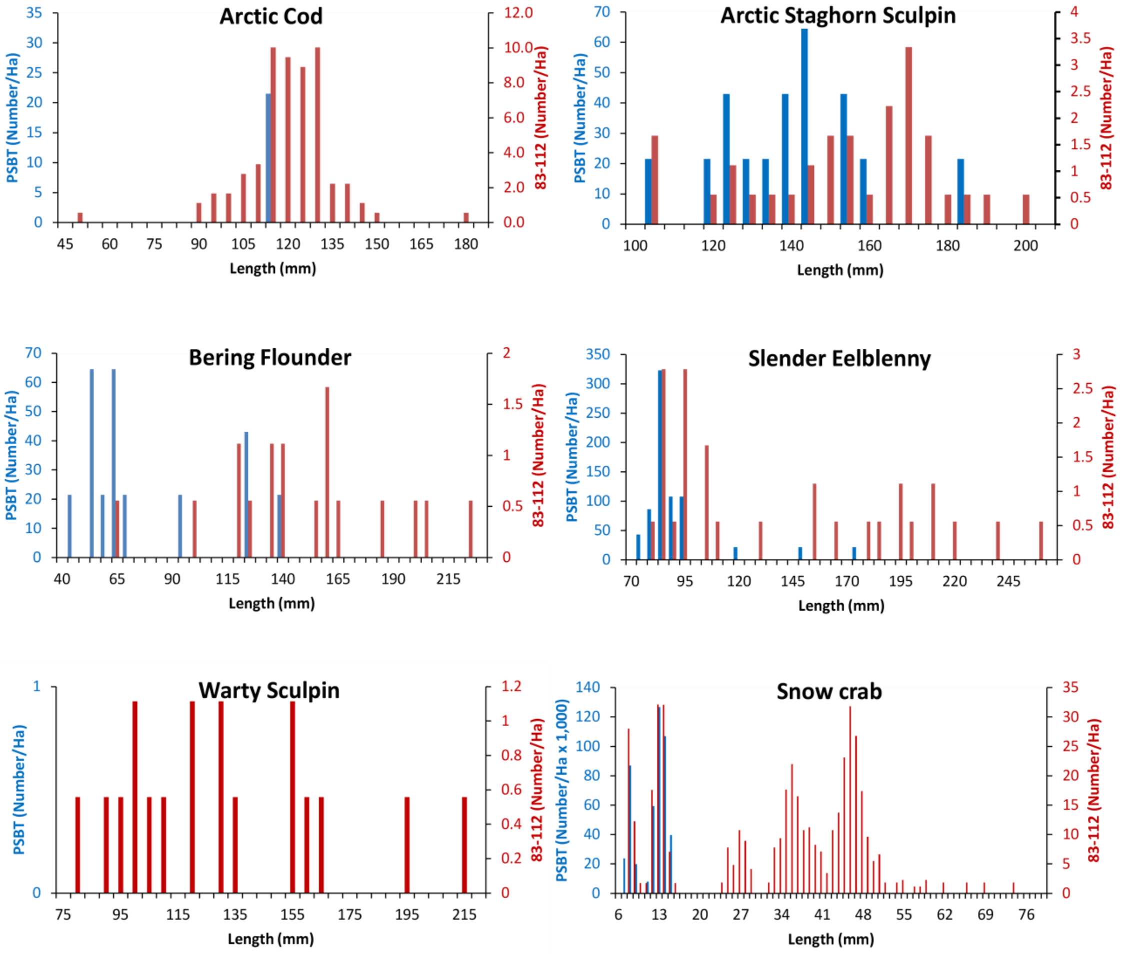
	83-112	PSBT	Difference
Area Sampled (ha)	1.796	0.047	97%
Depth (m)	37	39	-5%
Bottom Temperature (°C)	2.4	2.2	8%
Total Catch Weight (kg)	91.67	40.298	56%
Number Fish Species	11	8	27%
Unique Fish Species	4	1	75%
Number Invert Taxa	33	25	24%
Unique Invert Taxa	17	9	47%

Table 2. Catch per unit effort (per hectare) comparison for station C-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	1.70	123.05	0.26	21.51
Arctic staghorn sculpin	0.56	19.49	5.08	322.62
Bering flounder	0.41	10.02	1.68	279.60
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	0.16	16.70	2.24	731.27
stout eelblenny	-	-	0.34	193.57
variegated snailfish	0.59	5.01	1.16	21.51
warty sculpin	0.38	10.02	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station C-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	4.47	26.72	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	8.95	451.54	536.02	473,327.86
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	2.46	13.36	9.76	86.03
Neptunea heros	20.82	145.32	60.44	838.81
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	0.08	16.70	-	-
Pagurus rathbuni	0.16	15.03	0.22	21.51
Pagurus trigonocheirus	4.03	152.00	23.98	1,613.10
Strongylocentrotus droebachiensis	0.05	0.56	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station C-01.

Station C-02

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

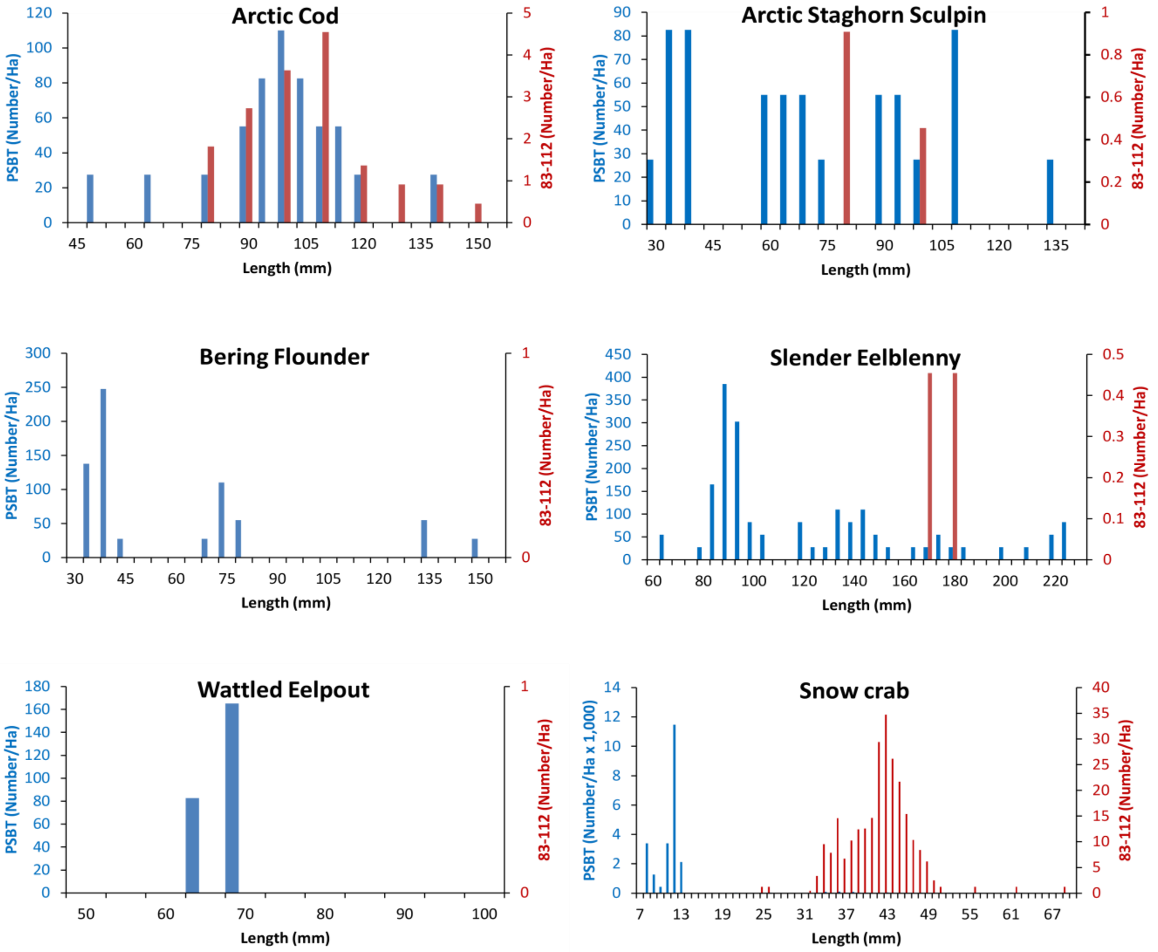
	83-112	PSBT	Difference
Area Sampled (ha)	2.202	0.036	98%
Depth (m)	38	39	-3%
Bottom Temperature (°C)	2	2	0%
Total Catch Weight (kg)	66.492	16.935	75%
Number Fish Species	6	11	-83%
Unique Fish Species	2	7	-250%
Number Invert Taxa	28	33	-18%
Unique Invert Taxa	9	14	-56%

Table 2. Catch per unit effort (per hectare) comparison for station C-02 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.19	16.35	5.23	577.91
Arctic staghorn sculpin	0.02	1.36	4.84	632.95
Bering flounder	-	-	2.64	687.99
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	0.01	0.91	12.77	1,953.89
stout eelblenny	-	-	1.38	330.24
variegated snailfish	0.09	0.45	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station C-02 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	2.28	9.08	29.12	110.08
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	6.60	254.32	27.44	22,676.17
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	2.48	19.53	7.87	55.04
Neptunea heros	7.80	68.12	48.93	632.95
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	2.36	311.08	228.28	60,075.35
Pagurus rathbuni	0.004	0.45	2.15	247.68
Pagurus trigonocheirus	2.17	61.31	21.91	1,568.62
Strongylocentrotus droebachiensis	-	-	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station C-02.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.075	0.047	98%
Depth (m)	24	24	0%
Bottom Temperature (°C)	8.2	8.1	1%
Total Catch Weight (kg)	114.179	3.075	97%
Number Fish Species	14	9	36%
Unique Fish Species	9	4	56%
Number Invert Taxa	29	14	52%
Unique Invert Taxa	21	6	71%

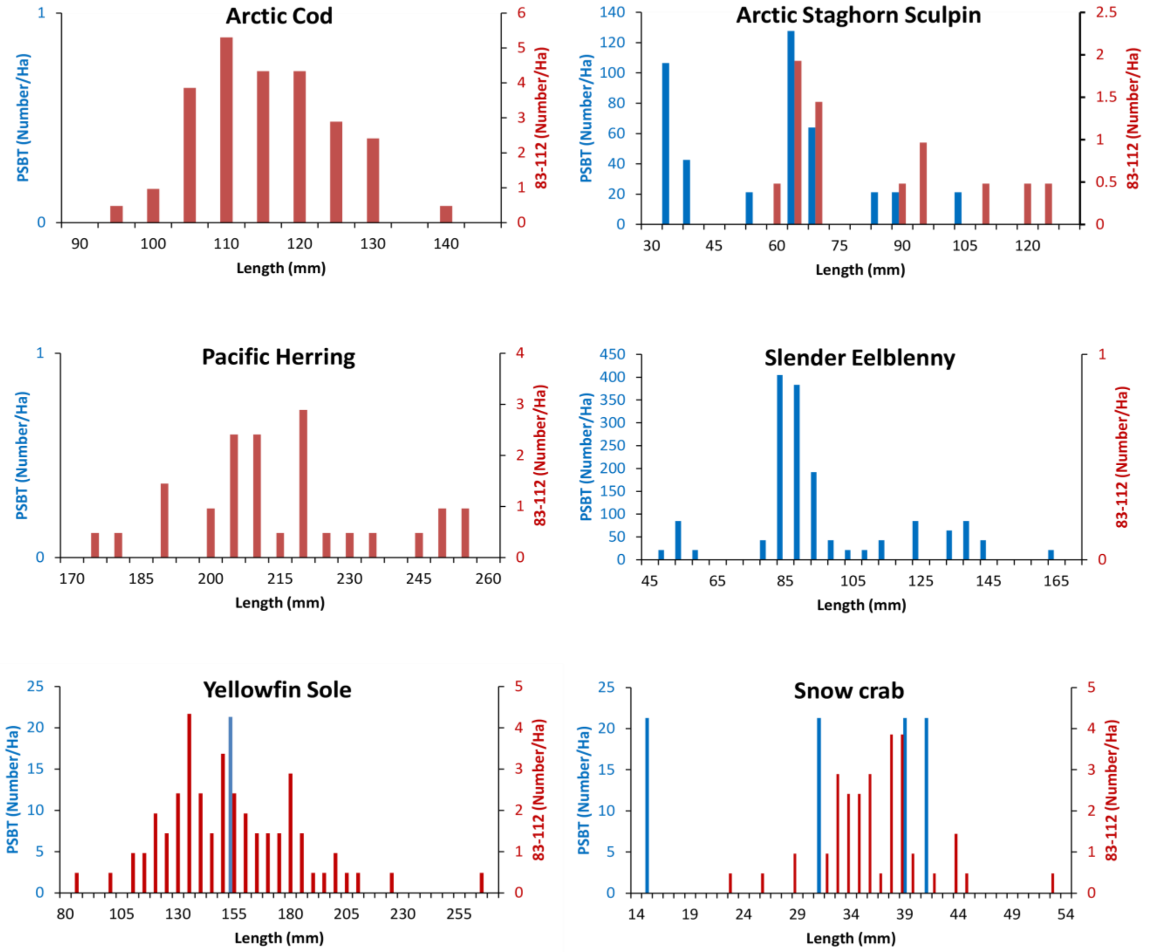
Table 2. Catch per unit effort (per hectare) comparison for station C-03 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.75	61.20	-	-
Arctic staghorn sculpin	0.08	6.75	1.36	426.03
Bering flounder	0.06	0.96	-	-
Pacific herring	1.57	15.42	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	5.37	1,576.29
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	0.12	1.93	0.04	42.60
yellowfin sole	1.87	37.11	1.02	21.30

Table 3. Catch per unit effort (per hectare) comparison for station C-03 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	27.89	815.41	38.13	1,214.17
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.80	25.54	2.00	85.21
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	0.04	0.48	-	-
Neptunea heros	-	-	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	0.10	5.78	-	-
Strongylocentrotus droebachiensis	0.17	2.89	-	-

Station C-03



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station C-03.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.216	0.048	98%
Depth (m)	14	14	0%
Bottom Temperature (°C)	10.7	10.6	1%
Total Catch Weight (kg)	148.752	6.687	96%
Number Fish Species	17	9	47%
Unique Fish Species	10	2	80%
Number Invert Taxa	33	21	36%
Unique Invert Taxa	18	6	67%

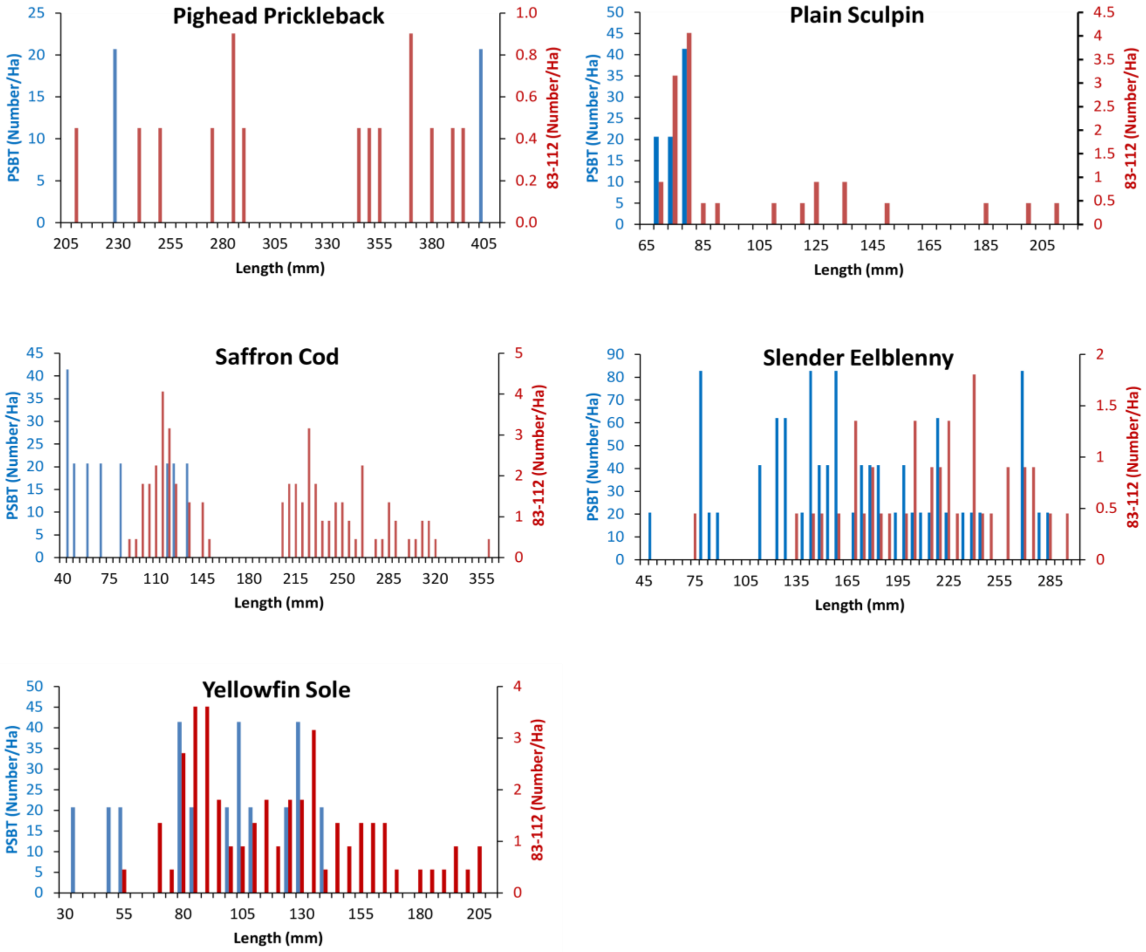
Table 2. Catch per unit effort (per hectare) comparison for station C-05 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.01	0.45	-	-
Arctic staghorn sculpin	-	-	0.17	82.82
Bering flounder	-	-	-	-
Pacific herring	-	-	-	-
saffron cod	7.43	92.06	1.08	186.34
slender eelblenny	0.66	32.94	14.12	1,118.02
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	4.37	185.48	4.55	289.86

Table 3. Catch per unit effort (per hectare) comparison for station C-05 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	17.77	303.26	52.59	19,482.48
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	-	-	-	-
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	2.55	19.41	-	-
Neptunea heros	0.54	5.87	0.70	20.70
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	0.04	2.71	-	-
Strongylocentrotus droebachiensis	0.65	13.09	-	-

Station C-05



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station C-05.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.273	0.056	98%
Depth (m)	47	49	-4%
Bottom Temperature (°C)	1.3	1.3	0%
Total Catch Weight (kg)	150.26	37.907	75%
Number Fish Species	8	9	-13%
Unique Fish Species	4	5	-25%
Number Invert Taxa	30	29	3%
Unique Invert Taxa	9	8	11%

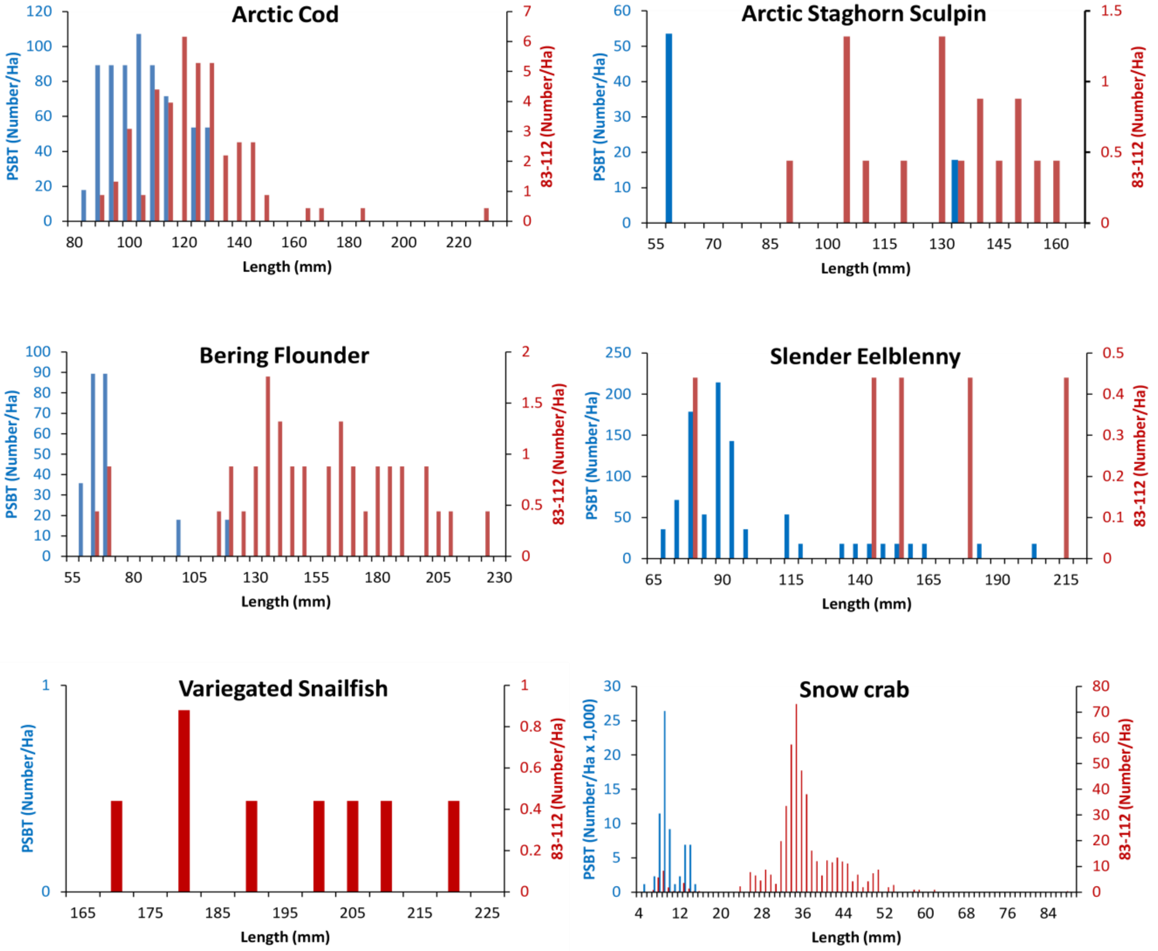
Table 2. Catch per unit effort (per hectare) comparison for station D-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	2.15	142.08	5.54	661.03
Arctic staghorn sculpin	0.28	7.48	0.93	71.46
Bering flounder	0.76	17.16	1.00	250.12
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	0.02	2.20	3.64	964.74
stout eelblenny	-	-	1.82	661.03
variegated snailfish	0.39	3.52	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station D-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	8.46	468.47	53.08	69,568.51
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	43.95	344.86	46.88	482.37
Neptunea heros	0.47	3.96	6.32	35.73
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	1.79	714.62
Ophiura sarsi	5.26	521.69	94.74	9,790.33
Pagurus rathbuni	0.53	33.43	378.96	-
Pagurus trigonocheirus	0.20	10.12	0.21	35.73
Strongylocentrotus droebachiensis	-	-	-	-

Station D-01



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station D-01.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.055	0.034	98%
Depth (m)	46	45	2%
Bottom Temperature (°C)	1.7	2.1	-24%
Total Catch Weight (kg)	62.213	17.279	72%
Number Fish Species	6	11	-83%
Unique Fish Species	1	6	-500%
Number Invert Taxa	35	32	9%
Unique Invert Taxa	16	13	19%

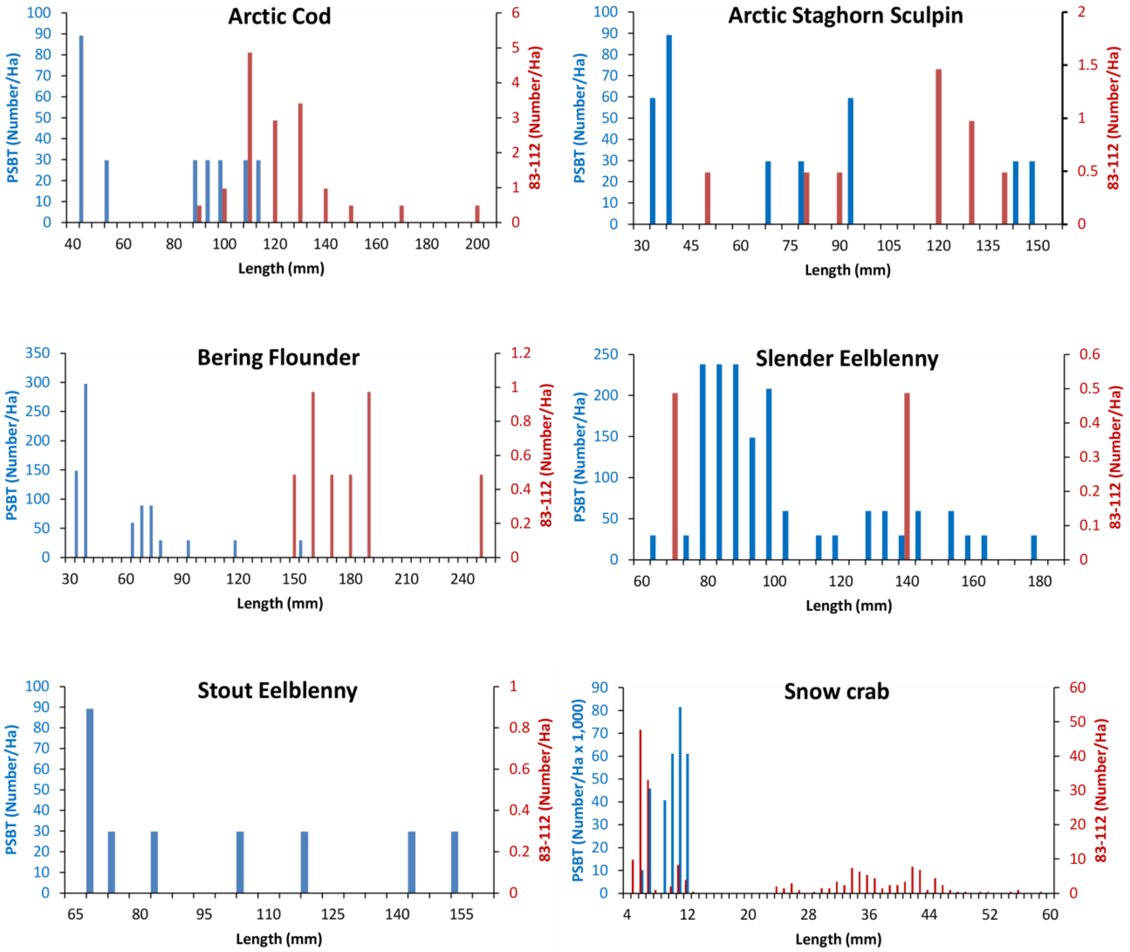
Table 2. Catch per unit effort (per hectare) comparison for station D-02 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.27	15.09	1.25	267.62
Arctic staghorn sculpin	0.13	4.38	4.46	327.10
Bering flounder	0.29	3.89	2.80	802.87
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	0.004	0.97	5.89	1,605.74
stout eelblenny	-	-	0.95	267.62
variegated snailfish	-	-	-	-
warty sculpin	-	-	0.03	59.47
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station D-02 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	2.64	15.57	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	1.67	183.00	168.10	301,463.31
Gorgonocephalus sp. cf. *arcticus*	0.002	0.49	0.36	29.74
Leptasterias polaris	11.87	95.39	34.82	3,211.49
Neptunea heros	-	-	-	-
Nucula tenuis	-	-	88.17	105,800.60
Nuculana pernula	-	-	-	-
Ophiura sarsi	1.11	132.87	4.82	535.25
Pagurus rathbuni	0.35	16.55	10.35	624.46
Pagurus trigonocheirus	0.83	32.61	12.96	1,040.76
Strongylocentrotus droebachiensis	-	-	-	-

Station D-02



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station D-02.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.688	0.065	96%
Depth (m)	40	40	0%
Bottom Temperature (°C)	5	--	--
Total Catch Weight (kg)	133.012	13.352	90%
Number Fish Species	8	8	0%
Unique Fish Species	4	4	0%
Number Invert Taxa	37	37	0%
Unique Invert Taxa	17	17	0%

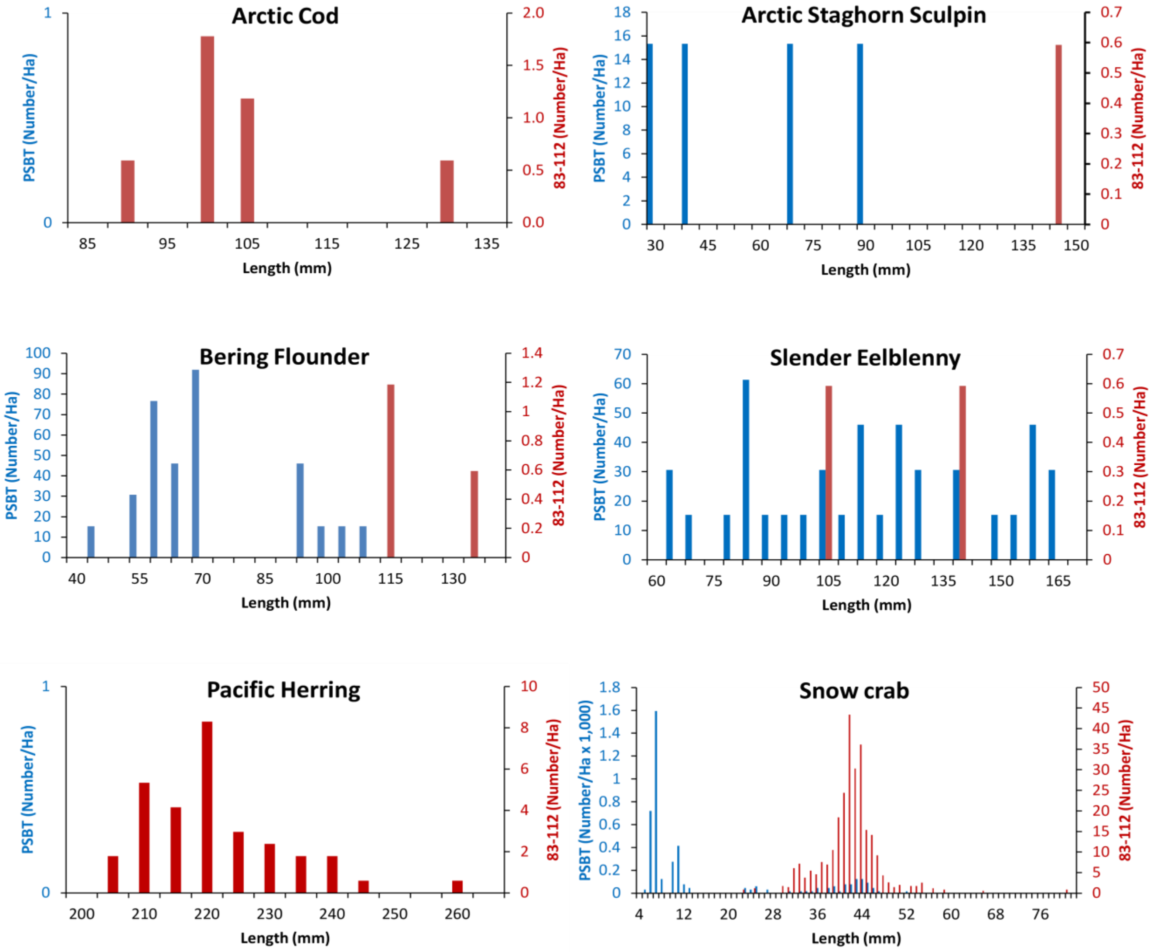
Table 2. Catch per unit effort (per hectare) comparison for station D-03 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.03	4.15	-	-
Arctic staghorn sculpin	0.02	0.59	0.21	61.32
Bering flounder	0.03	1.78	1.32	352.61
Pacific herring	14.94	128.59	-	-
saffron cod	-	-	-	-
slender eelblenny	0.01	1.19	1.93	490.59
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	0.01	0.59	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station D-03 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	6.07	89.48	30.94	199.30
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	8.11	268.43	27.07	4,246.69
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	0.99	9.48	3.10	45.99
Neptunea heros	1.31	13.63	11.28	245.30
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	0.21	107.32
Ophiura sarsi	0.001	0.59	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	13.76	62.81	14.84	2,759.58
Strongylocentrotus droebachiensis	0.08	1.19	-	-

Station D-03



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station D-03.

Station E-01

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

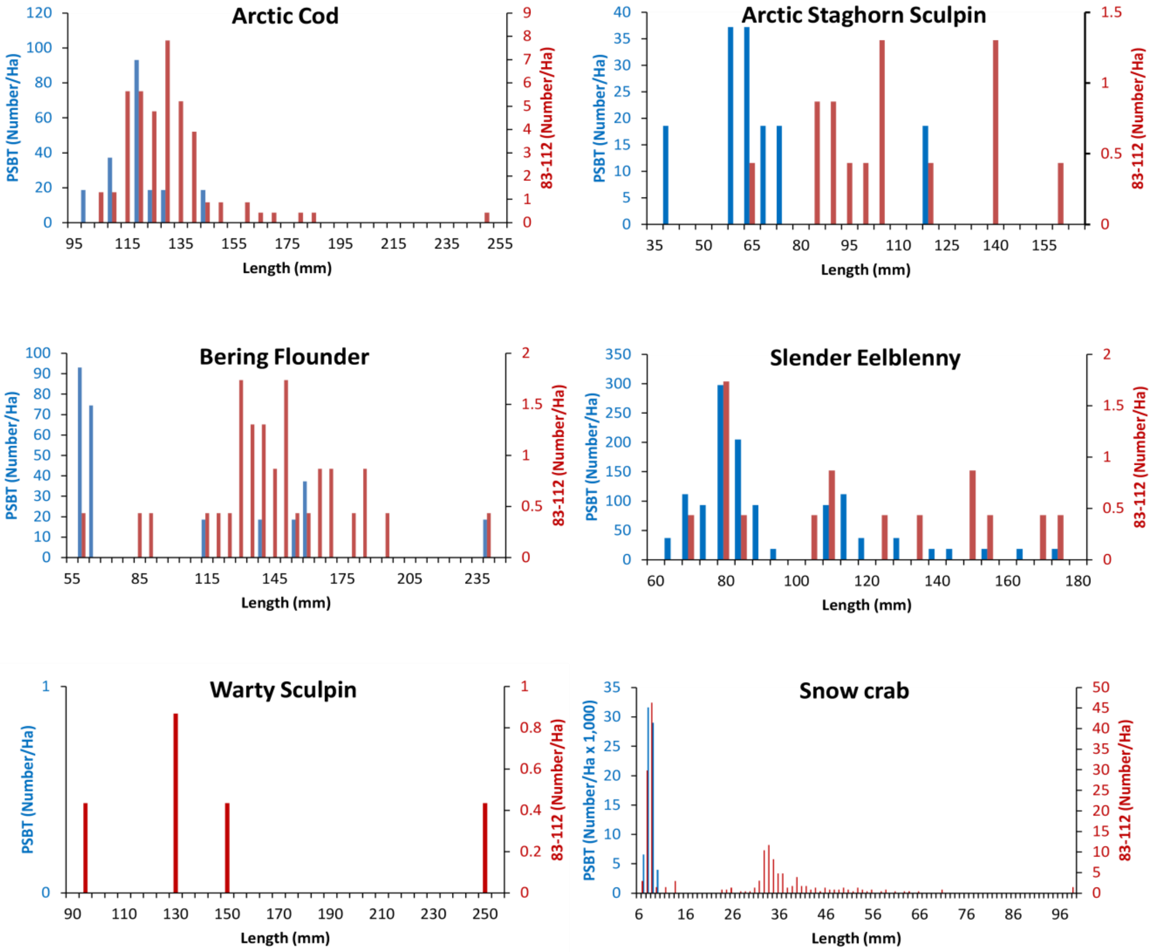
	83-112	PSBT	Difference
Area Sampled (ha)	2.302	0.054	98%
Depth (m)	58	58	0%
Bottom Temperature (°C)	1.5	1.5	0%
Total Catch Weight (kg)	147.968	18.406	88%
Number Fish Species	9	9	0%
Unique Fish Species	4	4	0%
Number Invert Taxa	38	24	37%
Unique Invert Taxa	18	4	78%

Table 2. Catch per unit effort (per hectare) comparison for station E-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	11.44	639.35	2.64	223.39
Arctic staghorn sculpin	0.14	6.52	0.78	148.93
Bering flounder	0.48	14.33	6.18	279.24
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	0.04	6.95	3.57	1,228.67
stout eelblenny	-	-	-	-
variegated snailfish	0.16	2.17	-	-
warty sculpin	0.14	2.17	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station E-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	9.79	18.62
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	1.98	162.01	38.18	71,374.58
Gorgonocephalus sp. cf. *arcticus*	0.44	7.82	-	-
Leptasterias polaris	14.94	99.46	14.93	297.86
Neptunea heros	9.25	66.02	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	5.67	983.78	170.12	30,809.84
Pagurus rathbuni	1.85	103.81	2.83	242.01
Pagurus trigonocheirus	2.70	105.98	3.61	223.39
Strongylocentrotus droebachiensis	-	-	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station E-01.

Station E-02

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

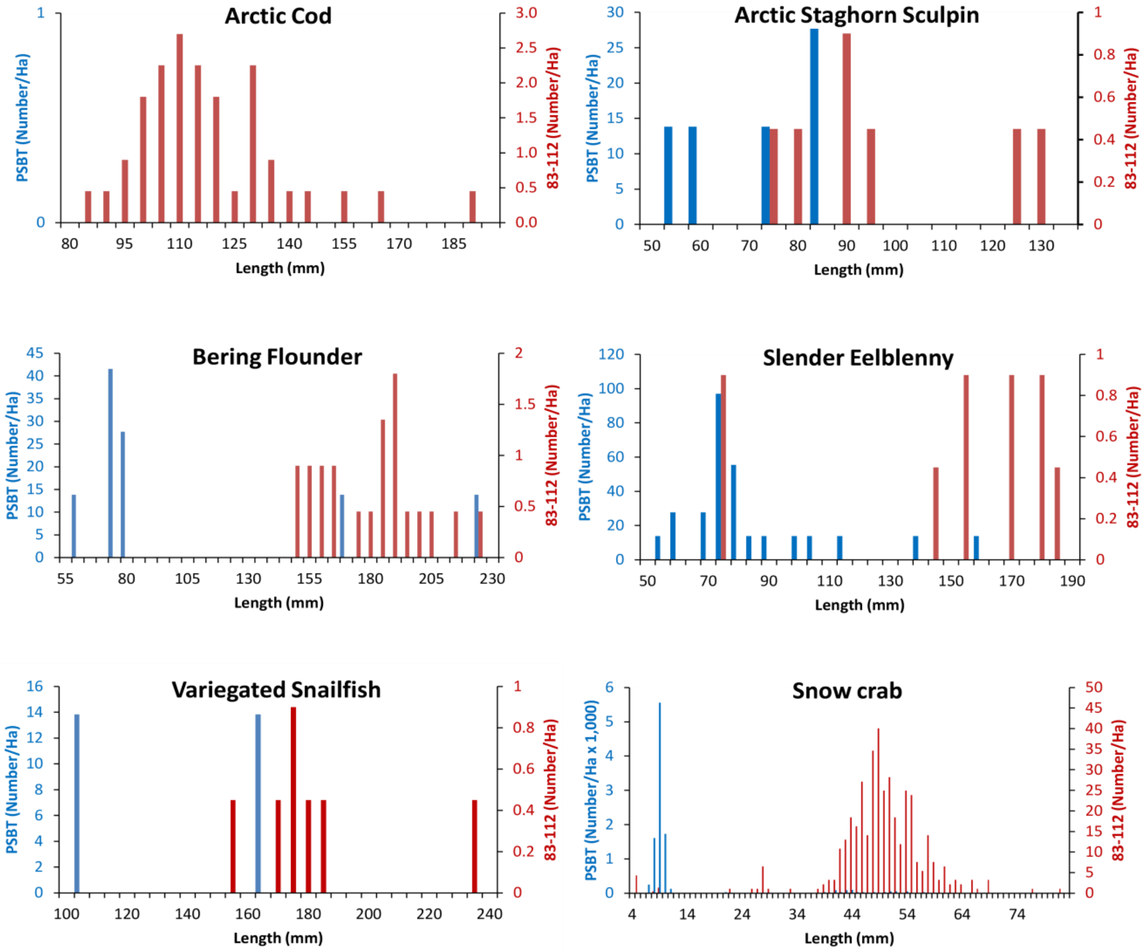
	83-112	PSBT	Difference
Area Sampled (ha)	2.222	0.072	97%
Depth (m)	56	56	0%
Bottom Temperature (°C)	2	1.6	20%
Total Catch Weight (kg)	859.511	42.36	95%
Number Fish Species	16	13	19%
Unique Fish Species	8	5	38%
Number Invert Taxa	60	71	-18%
Unique Invert Taxa	25	36	-44%

Table 2. Catch per unit effort (per hectare) comparison for station E-02 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.23	18.45	-	-
Arctic staghorn sculpin	0.04	3.15	0.53	69.23
Bering flounder	0.38	9.90	1.72	110.77
Pacific herring	0.05	0.45	-	-
saffron cod	-	-	-	-
slender eelblenny	0.04	4.50	0.75	318.45
stout eelblenny	-	-	0.11	13.85
variegated snailfish	0.28	3.15	1.14	27.69
warty sculpin	0.08	2.25	-	-
yellowfin sole	0.01	0.45	-	-

Table 3. Catch per unit effort (per hectare) comparison for station E-02 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	17.68	396.41	18.17	10,010.52
Gorgonocephalus sp. cf. *arcticus*	62.02	452.21	77.43	553.83
Leptasterias polaris	5.67	109.34	12.79	193.84
Neptunea heros	0.66	-	0.64	27.69
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	0.06	41.54
Ophiura sarsi	-	-	4.04	872.29
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	16.73	392.81	13.40	1,564.58
Strongylocentrotus droebachiensis	236.54	3,922.28	378.41	9,955.14



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station E-02.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.794	0.046	97%
Depth (m)	29	29	0%
Bottom Temperature (°C)	9.9	9.3	6%
Total Catch Weight (kg)	248.932	8.27	97%
Number Fish Species	17	10	41%
Unique Fish Species	11	4	64%
Number Invert Taxa	43	43	0%
Unique Invert Taxa	22	22	0%

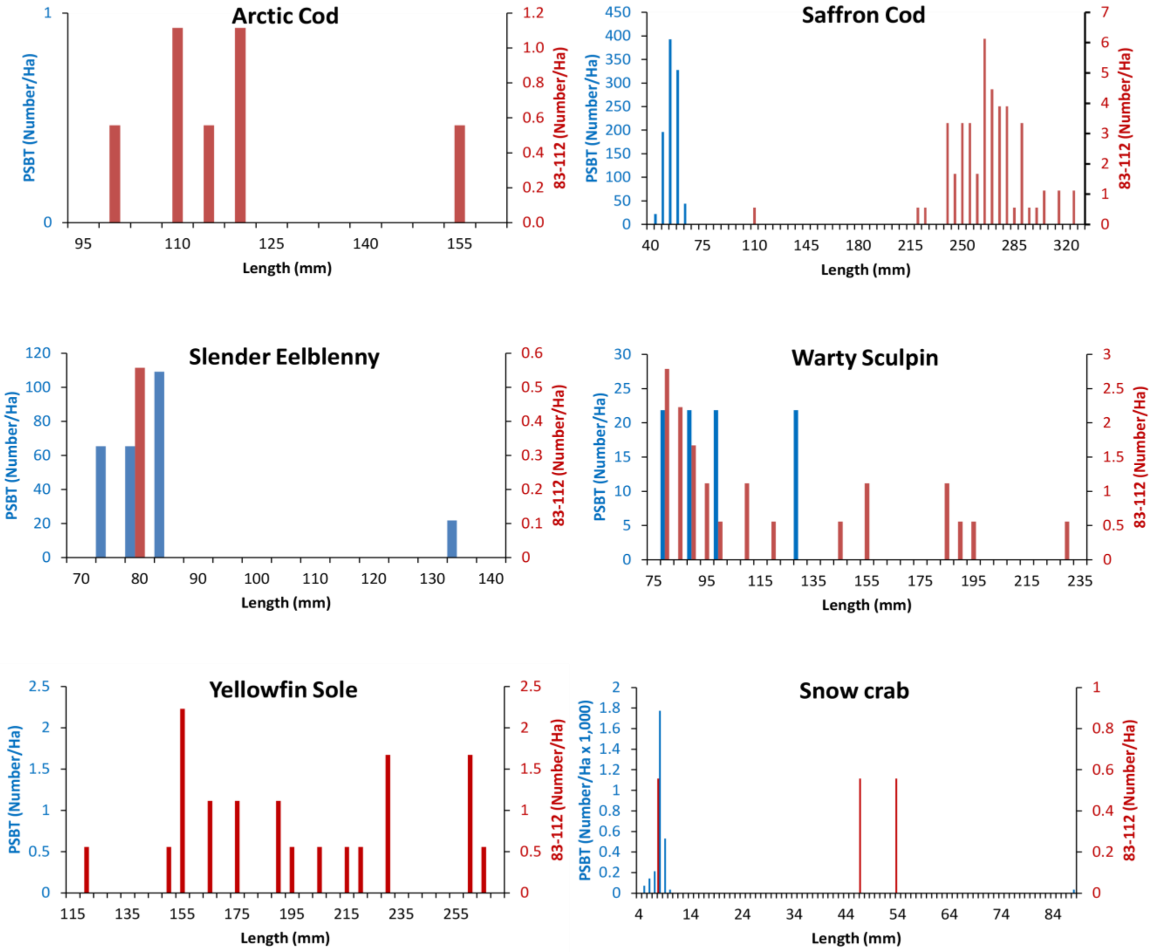
Table 2. Catch per unit effort (per hectare) comparison for station E-03 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.05	3.90	-	-
Arctic staghorn sculpin	0.03	0.56	0.04	65.48
Bering flounder	-	-	-	-
Pacific herring	6.66	65.21	-	-
saffron cod	38.64	242.46	1.27	982.17
slender eelblenny	0.001	0.56	0.48	261.91
stout eelblenny	-	-	-	-
variegated snailfish	0.04	0.56	-	-
warty sculpin	0.43	14.49	1.13	87.30
yellowfin sole	1.34	12.82	-	-

Table 3. Catch per unit effort (per hectare) comparison for station E-03 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	1.52	47.38	10.04	632.95
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.05	1.67	1.13	2,793.72
Gorgonocephalus sp. cf. *arcticus*	0.36	4.46	-	-
Leptasterias polaris	0.10	2.79	-	-
Neptunea heros	-	-	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	0.02	21.83
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	-	-	-	-
Strongylocentrotus droebachiensis	10.41	95.31	19.16	240.09

Station E-03



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station E-03.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.842	0.046	98%
Depth (m)	51	52	-2%
Bottom Temperature (°C)	2.3	2.3	0%
Total Catch Weight (kg)	70.348	1.964	97%
Number Fish Species	13	8	38%
Unique Fish Species	7	2	71%
Number Invert Taxa	34	24	29%
Unique Invert Taxa	21	11	48%

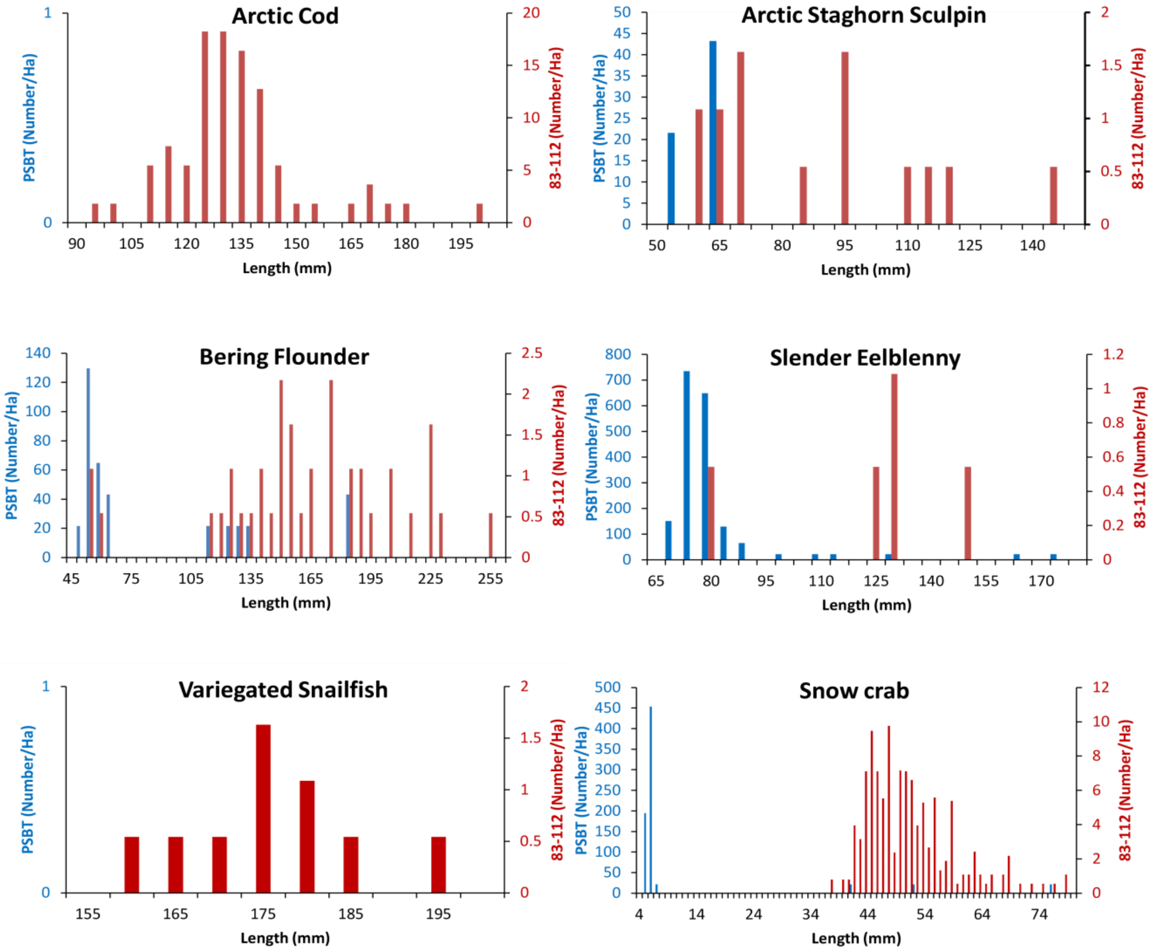
Table 2. Catch per unit effort (per hectare) comparison for station F-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	2.04	107.48	-	-
Arctic staghorn sculpin	0.08	8.14	0.09	64.84
Bering flounder	1.12	21.17	4.93	389.03
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	0.01	2.71	3.80	1,858.72
stout eelblenny	-	-	3.93	497.10
variegated snailfish	0.44	5.43	-	-
warty sculpin	0.02	1.63	0.30	21.61
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station F-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	0.38	1.09	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	7.60	111.83	6.70	734.84
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	4.40	60.26	2.07	43.23
Neptunea heros	5.66	45.06	0.13	21.61
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	0.44	38.54	0.35	86.45
Pagurus trigonocheirus	10.80	254.60	0.91	129.68
Strongylocentrotus droebachiensis	0.06	0.54	-	-

Station F-01



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station F-01.

Station G-01

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

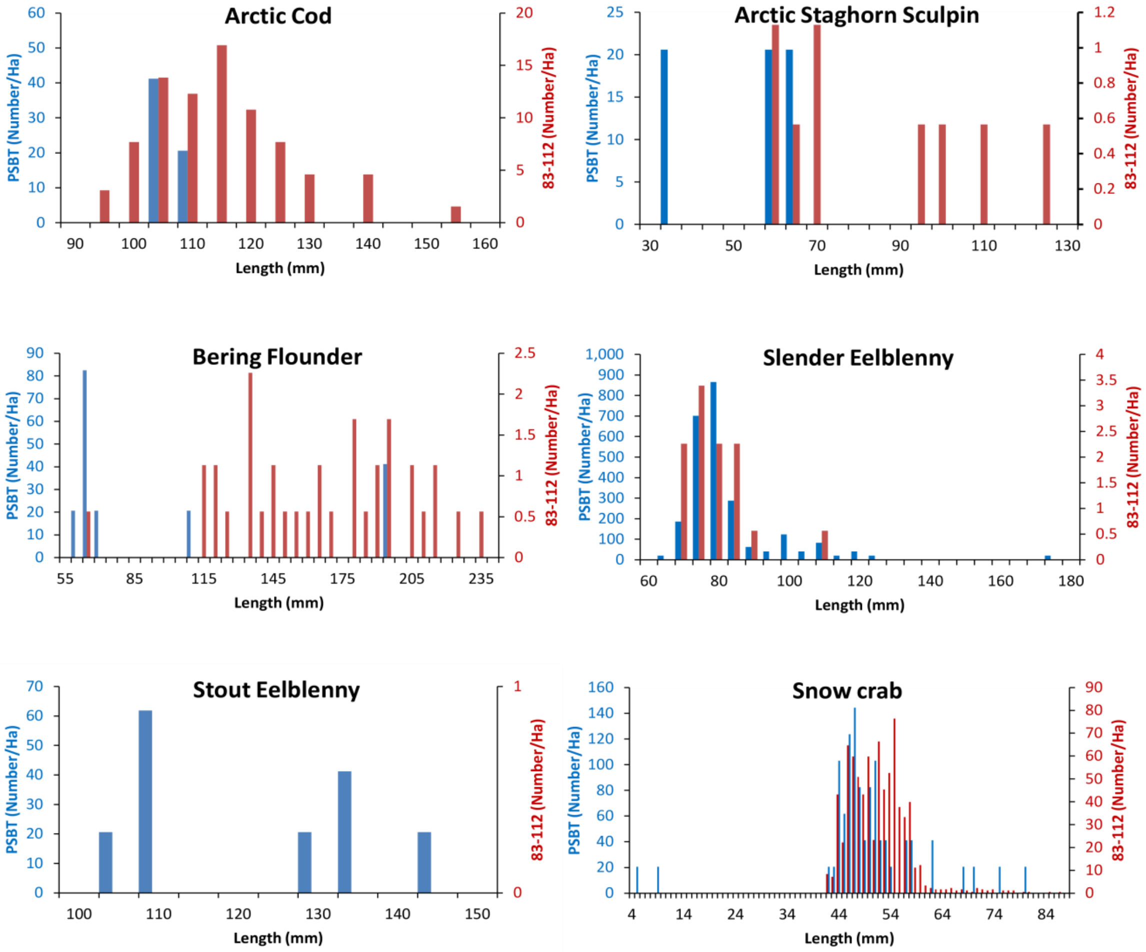
	83-112	PSBT	Difference
Area Sampled (ha)	1.770	0.049	97%
Depth (m)	51	53	-4%
Bottom Temperature (°C)	2.1	2	5%
Total Catch Weight (kg)	134.421	6.162	95%
Number Fish Species	13	12	8%
Unique Fish Species	6	5	17%
Number Invert Taxa	36	34	6%
Unique Invert Taxa	18	16	11%

Table 2. Catch per unit effort (per hectare) comparison for station G-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	1.01	83.06	0.54	61.82
Arctic staghorn sculpin	0.05	5.09	0.12	61.82
Bering flounder	1.01	19.78	3.30	185.47
Pacific herring	-	-	-	-
saffron cod	0.01	1.13	-	-
slender eelblenny	0.02	11.30	4.41	2,514.14
stout eelblenny	-	-	0.78	164.86
variegated snailfish	-	-	-	-
warty sculpin	0.10	1.70	-	-
yellowfin sole	0.00	0.57	-	-

Table 3. Catch per unit effort (per hectare) comparison for station G-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	43.22	787.63	59.45	1,133.42
Gorgonocephalus sp. cf. *arcticus*	0.62	3.96	-	-
Leptasterias polaris	6.55	83.06	13.15	247.29
Neptunea heros	6.47	51.42	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	0.20	23.73	0.58	144.25
Pagurus trigonocheirus	10.26	271.21	18.63	1,751.66
Strongylocentrotus droebachiensis	0.05	0.57	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station G-01.

Station G-03

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

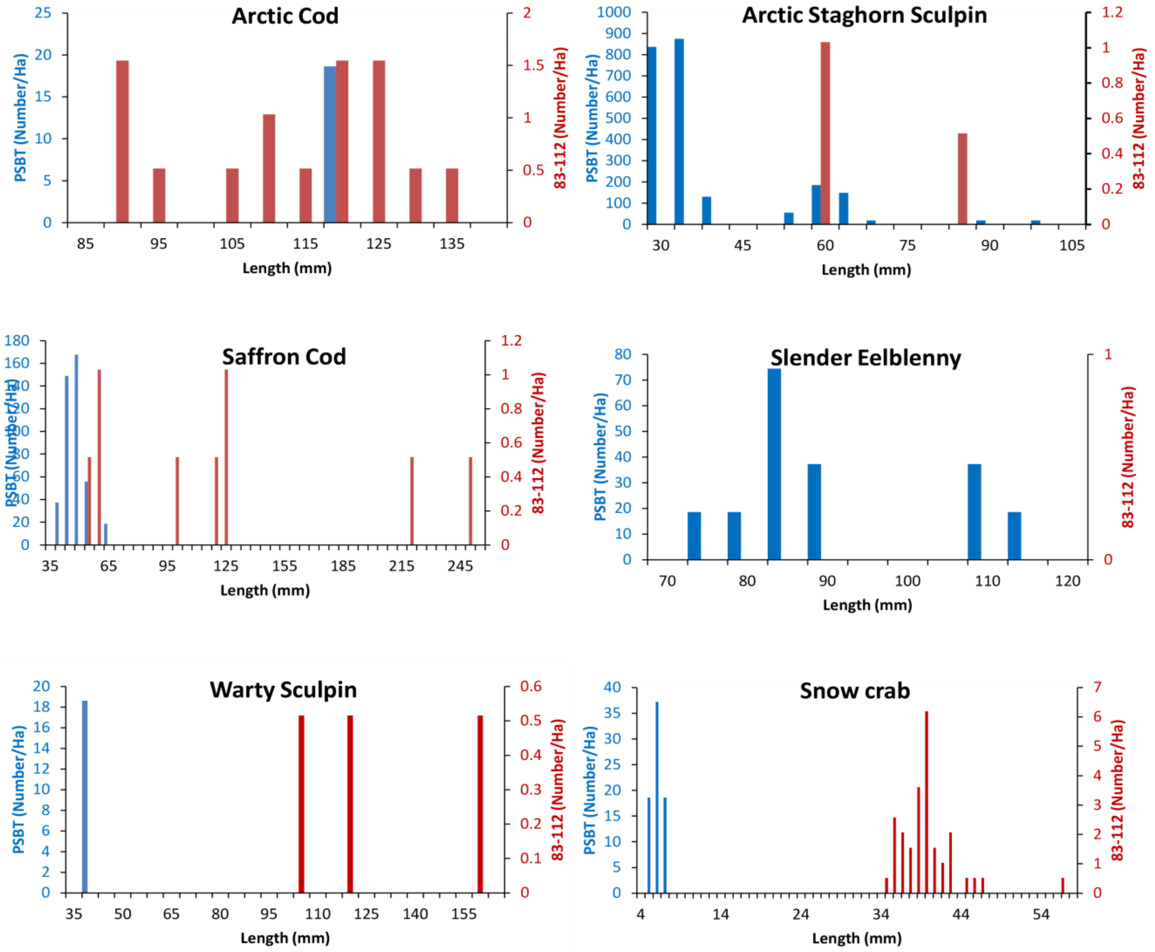
	83-112	PSBT	Difference
Area Sampled (ha)	1.939	0.054	97%
Depth (m)	21	21	0%
Bottom Temperature (°C)	9.1	9.2	-1%
Total Catch Weight (kg)	79.444	10.801	86%
Number Fish Species	12	9	25%
Unique Fish Species	8	5	38%
Number Invert Taxa	34	29	15%
Unique Invert Taxa	14	9	36%

Table 2. Catch per unit effort (per hectare) comparison for station G-03 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.07	8.25	0.26	18.62
Arctic staghorn sculpin	0.01	1.55	2.12	2,289.79
Bering flounder	-	-	-	-
Pacific herring	-	-	-	-
saffron cod	0.13	4.64	0.34	428.17
slender eelblenny	-	-	0.52	204.78
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	0.05	1.55	0.22	18.62
yellowfin sole	0.03	1.03	-	-

Table 3. Catch per unit effort (per hectare) comparison for station G-03 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	12.80	394.54	117.84	5,193.93
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.61	23.21	0.02	74.46
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	2.39	22.69	16.12	130.31
Neptunea heros	0.23	3.61	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	0.97	26.82	-	-
Strongylocentrotus droebachiensis	0.06	0.52	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station G-03.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.702	0.051	97%
Depth (m)	51	52	-2%
Bottom Temperature (°C)	3.8	4	-5%
Total Catch Weight (kg)	258.376	17.309	93%
Number Fish Species	11	10	9%
Unique Fish Species	6	5	17%
Number Invert Taxa	41	38	7%
Unique Invert Taxa	18	15	17%

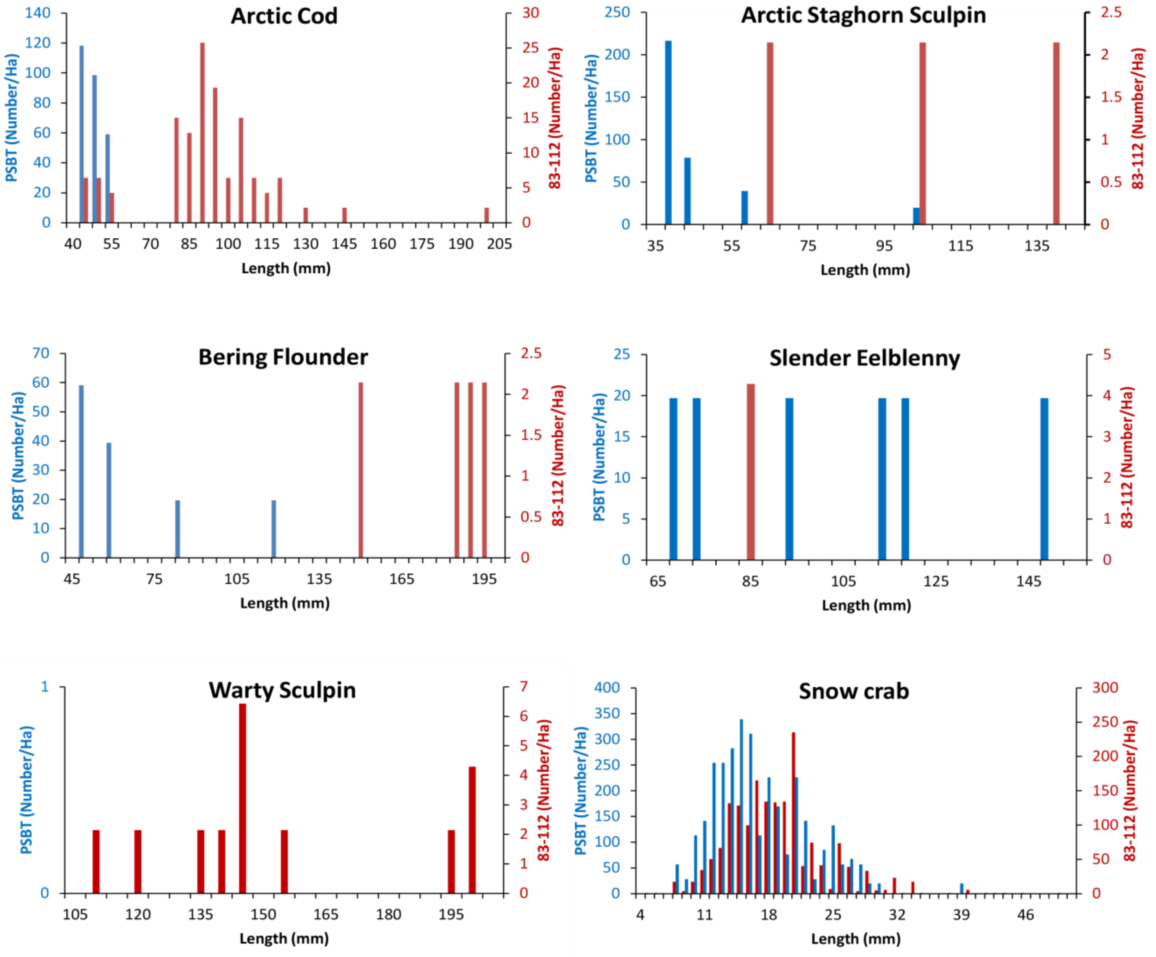
Table 2. Catch per unit effort (per hectare) comparison for station H-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	1.02	135.12	0.20	275.69
Arctic staghorn sculpin	0.03	1.76	0.43	354.45
Bering flounder	0.14	2.35	0.47	137.84
Pacific herring	-	-	-	-
saffron cod	0.01	1.76	-	-
slender eelblenny	0.002	1.17	0.39	118.15
stout eelblenny	-	-	0.04	39.38
variegated snailfish	-	-	-	-
warty sculpin	0.25	5.87	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station H-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.40	-	-	-
Chionoecetes opilio	88.36	1,730.13	117.03	3,209.77
Gorgonocephalus sp. cf. *arcticus*	6.38	35.25	19.34	177.23
Leptasterias polaris	6.66	96.93	12.48	177.23
Neptunea heros	4.10	38.77	4.57	19.69
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	0.05	6.46	-	-
Pagurus trigonocheirus	17.50	317.83	79.85	8,250.87
Strongylocentrotus droebachiensis	0.12	1.76	-	-

Station H-01



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station H-01.

Station H-02

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

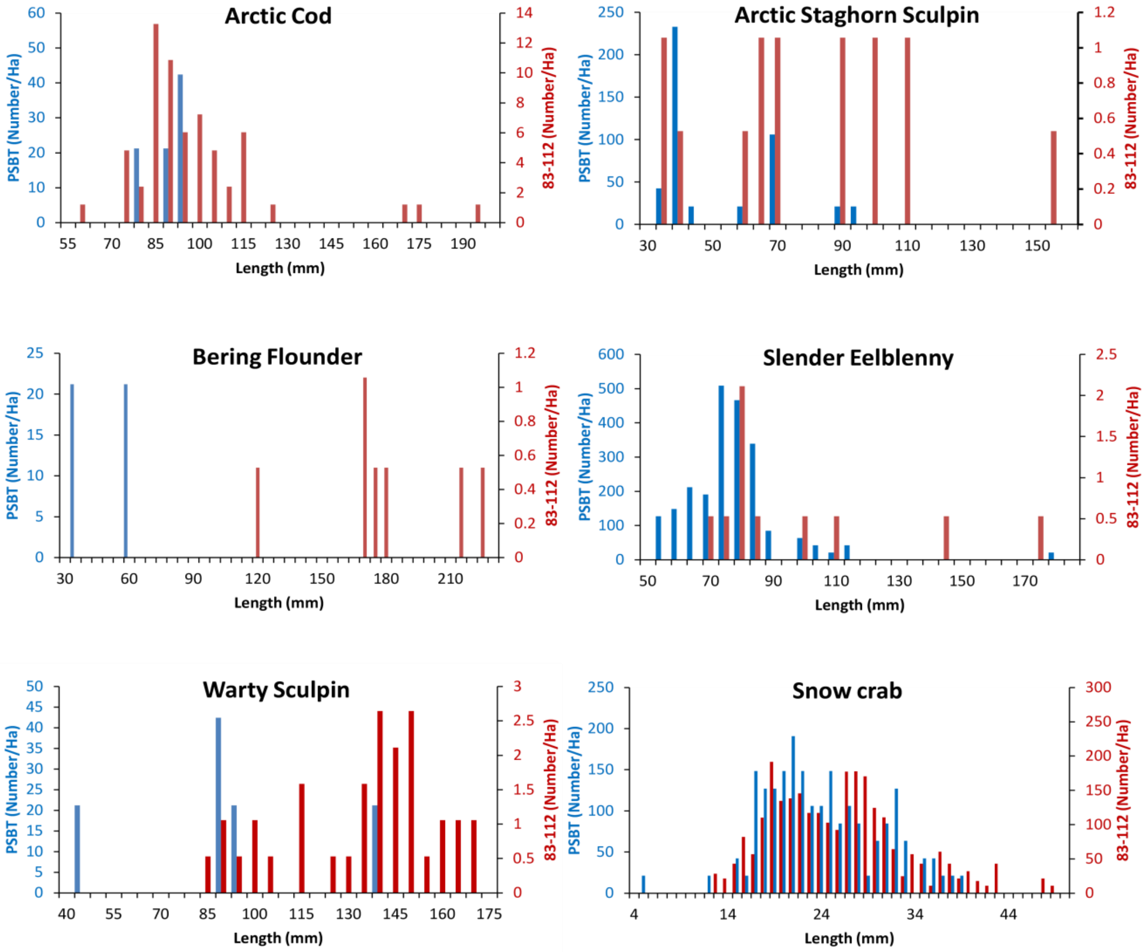
	83-112	PSBT	Difference
Area Sampled (ha)	1.892	0.047	98%
Depth (m)	47	47	0%
Bottom Temperature (°C)	5.7	5.4	5%
Total Catch Weight (kg)	505.341	16.021	97%
Number Fish Species	21	19	10%
Unique Fish Species	5	3	40%
Number Invert Taxa	55	49	11%
Unique Invert Taxa	24	18	25%

Table 2. Catch per unit effort (per hectare) comparison for station H-02 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.53	63.92	0.47	84.80
Arctic staghorn sculpin	0.07	7.92	0.93	466.39
Bering flounder	0.22	3.70	0.04	42.40
Pacific herring	0.59	3.70	-	-
saffron cod	0.02	3.17	-	-
slender eelblenny	0.02	5.81	2.93	2,268.33
stout eelblenny	0.003	0.53	1.27	211.99
variegated snailfish	0.02	0.53	0.59	21.20
warty sculpin	0.61	19.02	1.19	106.00
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station H-02 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	0.69	5.28	-	-
Boltenia ovifera	0.76	-	-	-
Chionoecetes opilio	125.08	2,601.88	89.50	2,141.13
Gorgonocephalus sp. cf. *arcticus*	5.47	47.55	2.97	42.40
Leptasterias polaris	19.01	195.47	20.52	190.79
Neptunea heros	11.36	117.81	5.85	211.99
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	54.80	574.79	19.23	6,190.20
Strongylocentrotus droebachiensis	0.06	0.53	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station H-02.

Station H-03

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

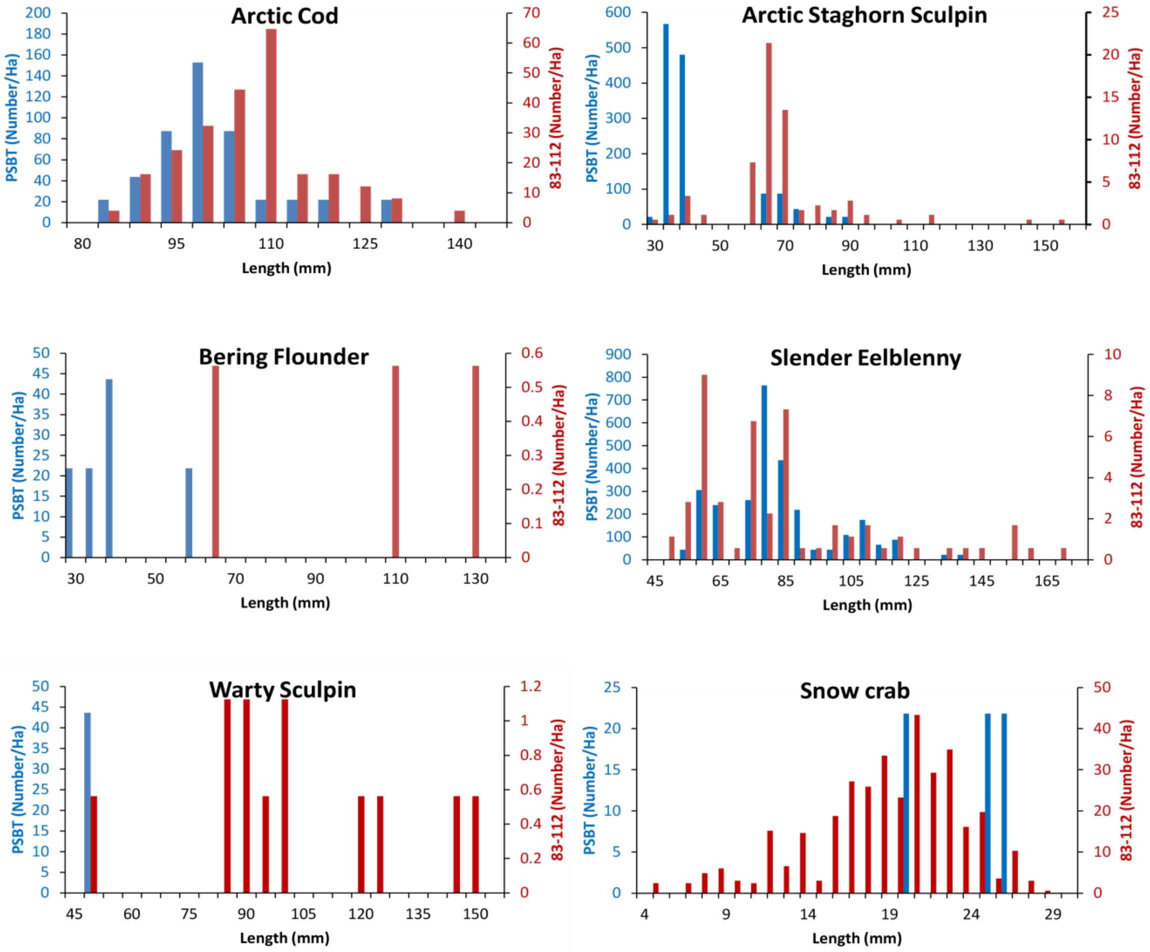
	83-112	PSBT	Difference
Area Sampled (ha)	1.777	0.046	97%
Depth (m)	35	36	-3%
Bottom Temperature (°C)	7.9	8.5	-8%
Total Catch Weight (kg)	329.977	14.703	96%
Number Fish Species	18	16	11%
Unique Fish Species	6	4	33%
Number Invert Taxa	35	32	9%
Unique Invert Taxa	17	14	18%

Table 2. Catch per unit effort (per hectare) comparison for station H-03 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	2.12	242.59	3.49	480.17
Arctic staghorn sculpin	0.29	60.79	1.57	1,331.38
Bering flounder	0.02	1.69	0.09	109.13
Pacific herring	8.53	58.54	-	-
saffron cod	0.01	3.94	0.04	21.83
slender eelblenny	0.10	45.03	21.56	10,782.00
stout eelblenny	0.003	0.56	0.09	21.83
variegated snailfish	0.01	0.56	2.92	21.83
warty sculpin	0.10	6.75	0.04	43.65
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station H-03 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	4.35	29.27	4.32	21.83
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	7.61	350.10	2.01	65.48
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	23.92	242.59	39.50	109.13
Neptunea heros	52.80	510.52	50.07	283.74
Nucula tenuis	-	-	-	-
Nuculana pernula	0.002	NA	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	62.31	884.26	95.64	1,156.77
Strongylocentrotus droebachiensis	0.36	4.50	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station H-03.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.420	0.026	98%
Depth (m)	42	44	-5%
Bottom Temperature (°C)	0.7	0.6	14%
Total Catch Weight (kg)	589.482	7.459	99%
Number Fish Species	8	9	-13%
Unique Fish Species	2	3	-50%
Number Invert Taxa	58	20	66%
Unique Invert Taxa	41	3	93%

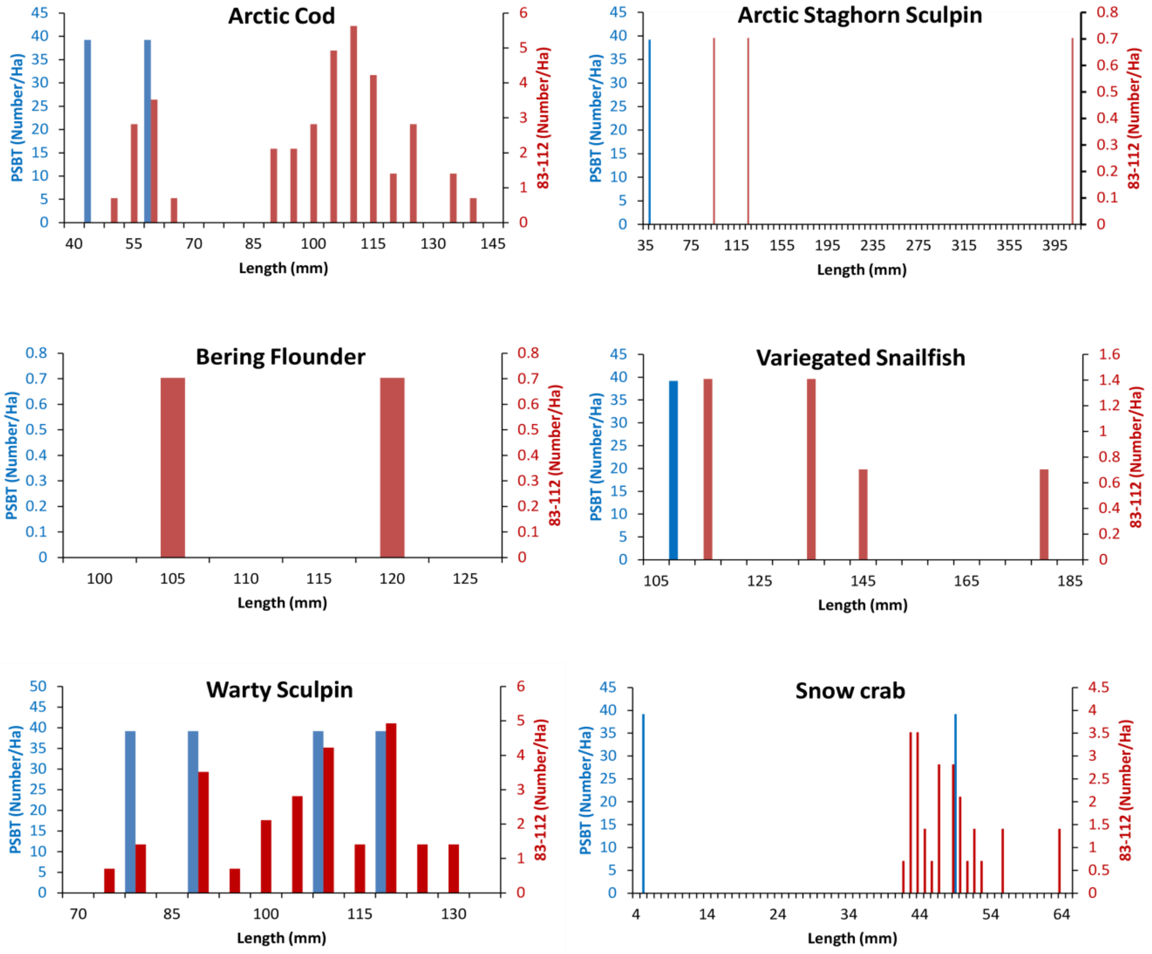
Table 2. Catch per unit effort (per hectare) comparison for station I-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.29	35.90	0.08	78.42
Arctic staghorn sculpin	0.03	2.11	0.04	39.21
Bering flounder	0.01	1.41	-	-
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	-	-
stout eelblenny	-	-	-	-
variegated snailfish	0.15	4.22	0.86	39.21
warty sculpin	0.38	24.64	2.12	156.84
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station I-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	233.68	-	158.25	-
Chionoecetes opilio	0.97	23.23	1.57	78.42
Gorgonocephalus sp. cf. *arcticus*	0.08	2.11	-	-
Leptasterias polaris	0.28	1.41	-	-
Neptunea heros	1.40	21.12	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	2.96	52.80	0.16	78.42
Strongylocentrotus droebachiensis	51.55	1,187.67	11.76	196.05

Station I-01



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station I-01.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.244	0.066	97%
Depth (m)	40	42	-5%
Bottom Temperature (°C)	5.4	5.4	0%
Total Catch Weight (kg)	254.603	7.216	97%
Number Fish Species	12	14	-17%
Unique Fish Species	5	7	-40%
Number Invert Taxa	42	35	17%
Unique Invert Taxa	21	14	33%

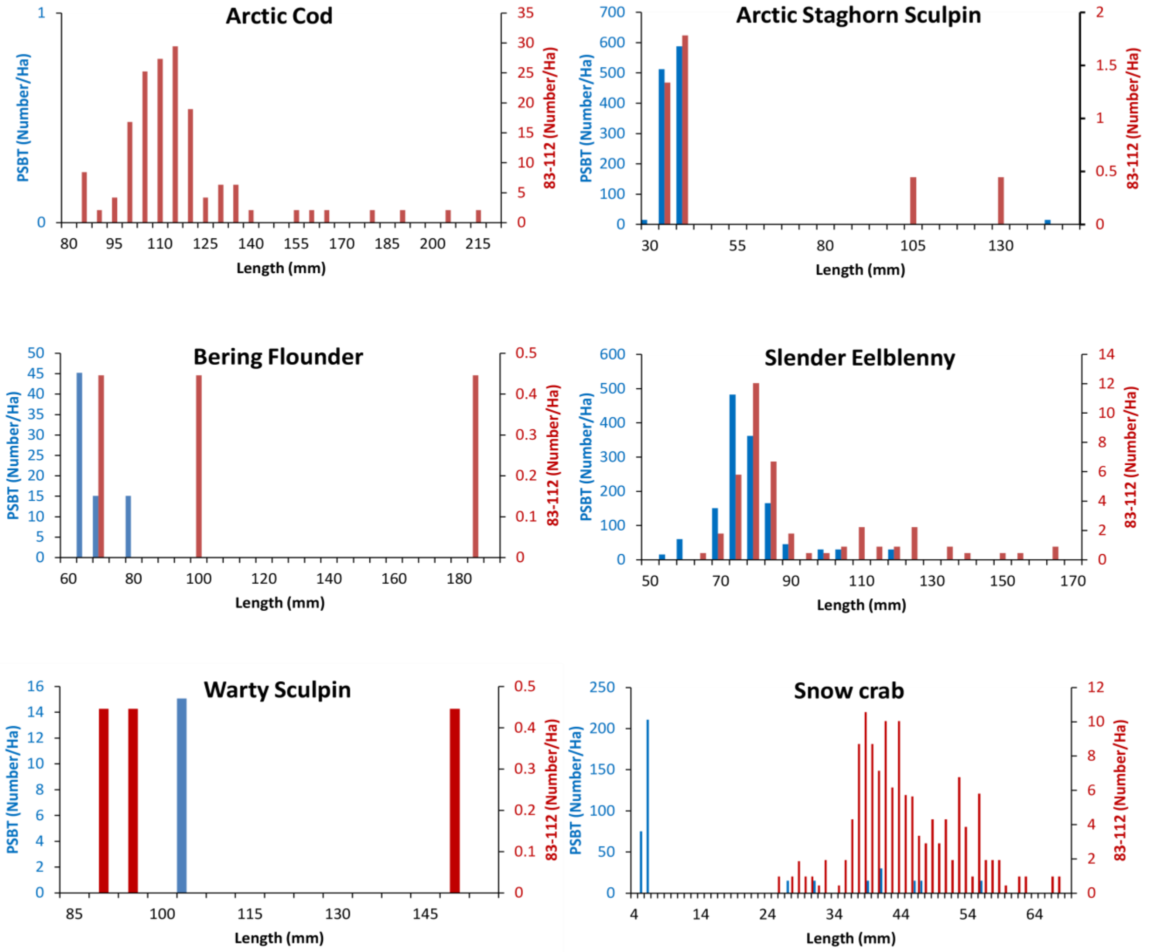
Table 2. Catch per unit effort (per hectare) comparison for station I-03 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	2.16	166.23	-	-
Arctic staghorn sculpin	0.02	4.01	2.20	2,109.84
Bering flounder	0.03	1.34	0.23	90.42
Pacific herring	-	-	-	-
saffron cod	0.001	0.45	-	-
slender eelblenny	0.10	39.66	1.96	1,371.39
stout eelblenny	-	-	0.03	15.07
variegated snailfish	-	-	-	-
warty sculpin	0.03	1.34	0.03	15.07
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station I-03 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.30	12.92	-	-
Chionoecetes opilio	6.47	134.58	5.37	406.90
Gorgonocephalus sp. cf. *arcticus*	3.72	18.72	-	-
Leptasterias polaris	7.61	102.94	4.97	90.42
Neptunea heros	3.68	37.43	2.59	45.21
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	0.03	15.07
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	1.94	135.63
Pagurus trigonocheirus	61.36	863.66	41.19	2,170.12
Strongylocentrotus droebachiensis	-	-	-	-

Station I-03



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station I-03.

Station I-04

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

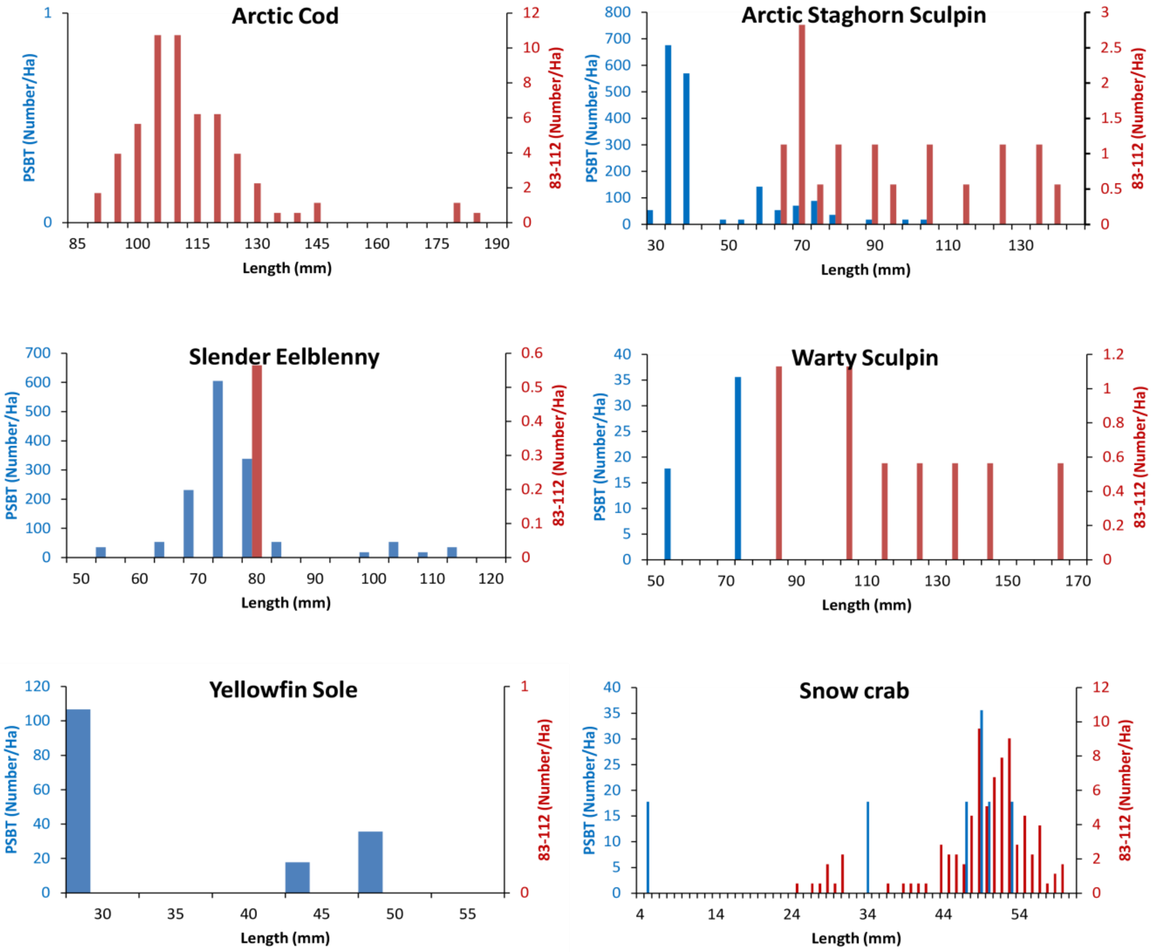
	83-112	PSBT	Difference
Area Sampled (ha)	1.771	0.056	97%
Depth (m)	31	33	-6%
Bottom Temperature (°C)	7	6.8	3%
Total Catch Weight (kg)	508.637	17.307	97%
Number Fish Species	11	13	-18%
Unique Fish Species	4	6	-50%
Number Invert Taxa	42	35	17%
Unique Invert Taxa	18	11	39%

Table 2. Catch per unit effort (per hectare) comparison for station I-04 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.60	55.33	-	-
Arctic staghorn sculpin	0.17	11.86	5.12	3,469.79
Bering flounder	0.02	0.56	0.04	17.79
Pacific herring	-	-	-	-
saffron cod	-	-	0.04	17.79
slender eelblenny	0.001	0.56	3.77	2,829.22
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	0.12	5.08	0.21	53.38
yellowfin sole	-	-	0.07	160.14

Table 3. Catch per unit effort (per hectare) comparison for station I-04 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	2.71	10.16	-	-
Boltenia ovifera	1.24	41.21	0.34	88.97
Chionoecetes opilio	3.92	77.91	4.56	124.56
Gorgonocephalus sp. cf. *arcticus*	3.78	44.04	5.94	142.35
Leptasterias polaris	2.39	19.19	1.99	17.79
Neptunea heros	28.90	329.14	2.10	35.59
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	23.51	720.37	17.44	338.08
Strongylocentrotus droebachiensis	-	-	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station I-04.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.773	0.031	98%
Depth (m)	39	40	-3%
Bottom Temperature (°C)	0.1	0.1	0%
Total Catch Weight (kg)	353.466	1.339	100%
Number Fish Species	12	10	17%
Unique Fish Species	7	5	29%
Number Invert Taxa	55	21	62%
Unique Invert Taxa	46	12	74%

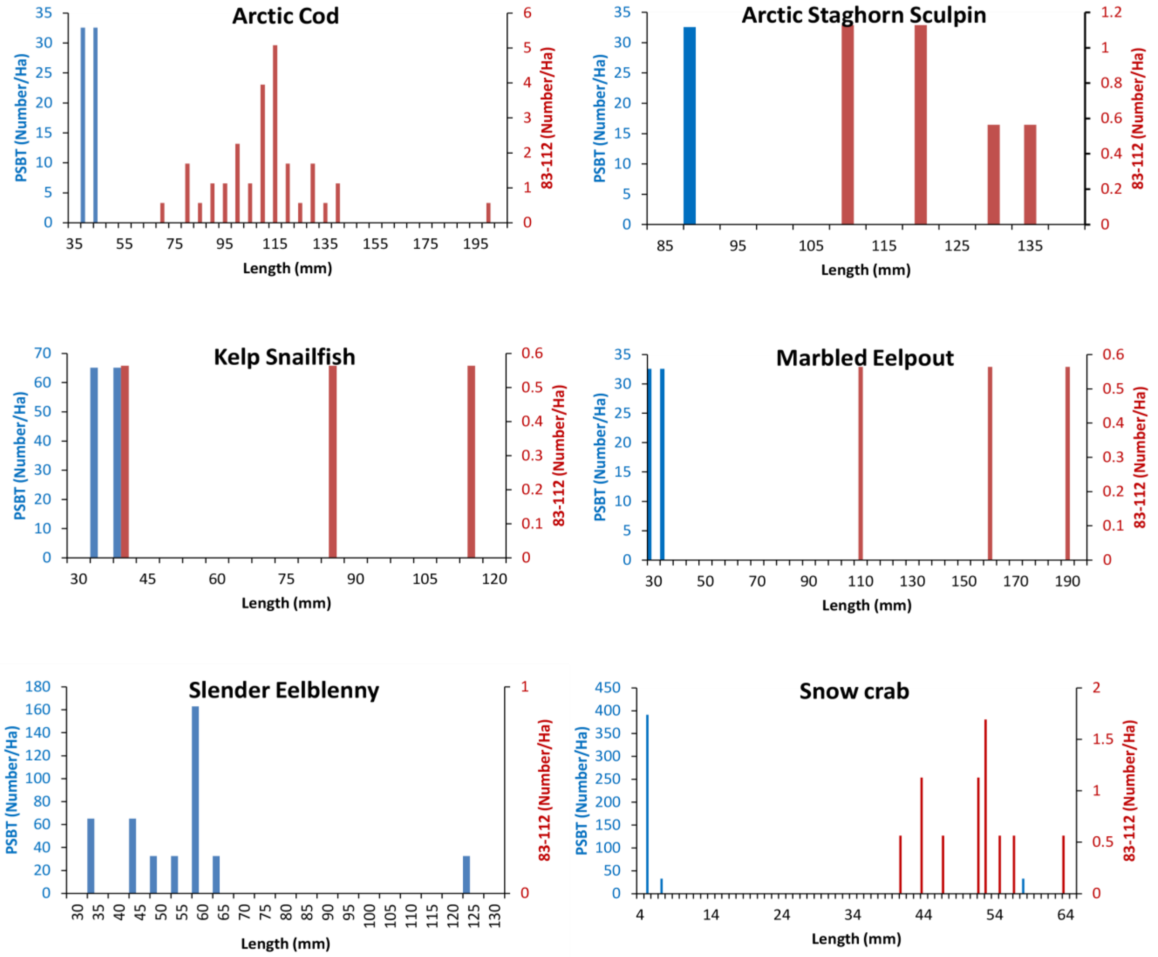
Table 2. Catch per unit effort (per hectare) comparison for station J-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.26	23.69	0.07	65.16
Arctic staghorn sculpin	0.08	3.38	0.26	32.58
Bering flounder	-	-	-	-
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	0.20	228.05
stout eelblenny	-	-	0.20	32.58
variegated snailfish	0.03	1.13	-	-
warty sculpin	0.01	0.56	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station J-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	4.64	-	-	-
Chionoecetes opilio	0.30	6.77	2.02	456.10
Gorgonocephalus sp. cf. *arcticus*	0.28	3.38	-	-
Leptasterias polaris	1.43	24.26	-	-
Neptunea heros	27.61	234.12	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	46.56	837.74	-	-
Strongylocentrotus droebachiensis	0.29	3.38	-	-

Station J-01



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station J-01.

Station J-04

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

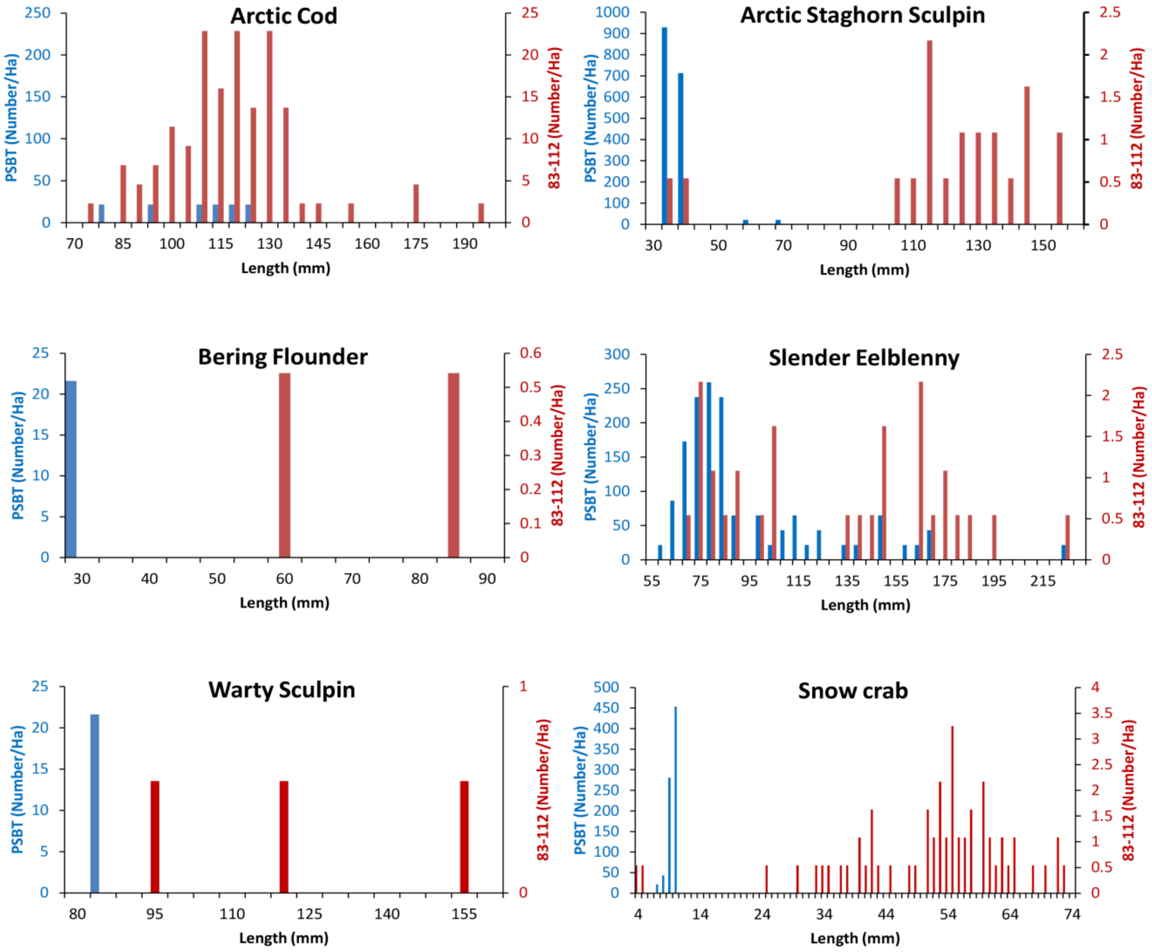
	83-112	PSBT	Difference
Area Sampled (ha)	1.845	0.046	98%
Depth (m)	43	43	0%
Bottom Temperature (°C)	6.2	6.1	2%
Total Catch Weight (kg)	241.495	5.561	98%
Number Fish Species	16	17	-6%
Unique Fish Species	5	6	-20%
Number Invert Taxa	52	32	38%
Unique Invert Taxa	31	11	65%

Table 2. Catch per unit effort (per hectare) comparison for station J-04 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	2.29	166.90	1.25	129.68
Arctic staghorn sculpin	0.35	11.38	0.82	1,685.81
Bering flounder	0.01	1.08	0.02	21.61
Pacific herring	6.45	37.93	-	-
saffron cod	0.002	0.54	0.02	21.61
slender eelblenny	0.13	16.80	5.10	1,556.13
stout eelblenny	0.004	0.54	0.30	172.90
variegated snailfish	-	-	-	-
warty sculpin	0.05	1.63	0.22	21.61
yellowfin sole	-	-	0.02	21.61

Table 3. Catch per unit effort (per hectare) comparison for station J-04 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.22	-	-	-
Chionoecetes opilio	1.85	32.51	0.26	799.68
Gorgonocephalus sp. cf. *arcticus*	51.65	426.46	46.34	670.00
Leptasterias polaris	3.80	36.31	8.90	21.61
Neptunea heros	4.87	82.37	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	10.66	1,812.58	3.11	497.10
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	14.19	389.61	5.36	129.68
Strongylocentrotus droebachiensis	0.05	0.54	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station J-04.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.299	0.028	99%
Depth (m)	46	47	-2%
Bottom Temperature (°C)	0	0	--
Total Catch Weight (kg)	32.912	3.764	89%
Number Fish Species	4	12	-200%
Unique Fish Species	0	8	--
Number Invert Taxa	34	27	21%
Unique Invert Taxa	14	7	50%

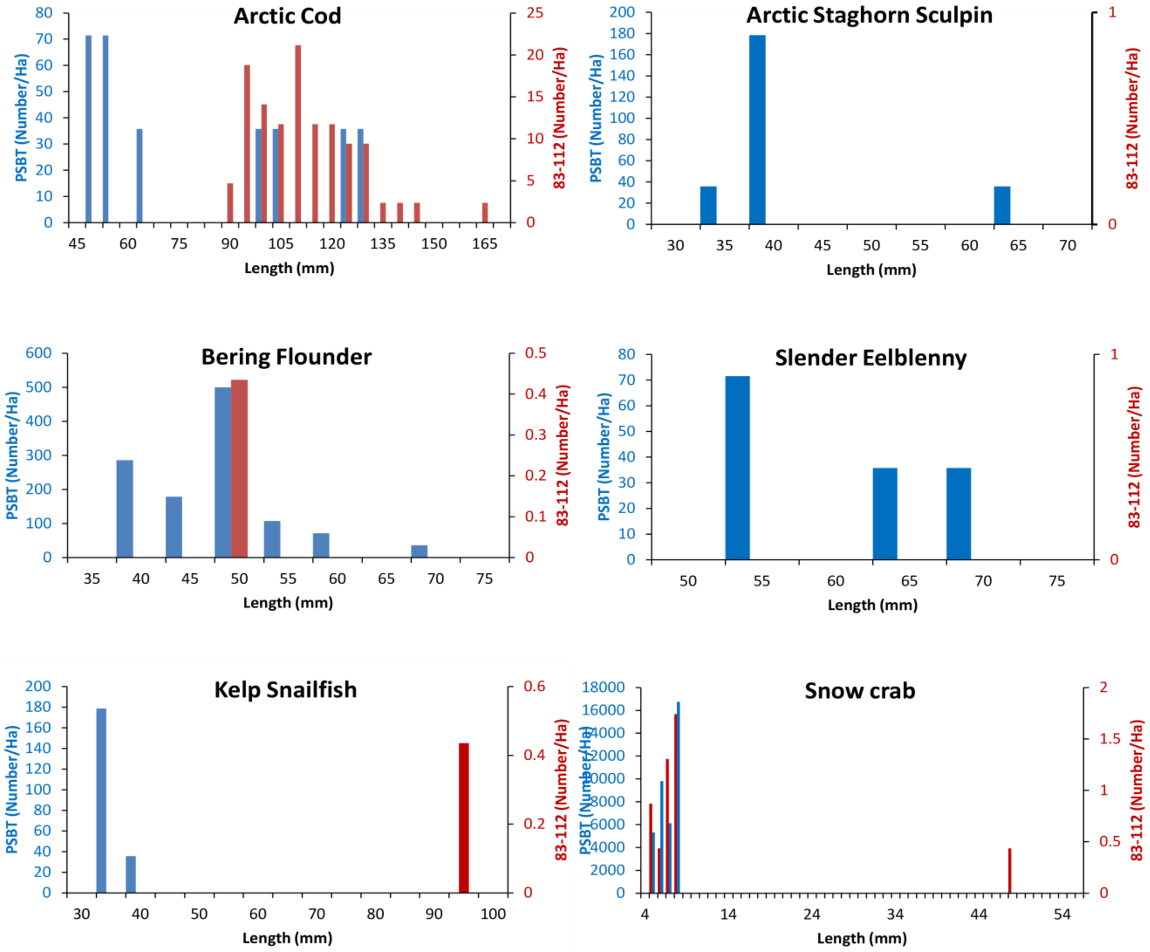
Table 2. Catch per unit effort (per hectare) comparison for station K-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	1.39	122.24	1.64	321.58
Arctic staghorn sculpin	-	-	0.21	250.12
Bering flounder	0.0004	0.44	0.93	1,179.13
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	0.07	142.92
stout eelblenny	-	-	0.64	-
variegated snailfish	-	-	1.29	35.73
warty sculpin	-	-	-	-
yellowfin sole	-	-	0.04	35.73

Table 3. Catch per unit effort (per hectare) comparison for station K-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.02	4.79	9.83	38,089.38
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	2.55	21.75	-	-
Neptunea heros	2.88	27.84	1.43	71.46
Nucula tenuis	-	-	-	-
Nuculana pernula	0.002	1.31	62.35	74,249.29
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	1.64	91.36	1.79	643.16
Pagurus trigonocheirus	2.28	77.87	0.14	35.73
Strongylocentrotus droebachiensis	-	-	-	-

Station K-01



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station K-01.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.693	0.034	98%
Depth (m)	41	42	-2%
Bottom Temperature (°C)	0.5	0.5	0%
Total Catch Weight (kg)	72.523	5.151	93%
Number Fish Species	6	12	-100%
Unique Fish Species	1	7	-600%
Number Invert Taxa	51	40	22%
Unique Invert Taxa	26	15	42%

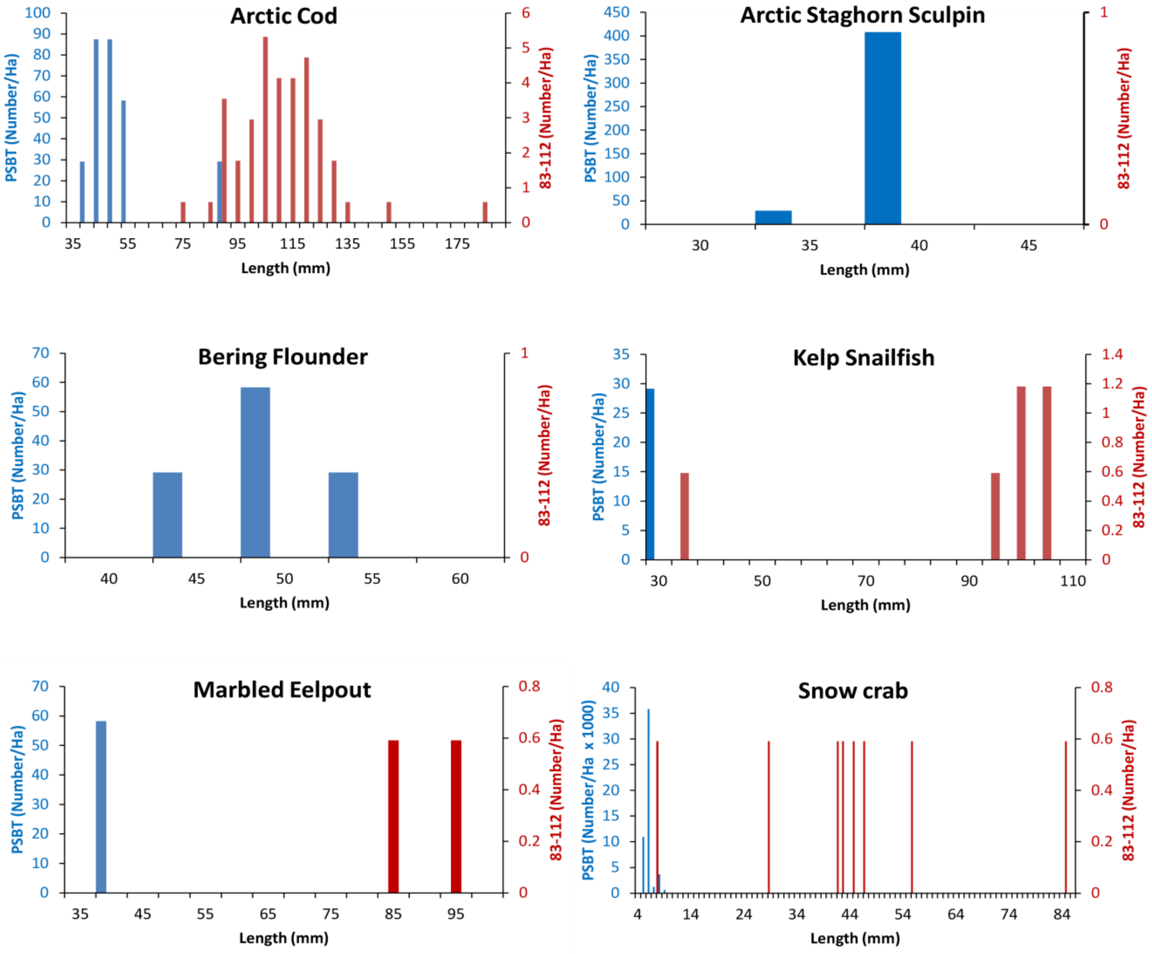
Table 2. Catch per unit effort (per hectare) comparison for station K-03 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.35	34.27	0.35	291.49
Arctic staghorn sculpin	-	-	0.29	437.24
Bering flounder	-	-	0.17	116.60
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	0.06	29.15
stout eelblenny	-	-	0.06	29.15
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station K-03 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.09	2.95	-	-
Chionoecetes opilio	0.25	4.73	7.29	52,235.15
Gorgonocephalus sp. cf. *arcticus*	1.66	29.54	0.17	29.15
Leptasterias polaris	3.72	59.08	10.32	145.75
Neptunea heros	0.56	24.22	1.52	29.15
Nucula tenuis	-	-	-	-
Nuculana pernula	0.002	0.59	-	-
Ophiura sarsi	-	-	0.06	29.15
Pagurus rathbuni	0.32	15.36	3.21	641.28
Pagurus trigonocheirus	16.46	235.73	41.86	2,710.86
Strongylocentrotus droebachiensis	0.05	0.59	-	-

Station K-03



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station K-03.

Station K-05

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

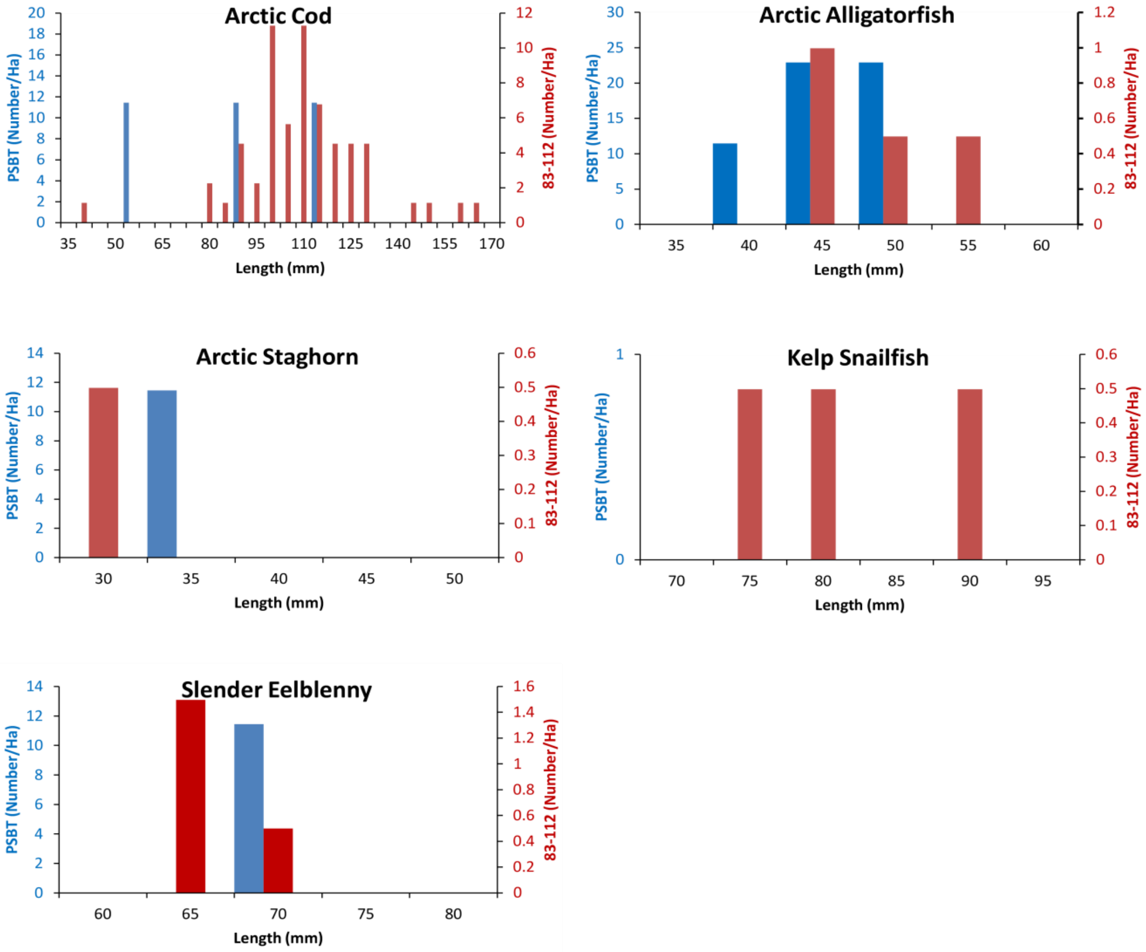
	83-112	PSBT	Difference
Area Sampled (ha)	2.006	0.087	96%
Depth (m)	45	45	0%
Bottom Temperature (°C)	2.2	1.9	14%
Total Catch Weight (kg)	281.065	16.245	94%
Number Fish Species	10	5	50%
Unique Fish Species	6	1	83%
Number Invert Taxa	58	20	66%
Unique Invert Taxa	43	5	88%

Table 2. Catch per unit effort (per hectare) comparison for station K-05 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.62	64.30	0.18	34.35
Arctic staghorn sculpin	0.0005	0.50	0.01	11.45
Bering flounder	-	-	-	-
Pacific herring	-	-	-	-
saffron cod	0.002	0.50	-	-
slender eelblenny	0.001	1.99	0.02	11.45
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	-	-	31.90	11.45
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station K-05 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.35	6.98	-	-
Chionoecetes opilio	-	-	-	-
Gorgonocephalus sp. cf. *arcticus*	73.29	523.34	42.25	583.89
Leptasterias polaris	-	-	-	-
Neptunea heros	2.49	47.85	1.79	34.35
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	0.08	63.30	86.51	65,063.16
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	1.86	114.64	1.43	354.91
Strongylocentrotus droebachiensis	0.10	1.50	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station K-05.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.006	0.087	96%
Depth (m)	45	45	0%
Bottom Temperature (°C)	2.2	1.9	14%
Total Catch Weight (kg)	281.065	16.245	94%
Number Fish Species	10	5	50%
Unique Fish Species	6	1	83%
Number Invert Taxa	58	20	66%
Unique Invert Taxa	43	5	88%

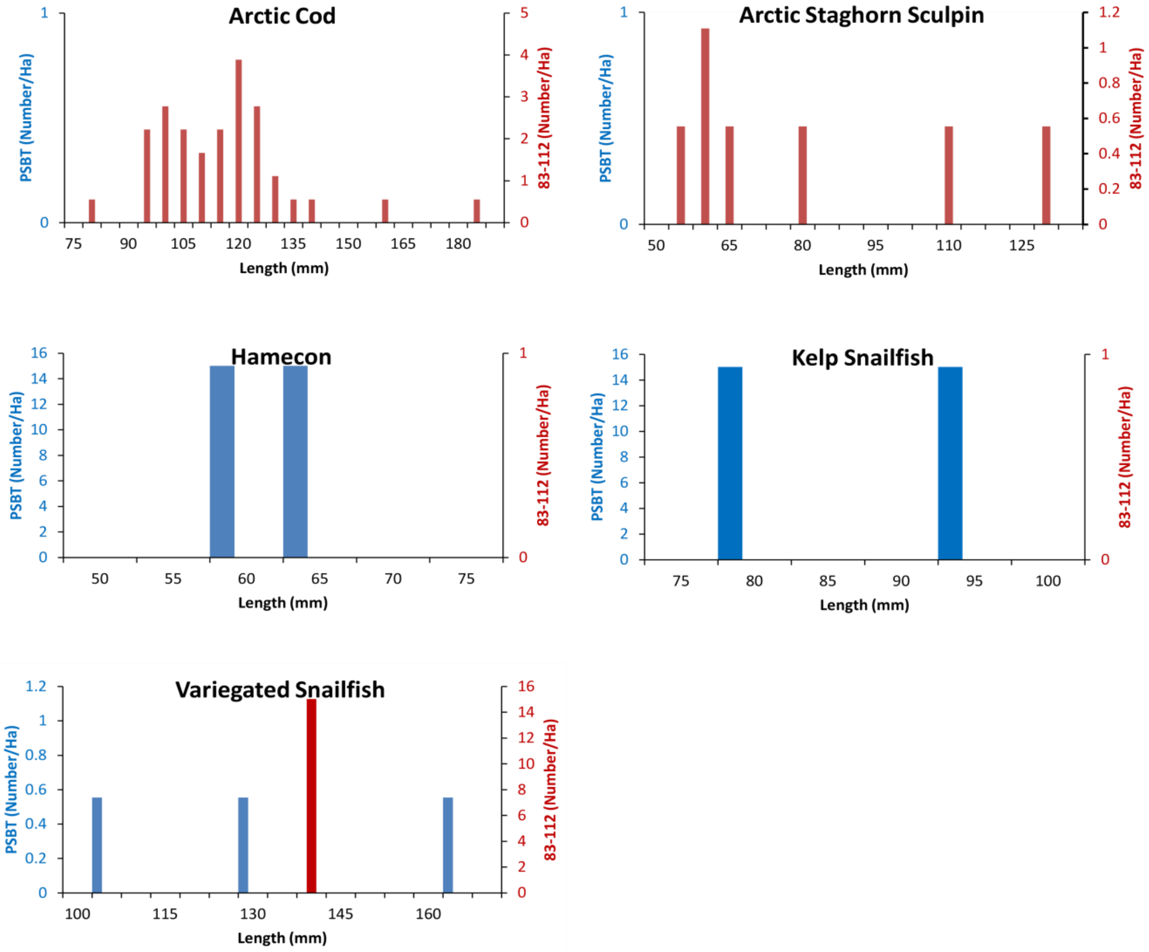
Table 2. Catch per unit effort (per hectare) comparison for station K-06 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.62	64.30	0.18	34.35
Arctic staghorn sculpin	0.00	0.50	0.01	11.45
Bering flounder	-	-	-	-
Pacific herring	-	-	-	-
saffron cod	0.00	0.50	-	-
slender eelblenny	0.00	1.99	0.02	11.45
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	-	-	31.90	11.45
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station K-06 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.35	6.98	-	-
Chionoecetes opilio	-	-	-	-
Gorgonocephalus sp. cf. *arcticus*	73.29	523.34	42.25	583.89
Leptasterias polaris	-	-	-	-
Neptunea heros	2.49	47.85	1.79	34.35
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	0.08	63.30	86.51	65,063.16
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	1.86	114.64	1.43	354.91
Strongylocentrotus droebachiensis	0.10	1.50	-	-

Station K-06



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station K-06.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.296	0.027	99%
Depth (m)	49	49	0%
Bottom Temperature (°C)	-0.3	-0.3	0%
Total Catch Weight (kg)	86.634	26.266	70%
Number Fish Species	5	8	-60%
Unique Fish Species	2	5	-150%
Number Invert Taxa	37	34	8%
Unique Invert Taxa	7	4	43%

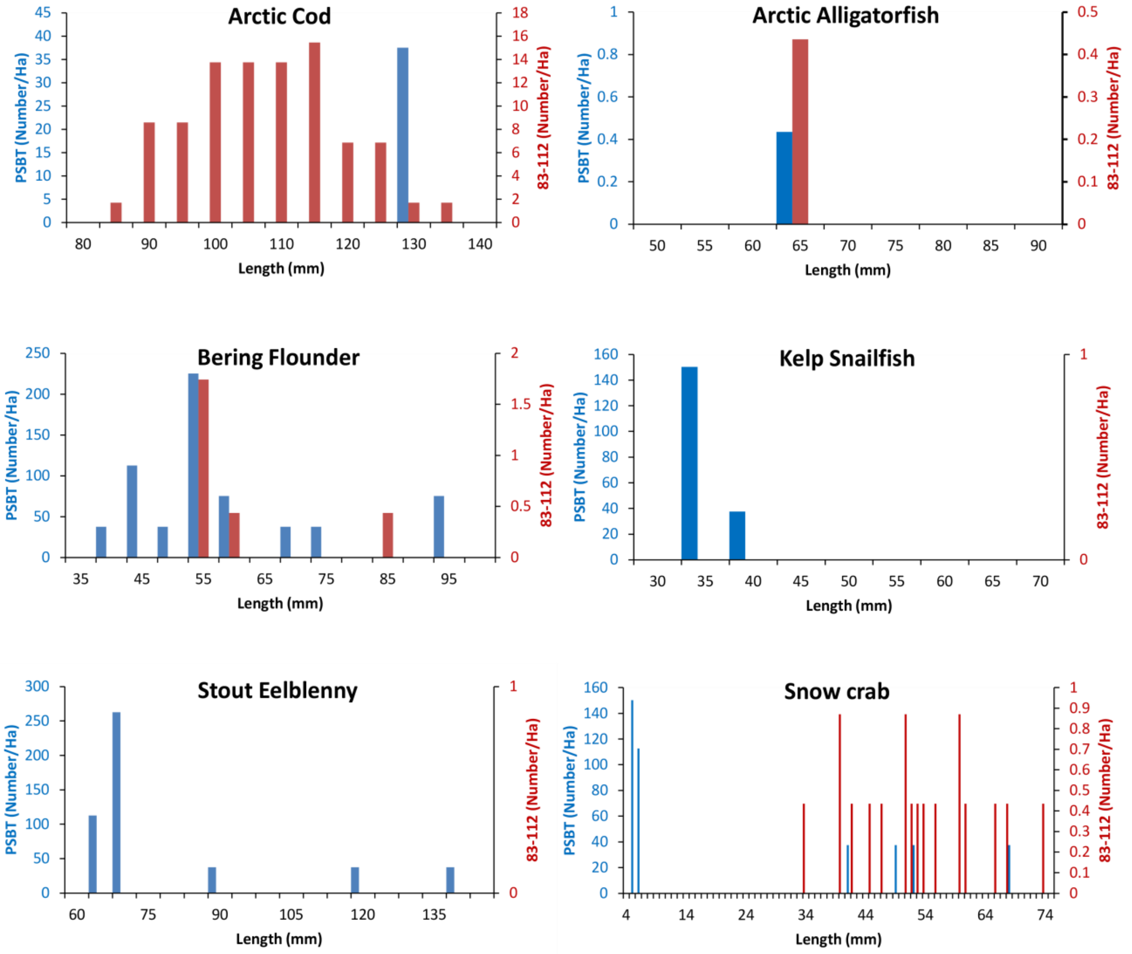
Table 2. Catch per unit effort (per hectare) comparison for station L-01 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.82	92.76	0.68	37.55
Arctic staghorn sculpin	-	-	0.04	37.55
Bering flounder	0.01	2.61	1.13	638.32
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	-	-
stout eelblenny	-	-	0.98	488.12
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	0.04	37.55

Table 3. Catch per unit effort (per hectare) comparison for station L-01 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.05	0.44	-	-
Chionoecetes opilio	0.46	7.84	9.09	413.03
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	6.91	83.62	92.07	1,013.80
Neptunea heros	0.69	25.70	5.18	75.10
Nucula tenuis	-	-	-	-
Nuculana pernula	0.04	24.82	635.80	397,370.14
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	0.78	40.50	18.77	2,365.52
Pagurus trigonocheirus	1.01	27.87	13.89	600.77
Strongylocentrotus droebachiensis	-	-	-	-

Station L-01



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station L-01.

Station L-03

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

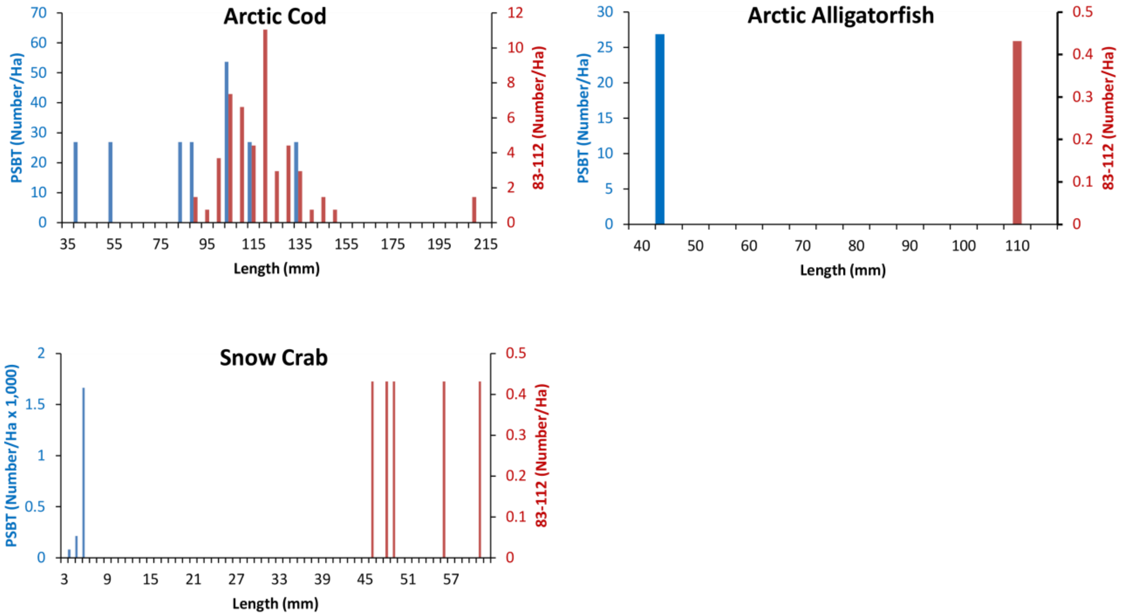
	83-112	PSBT	Difference
Area Sampled (ha)	2.317	0.037	98%
Depth (m)	42	43	-2%
Bottom Temperature (°C)	-0.6	-0.6	0%
Total Catch Weight (kg)	14.582	4.482	69%
Number Fish Species	2	7	-250%
Unique Fish Species	0	5	--
Number Invert Taxa	45	41	9%
Unique Invert Taxa	21	17	19%

Table 2. Catch per unit effort (per hectare) comparison for station L-03 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.66	50.06	1.45	214.82
Arctic staghorn sculpin	0.01	0.43	0.03	26.85
Bering flounder	-	-	0.03	26.85
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	0.03	26.85
stout eelblenny	-	-	-	-
variegated snailfish	-	-	0.64	26.85
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station L-03 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.11	2.16	0.27	1,960.23
Gorgonocephalus sp. cf. *arcticus*	1.45	32.79	1.24	53.70
Leptasterias polaris	0.67	7.34	6.87	53.70
Neptunea heros	0.89	11.22	2.09	26.85
Nucula tenuis	-	-	0.46	1,396.33
Nuculana pernula	0.01	3.88	-	-
Ophiura sarsi	0.003	2.59	67.83	36,868.46
Pagurus rathbuni	0.81	41.42	8.81	510.20
Pagurus trigonocheirus	0.14	8.20	0.27	107.41
Strongylocentrotus droebachiensis	-	-	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station L-03.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.241	0.051	98%
Depth (m)	44	45	-2%
Bottom Temperature (°C)	-1.1	-1.1	0%
Total Catch Weight (kg)	32.803	22.892	30%
Number Fish Species	6	7	-17%
Unique Fish Species	2	3	-50%
Number Invert Taxa	53	49	8%
Unique Invert Taxa	28	24	14%

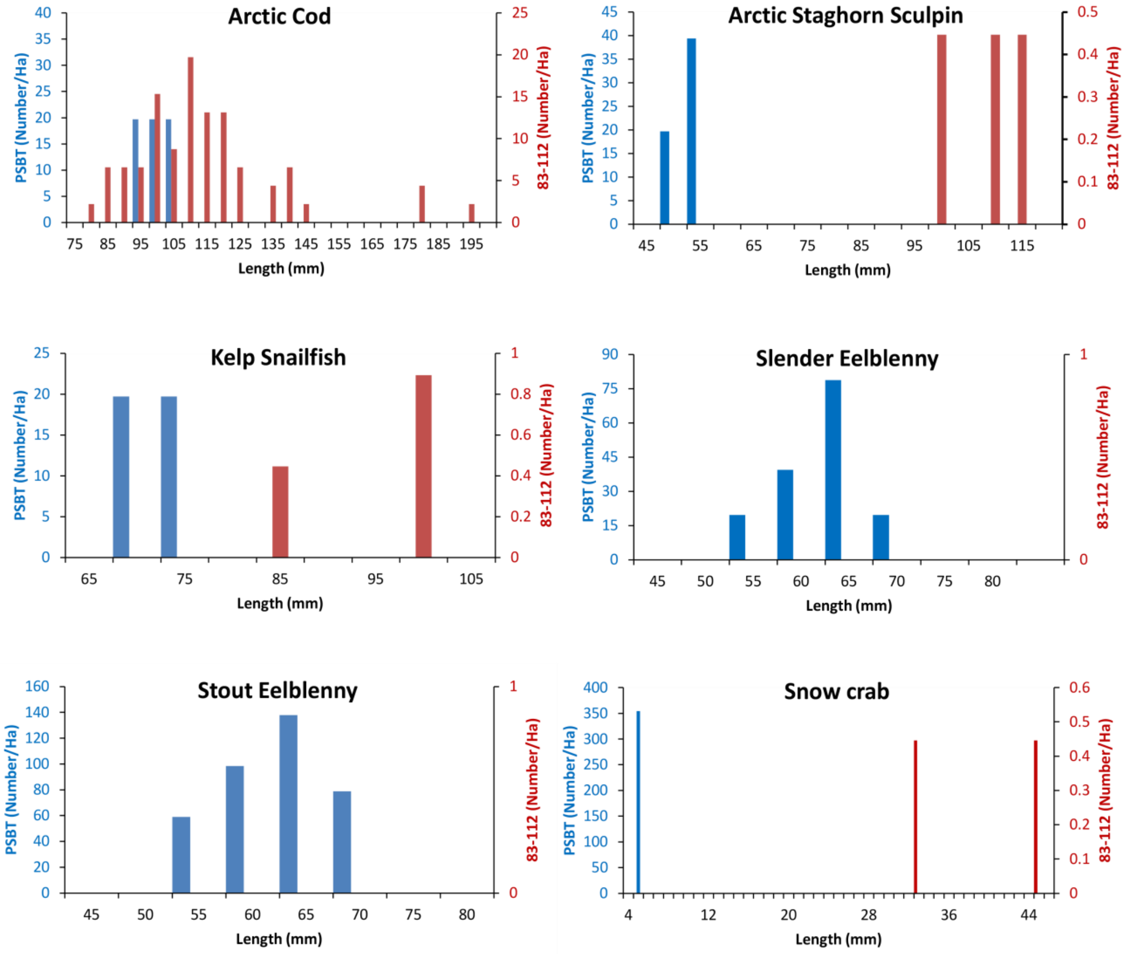
Table 2. Catch per unit effort (per hectare) comparison for station L-04 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	1.36	118.26	0.35	59.08
Arctic staghorn sculpin	0.02	1.34	0.08	59.08
Bering flounder	-	-	0.04	19.69
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	0.20	157.53
stout eelblenny	-	-	0.28	374.14
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station L-04 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.02	0.89	0.08	354.45
Gorgonocephalus sp. cf. *arcticus*	4.50	142.81	0.16	19.69
Leptasterias polaris	0.25	2.68	-	-
Neptunea heros	1.03	12.94	5.08	59.08
Nucula tenuis	-	-	19.77	33,771.48
Nuculana pernula	-	-	-	-
Ophiura sarsi	0.53	366.84	319.62	119,253.68
Pagurus rathbuni	0.40	7.14	2.56	452.91
Pagurus trigonocheirus	0.01	0.89	-	-
Strongylocentrotus droebachiensis	-	-	-	-

Station L-04



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station L-04.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.115	0.028	99%
Depth (m)	50	53	-6%
Bottom Temperature (°C)	-1.7	-1.7	0%
Total Catch Weight (kg)	29.034	20.886	28%
Number Fish Species	2	9	-350%
Unique Fish Species	0	7	--
Number Invert Taxa	57	47	18%
Unique Invert Taxa	29	19	34%

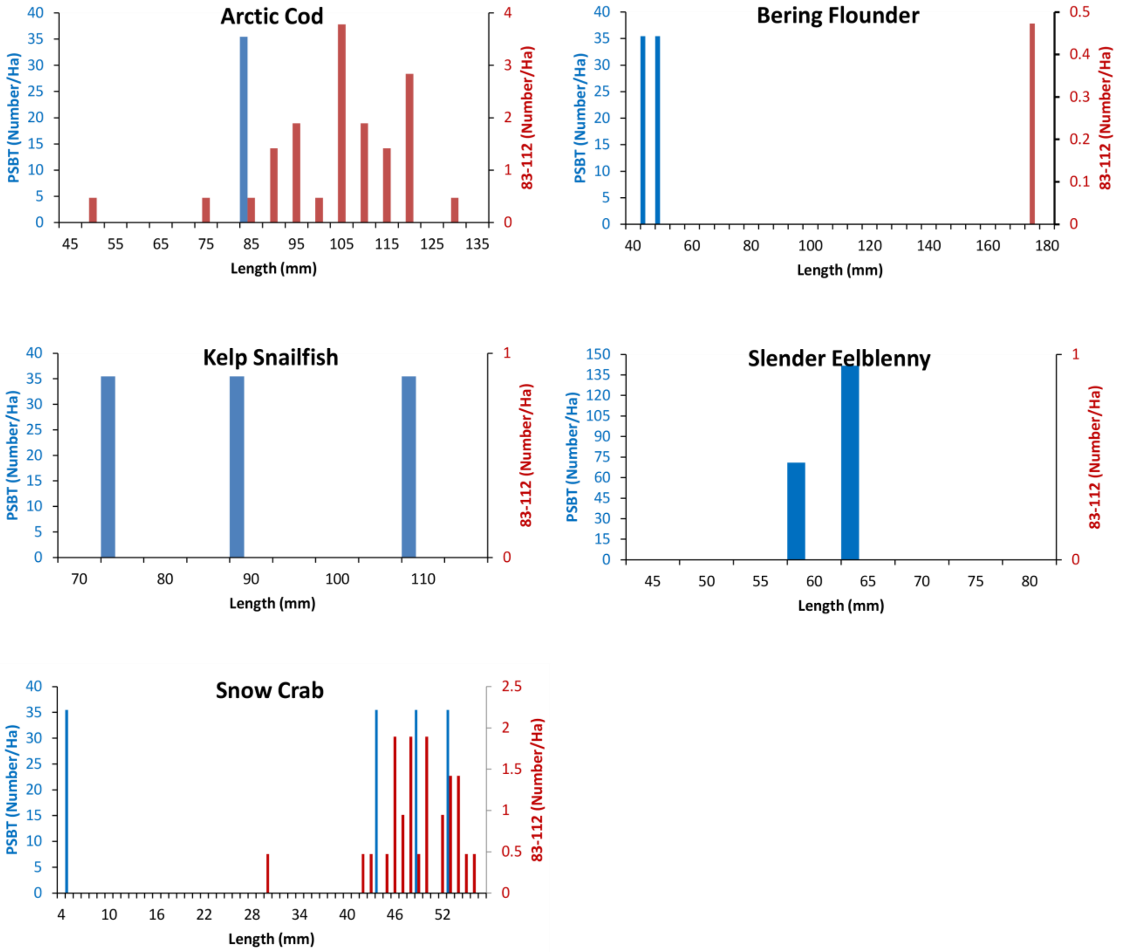
Table 2. Catch per unit effort (per hectare) comparison for station L-07 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.13	15.60	0.14	35.45
Arctic staghorn sculpin	-	-	-	-
Bering flounder	0.02	0.47	0.07	70.89
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	0.28	212.67
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station L-07 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.003	0.47	-	-
Chionoecetes opilio	0.55	13.71	4.96	141.78
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	-	-	-	-
Neptunea heros	0.50	5.67	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	0.001	0.47	-	-
Ophiura sarsi	0.91	235.49	604.31	169,747.45
Pagurus rathbuni	0.03	4.73	2.84	673.46
Pagurus trigonocheirus	0.20	15.60	0.07	35.45
Strongylocentrotus droebachiensis	-	-	-	-

Station L-07



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station L-07.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.733	0.049	97%
Depth (m)	90	90	0%
Bottom Temperature (°C)	-1.7	-1.7	0%
Total Catch Weight (kg)	72.163	3.908	95%
Number Fish Species	6	5	17%
Unique Fish Species	3	2	33%
Number Invert Taxa	61	21	66%
Unique Invert Taxa	48	8	83%

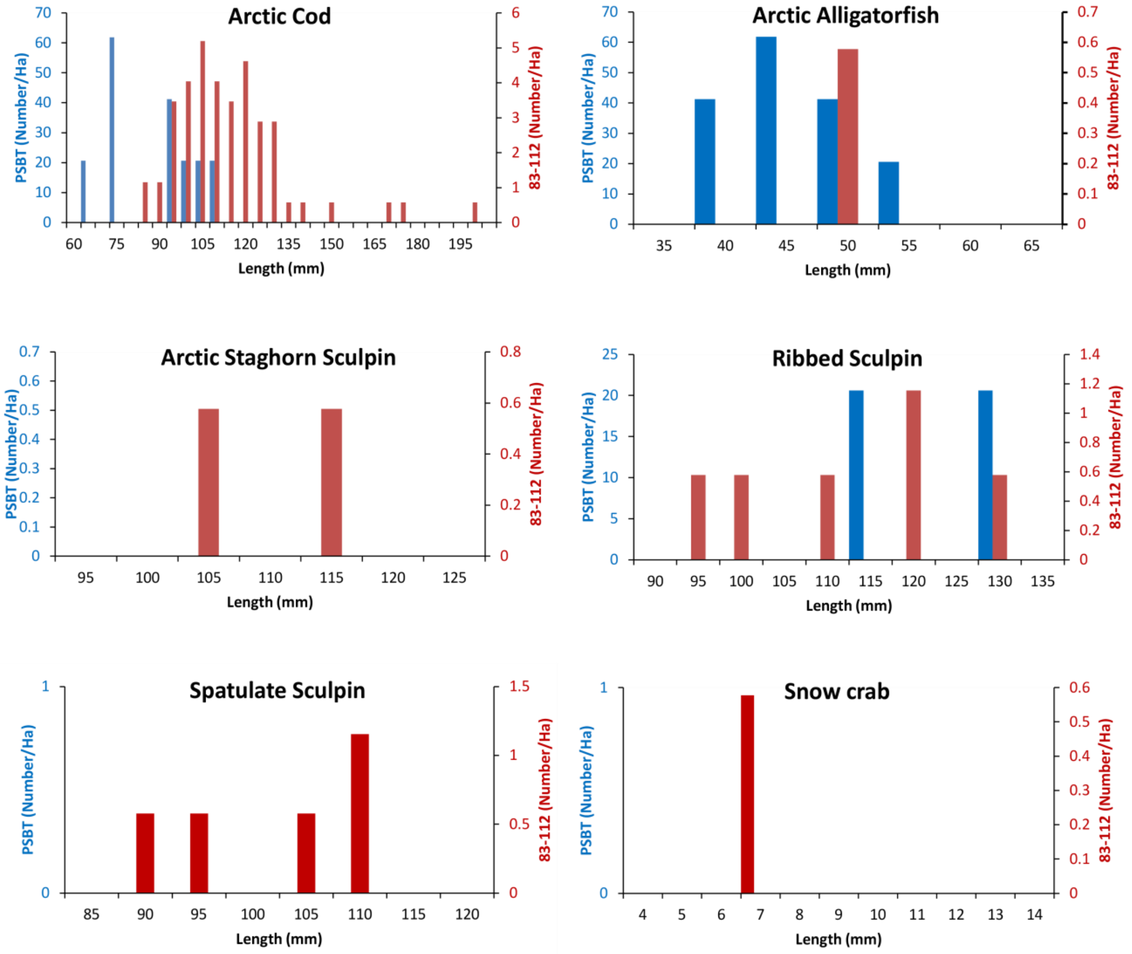
Table 2. Catch per unit effort (per hectare) comparison for station L-08 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.40	36.36	0.87	185.47
Arctic staghorn sculpin	0.02	1.15	-	-
Bering flounder	-	-	-	-
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	0.04	20.61
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station L-08 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.15	2.89	-	-
Chionoecetes opilio	0.02	0.58	-	-
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	-	-	-	-
Neptunea heros	0.56	7.50	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	2.96	4,728.88	44.68	73,033.77
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	0.33	17.32	0.08	61.82
Strongylocentrotus droebachiensis	0.18	2.31	-	-

Station L-08



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station L-08.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	2.470	0.023	99%
Depth (m)	47	48	-2%
Bottom Temperature (°C)	-0.8	-0.8	0%
Total Catch Weight (kg)	13.538	6.888	49%
Number Fish Species	5	6	-20%
Unique Fish Species	2	3	-50%
Number Invert Taxa	30	28	7%
Unique Invert Taxa	15	13	13%

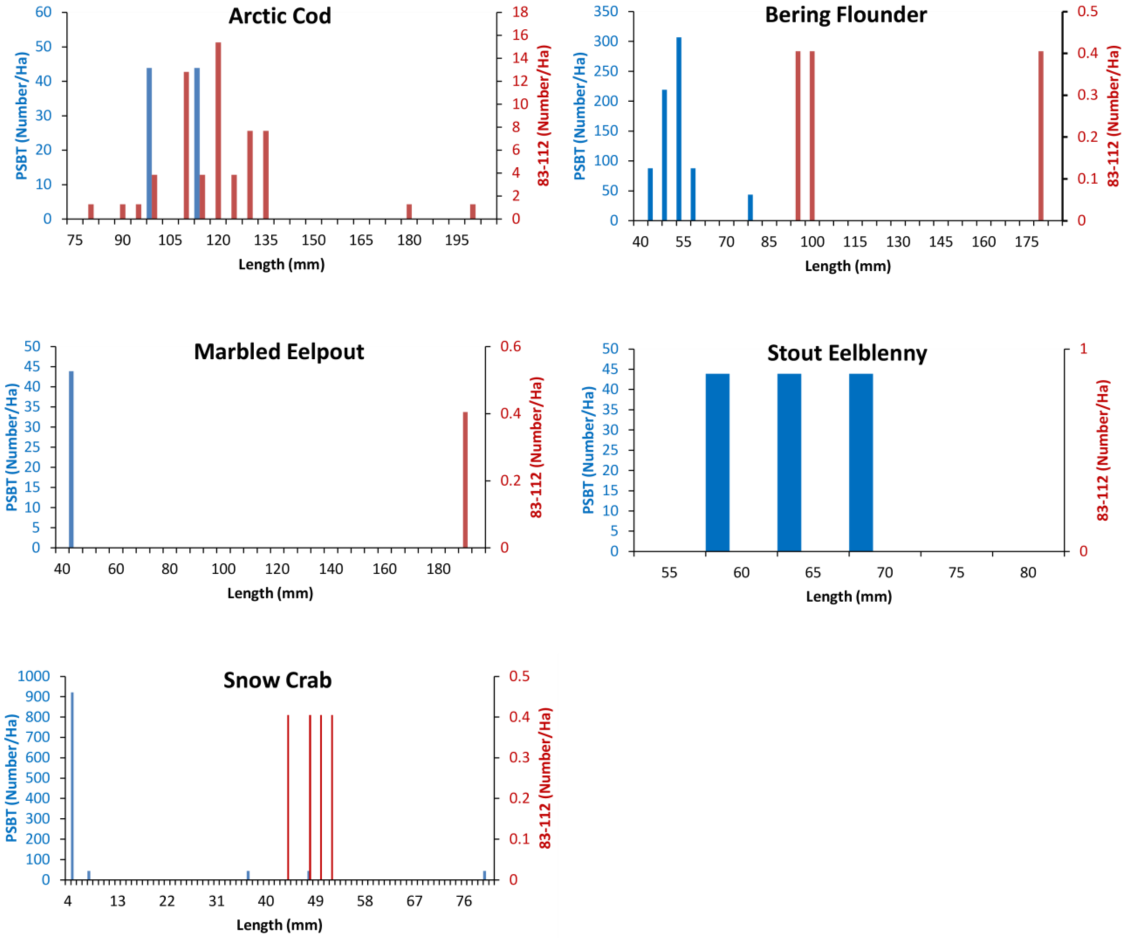
Table 2. Catch per unit effort (per hectare) comparison for station M-02 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.80	61.54	0.79	87.74
Arctic staghorn sculpin	0.002	0.40	-	-
Bering flounder	0.03	1.21	0.97	745.75
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	-	-
stout eelblenny	-	-	0.09	131.60
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station M-02 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.06	1.62	11.93	1,096.70
Gorgonocephalus sp. cf. *arcticus*	0.14	1.21	-	-
Leptasterias polaris	1.43	17.00	-	-
Neptunea heros	0.47	4.05	-	-
Nucula tenuis	-	-	3.99	7,940.09
Nuculana pernula	-	-	198.94	339,099.04
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	0.74	50.20	38.60	833.49
Pagurus trigonocheirus	0.40	9.72	0.88	87.74
Strongylocentrotus droebachiensis	-	-	-	-

Station M-02



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station M-02.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.657	0.027	98%
Depth (m)	39	40	-3%
Bottom Temperature (°C)	-1.2	-1.1	8%
Total Catch Weight (kg)	34.812	3.63	90%
Number Fish Species	4	2	50%
Unique Fish Species	2	0	100%
Number Invert Taxa	38	38	0%
Unique Invert Taxa	14	14	0%

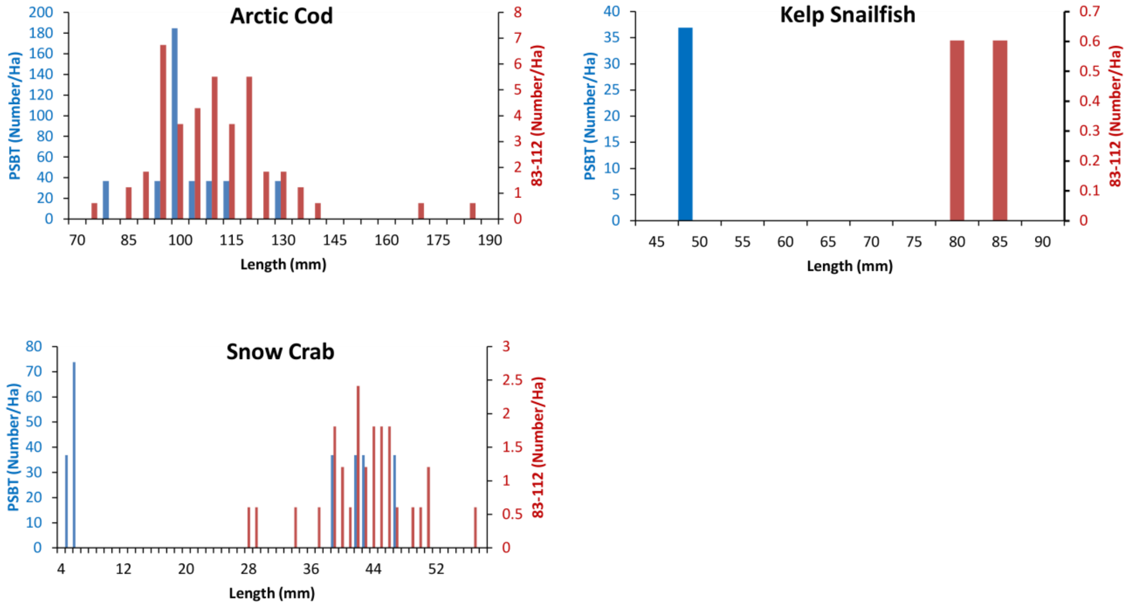
Table 2. Catch per unit effort (per hectare) comparison for station M-04 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.41	39.82	3.10	406.14
Arctic staghorn sculpin	-	-	-	-
Bering flounder	-	-	-	-
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	-	-
stout eelblenny	-	-	-	-
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station M-04 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.05	2.30	0.21	1,123.56
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	0.14	2.30	-	-
Neptunea heros	0.08	1.15	-	-
Nucula tenuis	-	-	1.95	-
Nuculana pernula	0.001	2.30	-	-
Ophiura sarsi	0.30	59.72	0.51	127.20
Pagurus rathbuni	-	-	0.04	21.20
Pagurus trigonocheirus	0.30	33.31	0.08	42.40
Strongylocentrotus droebachiensis	-	-	-	-

Station M-04



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station M-04.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.741	0.047	97%
Depth (m)	28	29	-4%
Bottom Temperature (°C)	-1.6	-1.6	0%
Total Catch Weight (kg)	9.948	1.376	86%
Number Fish Species	6	13	-117%
Unique Fish Species	2	9	-350%
Number Invert Taxa	38	27	29%
Unique Invert Taxa	20	9	55%

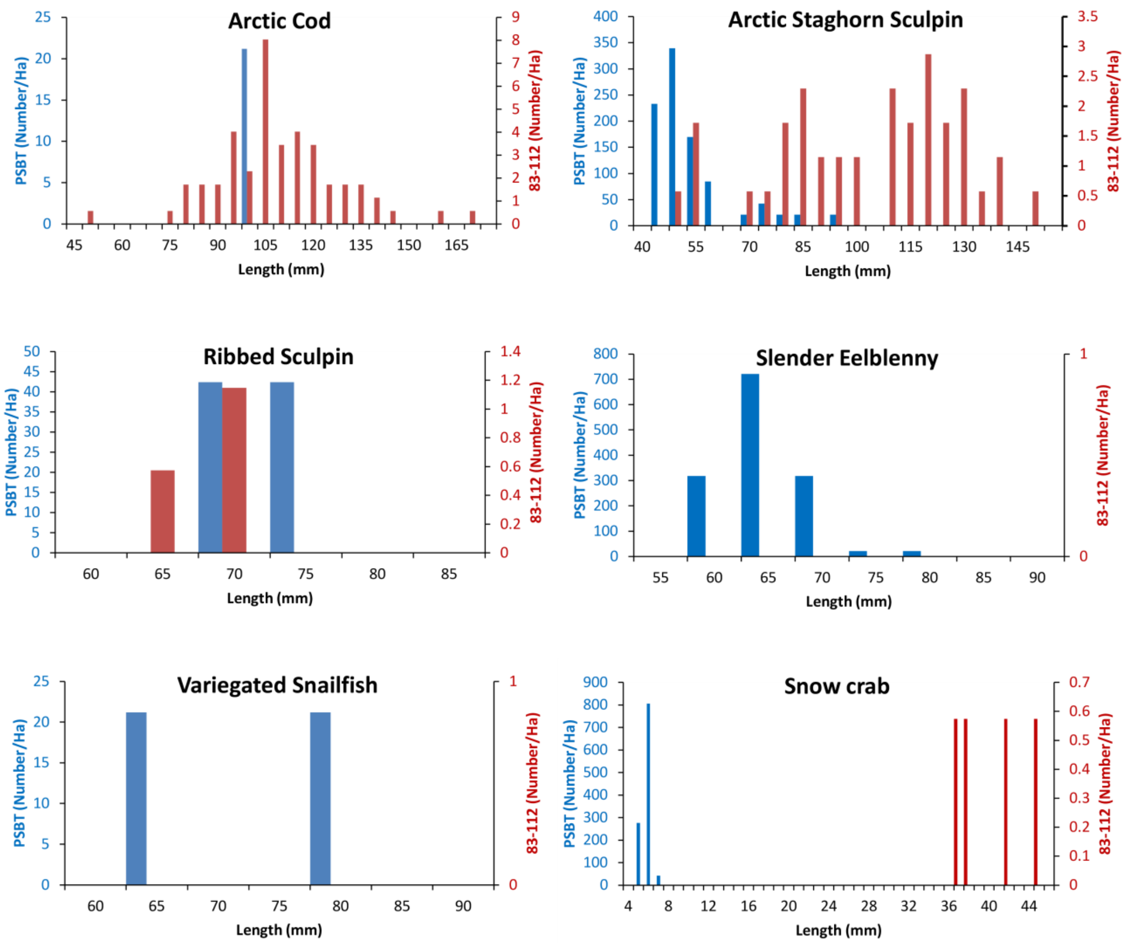
Table 2. Catch per unit effort (per hectare) comparison for station M-05 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.40	39.62	0.13	21.20
Arctic staghorn sculpin	0.44	24.12	1.95	953.97
Bering flounder	-	-	-	-
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	0.93	1,399.16
stout eelblenny	-	-	-	-
variegated snailfish	-	-	0.17	42.40
warty sculpin	-	-	-	-
yellowfin sole	-	-	0.02	21.20

Table 3. Catch per unit effort (per hectare) comparison for station M-05 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	0.15	2.89	-	-
Chionoecetes opilio	0.02	0.58	-	-
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	-	-	-	-
Neptunea heros	0.56	7.50	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	-	-	-	-
Ophiura sarsi	2.96	4,728.88	44.68	73,033.77
Pagurus rathbuni	-	-	-	-
Pagurus trigonocheirus	0.33	17.32	0.08	61.82
Strongylocentrotus droebachiensis	0.18	2.31	-	-

Station M-05



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station M-05.

Station N-02

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

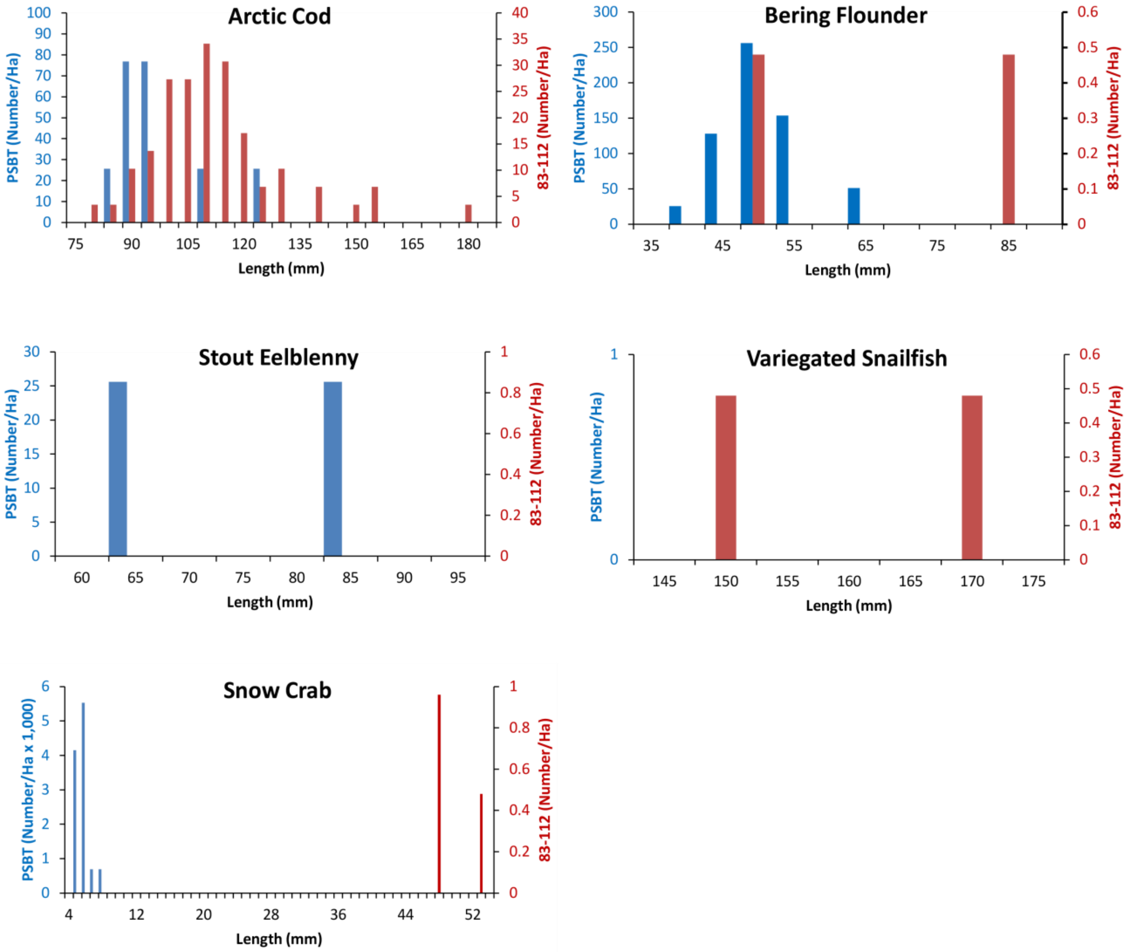
	83-112	PSBT	Difference
Area Sampled (ha)	2.084	0.039	98%
Depth (m)	50	51	-2%
Bottom Temperature (°C)	-0.8	-0.8	0%
Total Catch Weight (kg)	36.155	7.34	80%
Number Fish Species	4	4	0%
Unique Fish Species	2	2	0%
Number Invert Taxa	34	30	12%
Unique Invert Taxa	12	8	33%

Table 2. Catch per unit effort (per hectare) comparison for station N-02 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	2.15	204.93	1.43	230.50
Arctic staghorn sculpin	-	-	-	-
Bering flounder	0.00	0.96	0.61	614.66
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	-	-
stout eelblenny	-	-	0.05	51.22
variegated snailfish	0.05	0.96	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station N-02 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.06	1.44	1.38	11,063.85
Gorgonocephalus sp. cf. *arcticus*	5.47	70.07	6.51	128.05
Leptasterias polaris	-	-	-	-
Neptunea heros	0.18	1.44	-	-
Nucula tenuis	-	-	-	-
Nuculana pernula	1.18	818.27	20.74	27,659.61
Ophiura sarsi	2.18	395.94	84.34	17,978.75
Pagurus rathbuni	0.66	51.83	6.61	1,306.15
Pagurus trigonocheirus	0.16	5.28	0.41	25.61
Strongylocentrotus droebachiensis	-	-	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station N-02.

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

	83-112	PSBT	Difference
Area Sampled (ha)	1.631	0.030	98%
Depth (m)	42	44	-5%
Bottom Temperature (°C)	-1.2	-1.2	0%
Total Catch Weight (kg)	7.683	25.704	-235%
Number Fish Species	5	4	20%
Unique Fish Species	3	2	33%
Number Invert Taxa	29	27	7%
Unique Invert Taxa	14	12	14%

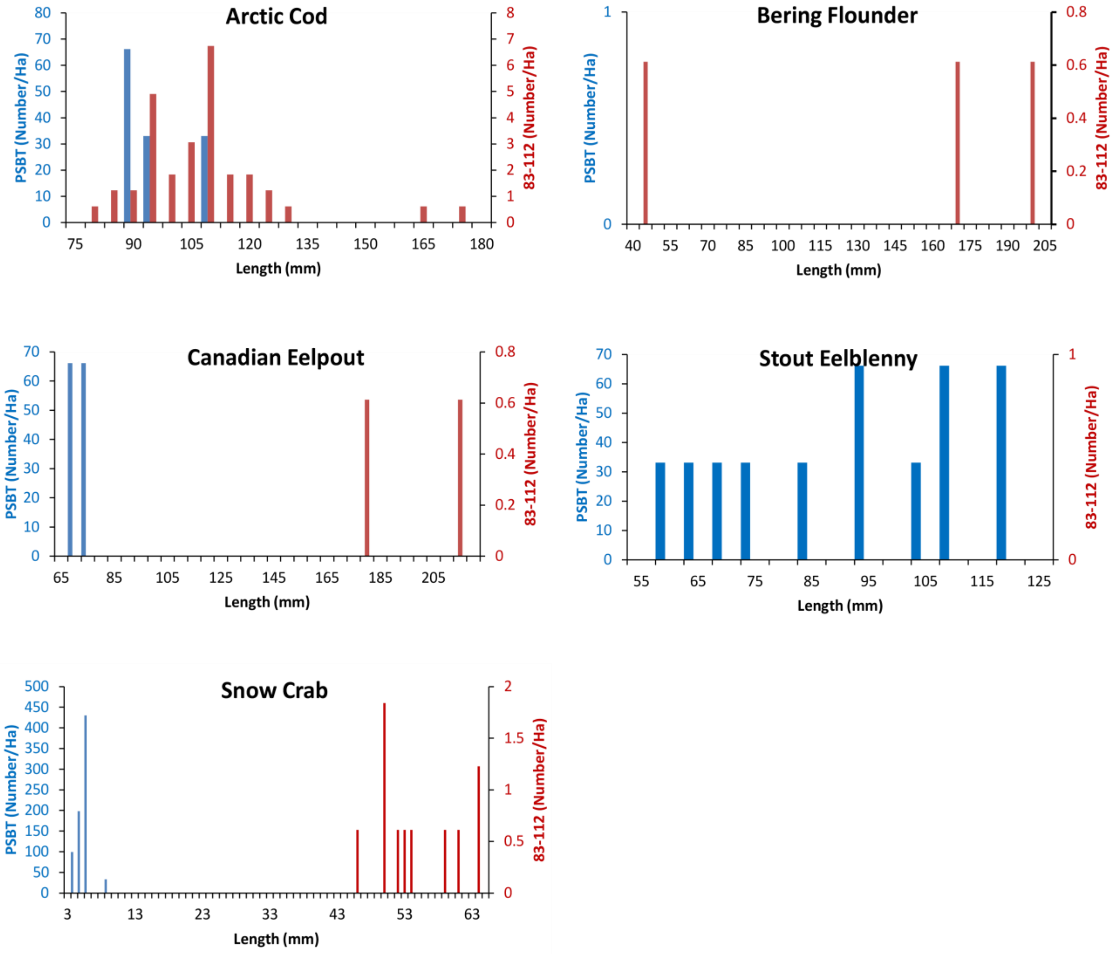
Table 2. Catch per unit effort (per hectare) comparison for station N-05 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.27	26.36	0.79	132.26
Arctic staghorn sculpin	-	-	-	-
Bering flounder	0.05	1.84	-	-
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	-	-
stout eelblenny	-	-	0.99	396.78
variegated snailfish	0.02	0.61	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station N-05 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	0.41	6.74	0.20	760.49
Gorgonocephalus sp. cf. *arcticus*	-	-	-	-
Leptasterias polaris	-	-	-	-
Neptunea heros	0.01	0.61	-	-
Nucula tenuis	-	-	519.35	2,073,912.67
Nuculana pernula	0.004	4.29	283.89	218,127.35
Ophiura sarsi	0.10	17.78	-	-
Pagurus rathbuni	0.31	19.00	1.06	330.65
Pagurus trigonocheirus	0.34	7.97	-	-
Strongylocentrotus droebachiensis	-	-	-	-

Station N-05



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station N-05.

Station O-02

Table 1. Differences in sample area and catch metrics for the 83-112 Eastern Bottom Trawl and the Plum Staff Beam Trawl.

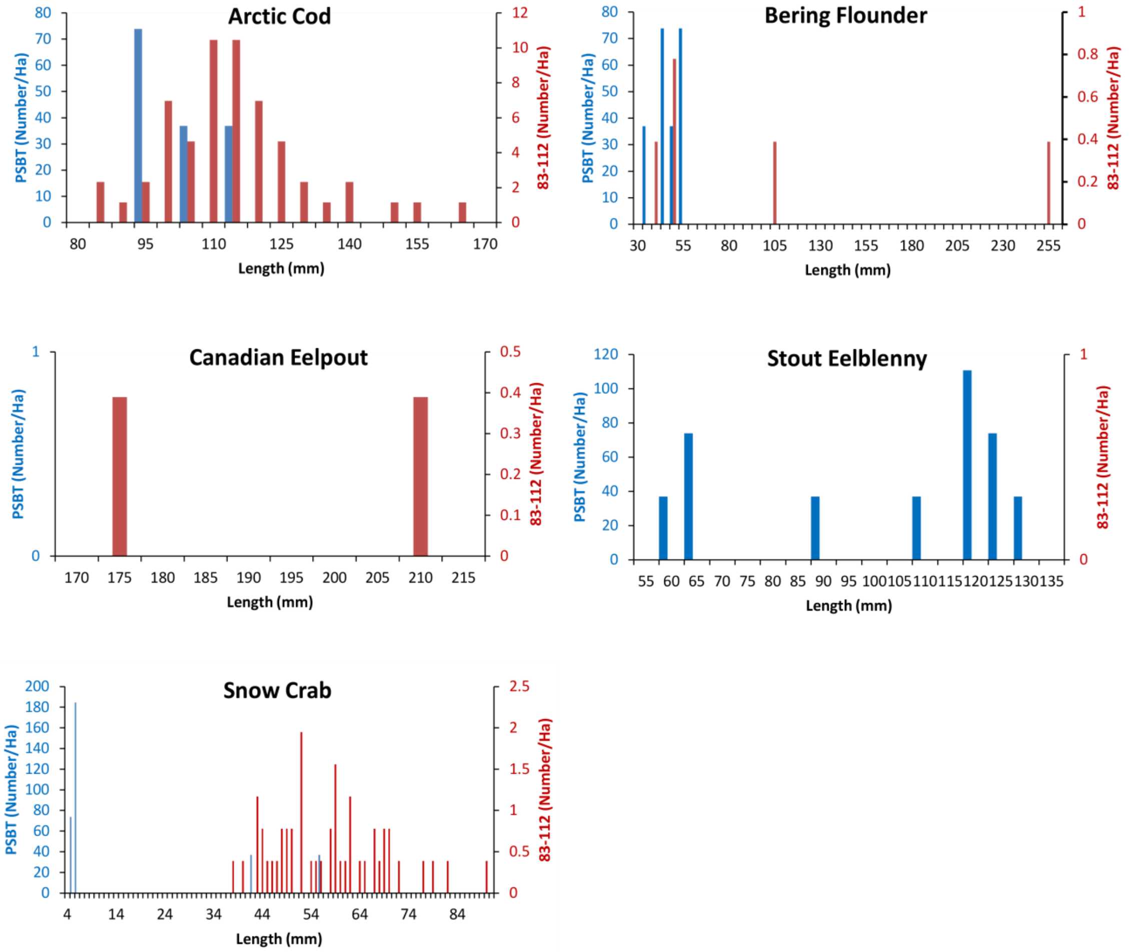
	83-112	PSBT	Difference
Area Sampled (ha)	2.567	0.027	99%
Depth (m)	59	60	-2%
Bottom Temperature (°C)	-1.4	-1.4	0%
Total Catch Weight (kg)	70.364	5.864	92%
Number Fish Species	5	3	40%
Unique Fish Species	3	1	67%
Number Invert Taxa	36	24	33%
Unique Invert Taxa	17	5	71%

Table 2. Catch per unit effort (per hectare) comparison for station O-02 of the top ten fish species caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Arctic cod	0.64	59.21	1.03	147.69
Arctic staghorn sculpin	0.01	0.39	-	-
Bering flounder	0.05	1.95	0.15	221.53
Pacific herring	-	-	-	-
saffron cod	-	-	-	-
slender eelblenny	-	-	-	-
stout eelblenny	-	-	1.26	406.14
variegated snailfish	-	-	-	-
warty sculpin	-	-	-	-
yellowfin sole	-	-	-	-

Table 3. Catch per unit effort (per hectare) comparison for station O-02 of the top twelve invertebrate taxa caught during the 2012 Arctic Eis Bottom Trawl survey.

	83-112		PSBT	
Taxon	Wt. (kg)	Number	Wt. (kg)	Number
Asterias amurensis	-	-	-	-
Boltenia ovifera	-	-	-	-
Chionoecetes opilio	1.33	19.09	3.40	332.30
Gorgonocephalus sp. cf. *arcticus*	0.0004	0.39	-	-
Leptasterias polaris	-	-	-	-
Neptunea heros	-	-	-	-
Nucula tenuis	-	-	19.72	21,230.25
Nuculana pernula	0.03	47.52	122.32	113,277.21
Ophiura sarsi	-	-	-	-
Pagurus rathbuni	0.39	26.49	5.02	738.44
Pagurus trigonocheirus	0.03	1.56	-	-
Strongylocentrotus droebachiensis	-	-	-	-



Standardized size frequency plots comparing major taxa captured by the Plumb Staff Beam Trawl (PSBT; blue) and the 83-112 Eastern Trawl (red) at station O-02.

Appendix B.

Ichthyoplankton Assemblages and Distribution Patterns in the Chukchi and Northern Bering Seas 2012-2013

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30 September 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
SBE	Sea Bird Electronics

List of Oral and Poster Presentations

Busby, M., Duffy-Anderson, J.T., Mier, K., and Tabisola, H. 2016. Ichthyoplankton assemblages and distribution in the Chukchi Sea (2012-2013). ASLO, Ocean Sciences. Poster Contribution. New Orleans, LA.

Tabisola, H., Busby, M., Duffy-Anderson, J.T., and Mier, K. 2016. Ocean Currents as Drivers of Ichthyoplankton Distribution in the Chukchi Sea. Alaska Marine Science Symposium. Poster Contribution. Anchorage, AK.

Proposed Objectives and Study Chronology

The primary objective of this project was to collect and identify the ichthyoplankton of the Eastern Chukchi and Northern Bering Seas and determine abundances and distribution patterns of major taxa. Analyses of assemblage structure were also conducted.

The study began in 2012. Ichthyoplankton were collected aboard the *F/V Bristol Explorer* with a 60 cm bongo sampler fitted with two 0.505 mm mesh nets with detachable cod ends at 138 stations in the Chukchi and Northern Bering Seas 7 August–24 September 2012 and 143 stations over the same date range in 2013. A flowmeter was fitted into the mouth of the net frame to determine volume filtered. Samples were preserved in 5% formaldehyde-sea water solution buffered with sodium borate. The bongo array was equipped with either a Seabird Electronics SBE 49 FastCAT or a SBE 19+ SeaCAT to monitor and record depth, temperature, and salinity data over the towed path. Samples were sorted and fish eggs, larvae, and juveniles identified to the lowest taxonomic level possible at the Plankton Sorting and Identification Center in Szczecin, Poland (ZSIOP). Taxonomic identifications were verified at the Alaska Fisheries Science Center (AFSC). A chronology of activities for each survey year follows:

2012 Survey

August - Prepared *F/V Bristol Explorer* for survey. Departed Dutch Harbor, AK for survey.

September - Completed survey, unloaded gear and samples. Samples shipped to Seattle, WA.

October - Samples arrived in Seattle, WA.

November - Samples shipped to ZSIOP (Szczecin, Poland).

December - Samples received by ZSIOP (Szczecin, Poland).

April (2013) - Sorted ichthyoplankton received from ZSIOP (Szczecin, Poland) in Seattle, WA.

October (2013) - Verifications of ichthyoplankton identifications completed.

April (2014) - Data editing complete and available on AFSC ECODAAT database.

June (2014) - Begin data analysis and mapping distributions and abundances of major species.

December (2015) - Metadata questionnaire completed and data submitted to AOOS website.

May (2016) - Metadata questionnaire and data revised.

2013 Survey

August - Prepared *F/V Bristol Explorer* for survey. Departed Dutch Harbor, AK for survey.

September - Completed survey, unloaded gear and samples. Samples shipped to Seattle, WA.

November- Samples arrived in Seattle, WA.

November - Samples shipped to ZSIOP (Szczecin, Poland).

December - Samples received by ZSIOP (Szczecin, Poland).

June (2014) - Sorted ichthyoplankton received from ZSIOP (Szczecin, Poland) in Seattle, WA.

August (2014) - Verifications of ichthyoplankton identifications completed.

February (2015) - Data editing complete and available on AFSC ECODAAT database.

June (2014) - Begin data analysis and mapping distributions and abundances of major species.

November (2015) - Completed and submitted final report.

December (2015) - Metadata questionnaire completed and data submitted to AOOS website.

June (2016) - Edits received on final report.

December (2015) - Metadata questionnaire completed and data submitted to AOOS website.

May (2016) - Metadata questionnaire and data revised.

September (2016) - Revisions to final report submitted.

In 2013 a significant problem occurred during the survey at sea where flooding of the factory processing deck that was being used as a laboratory flooded and the data forms that were used to record the flowmeter revolutions lost. This required a diligent effort headed by Dr. Alexei Pinchuk (University of Alaska, Fairbanks) and Wess Strasburger (NOAA/Alaska Fisheries Science Center) to reconstruct the distance fished based on data from the 2012 survey to calculate the volumes filtered for each tow. Quantitative filtered volume measurements were obtained and data were deemed appropriate for use in calculating quantitative catch of ichthyoplankton from the survey. Data are presented herein.

Specimens collected are housed in the collection of the Ichthyoplankton Laboratory, Recruitment Processes Program AFSC. Data will be publically accessible on the Ichthyoplankton Information System (IIS)website [http://access.afsc.noaa.gov/ichthyo/index/.php] and Arctic Eis AOOS [https://workspace.aoos.org/group/11050/projects].

1. Abstract

Ichthyoplankton surveys have become an integral component of ecosystem studies in the Pacific arctic over the past decade. In summer 2012 and 2013, large scale fisheries oceanographic surveys that included ichthyoplankton tows were conducted in the northern Bering and eastern Chukchi Seas as part of the Arctic Ecosystem Integrated Survey (Arctic Eis). Collections of pelagic fish eggs indicated potential spawning areas for *Limanda* spp. (probably yellowfin sole *L. aspera*) nearshore of the Seward Peninsula, and Bering flounder (*Hippoglossoides robustus*) to the west and offshore from Point Barrow in 2012. Similar but less pronounced trends in egg distributions for these two species were observed in 2013. Spatial and temporal analyses of larval fish abundances determined that yellowfin sole (*Limanda aspera*) was the most abundant larval fish species collected followed by Arctic cod (*Boreogadus saida*), an important forage fish in the food web of the Arctic ecosystem. Spatio-temporal composition of larval fish communities was examined. Cluster analyses showed *L. aspera* to be the dominant component of a southern, nearshore assemblage strongly associated with the northward moving Alaska Coastal Current (ACC) characterized by comparatively warm, low-salinity water. *Boreogadus saida* larvae dominated a more northern assemblage in close proximity to the ice edge and were more abundant in 2013 than 2012. Larvae of the forage fish species capelin (*Mallotus villosus*) and Arctic sand lance (*Ammodytes hexapterus*) were important assemblage components in 2012 and 2013, respectively.

2. Introduction

There is substantial interest in the effects of climate change on the Pacific arctic ecosystem, and determining relationships between physical processes in the environment and biological responses. Biological communities in Arctic ecosystems are changing dramatically as the result of rapid climate change manifested mostly by great reductions in sea ice cover both in quantity and seasonal extent and duration. The resulting increased potential for oil and gas development and expanded transportation routes have opened a floodgate for scientific investigations including species inventories and abundance estimates of regional fauna. Sensitivity of early life stages of fishes to these and other climate driven oceanographic phenomena potentially make marine fish larvae important indicators of regional climate variation and ecosystem change (Busby et al., 2014). Taking this into consideration, ichthyoplankton surveys have become an integral component of ecosystem studies in the Pacific Arctic over the past decade (Norcross et al. 2010; this study) as they most importantly describe the species comprising ichthyoplankton communities, provide baseline data on abundance and distribution of the species present, and may in some instances offer early insight into climate-mediated changes (northward expansions, phenological shifts, changes in spawning distributions of adults).

In this report, we document the species composition, abundance, and distribution of ichthyoplankton collected during two fisheries oceanography surveys of the Arctic Ecosystem Integrated Survey (Arctic Eis) program conducted in the eastern Chukchi and northern Bering Seas during the summers of 2012 and 2013. Although other ichthyoplankton surveys have been conducted in the Chukchi Sea e.g. the Russian- American Long-Term Census of the Arctic

(RUSALCA, Norcross et al. 2010; Busby et al. in prep.), the Arctic Eis Surveys are the most spatially comprehensive US Chukchi shelf surveys to date, and offer results at high spatial resolution. Species-specific results for selected nodal species are presented, and analyses and interpretation of analyses of assemblage structure and community ecology are also presented. We propose that species-specific patterns of distribution, and community-level patterns in larval fish composition, reflect species driven responses to oceanographic variables and that early life stages may be early indicators of broader ecosystem shifts.

3. Methods

Field collections

Ichthyoplankton was collected aboard the *F/V Bristol Explorer* with a 60 cm bongo sampler fitted with two 0.505 mm mesh nets with detachable cod ends at 138 stations in 2012 and 143 stations in 2013 (Figs. 1a and b, Table 1, Appendix 1). During all cruises, quantitative oblique tows were made to a maximum depth of 91 m (or to within 10 m of the substratum), allowing for vertically integrated estimates of larval fish abundance. The ship speed was monitored and adjusted (1.5 to 2.5 knots) throughout each tow to maintain a wire angle of 45° from the ship to the bongo net. The nets were equipped with a calibrated flow meter; therefore, catch rates were standardized to catch per unit effort (CPUE; number · 10 m^{-2}). Sampling occurred during daylight hours as per ship protocol. Samples were preserved in 5% formaldehyde-sea water solution buffered with sodium borate.

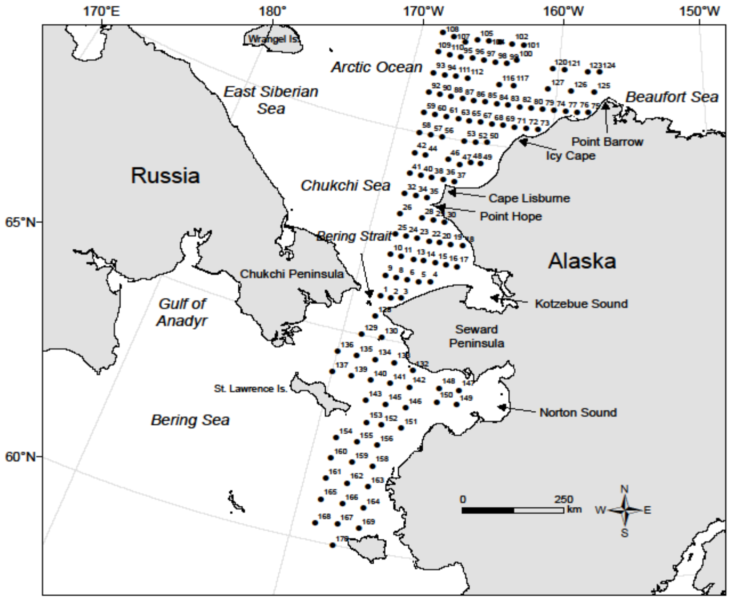

Fig. 1a. Bongo stations sampled 7 August – 24 September 2012.

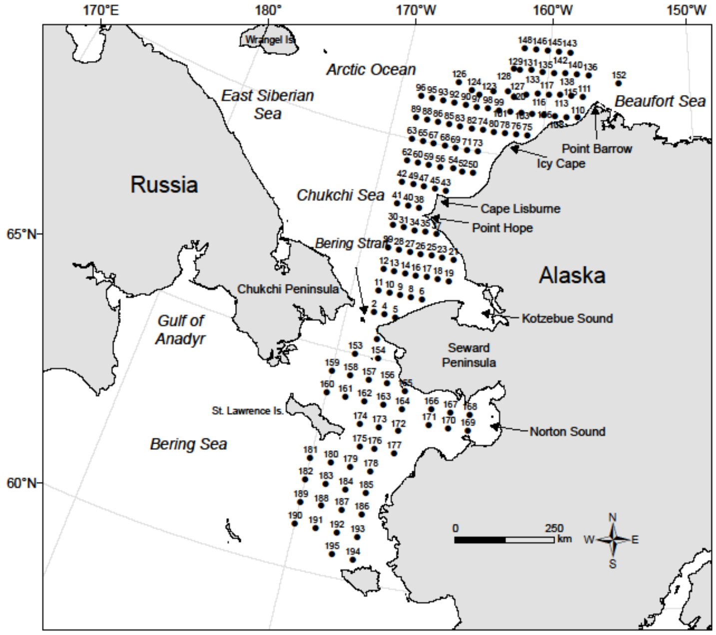

Fig. 1b. Bongo stations sampled 7 August – 24 September 2013.

Laboratory procedures

Samples were sorted and fish eggs, larvae, and juveniles identified to the lowest taxonomic level possible at the Plankton Sorting and Identification Center in Szczecin, Poland. Taxonomic identifications were verified at the Alaska Fisheries Science Center (AFSC), National Oceanic and Atmospheric Administration in Seattle, WA. Some fish eggs and larvae were categorized as taxonomic groups (e.g., *Limanda* spp., *Liparis* spp.) due to limitations associated with identifying eggs and larval stages to the species level. In some cases identifications of damaged specimens were only made at the family level. In these instances the identifications were not included in counts of species richness or diversity because they were considered to be of taxa that could normally be successfully identified. Fish were measured for standard length (SL) to the nearest 1.0 mm. The separation point between the larval and juvenile stages for *Gadus chalcogrammus* and *Boreogadus saida* is 25.0 mm SL based on the size at transformation of *G. chalcogrammus* determined by Brown *et al.,* (2001). For other taxa, definition of the juvenile stage follows Kendall et al. (1984) as a fish having complete adult compliments of fin elements, scales, and "the appearance of a small adult". Catch in each tow was converted to catch 10 m^{-2} of sea surface area.

Physical environment sampling

The bongo array was equipped with a Seabird Electronics SBE 49 FastCAT or a SBE 19+ SeaCAT to monitor and record depth (pressure), temperature, and conductivity data over the towed path. Depth-averaged temperature and salinity measurements were calculated at each station and compared with depth-integrated larval fish abundance estimates to evaluate influences of water column variables on fish community composition.

Sea ice data were collected using the special sensor microwave interferometer (SSMI) and obtained from the National Snow and Ice Data Center (NSIDC, http://nsidc.org/). Data were extracted into nominally diagonal 25 x 25 km regions, reported as percent ice coverage and mapped for each. Twelve ARGOS satellite tracked drifters drogued at 30 m depth were deployed south of Bering Strait in September 2012 and south of Point Hope in September 2013 to study circulation patterns.

Analytical methods

Taxa collected were reported in phylogenetic order for each family encountered and then by alphabetical order within each family (Table 1). Maps of the distribution and abundance, (reported as number/10m$^{2)}$ of eggs, larvae and juveniles of species occurring in high numbers or considered of ecological importance were created using ESRI ARC map software and are presented from high to lower abundance.

To test for differences in lengths of *B. saida* between years a two-sample t test (using average corrected length per station) which tests whether the means are different and a nonparametric two-sample KS (Kolmogorov Smirnov) test which tests whether the distributions are different between the 2 years were used.

Species assemblages were defined by applying both clustering and ordination techniques to abundance (no/10m^2) in both 2012 and 2013. A separate cluster analysis was applied to group stations and species. For the station analysis, a square root transform was applied to all species abundance to down-weight the effect of outliers (Clarke and Warwick, 2001). The Bray-Curtis (BC) similarity coefficient, calculated for each pair of stations, was used as input to a hierarchical cluster analysis using group average linkage. Clusters were determined from the resulting dendrogram based on highest similarity, length of branches (indicating stability), results of similarity profiles analysis (SIMPROF, a permutation test of randomness at each branch in dendrogram), as well as biological relevance. For the species analysis, relative abundance (standardized by species totals rather than transforming) was used and rare species were eliminated (occurring at only 1 station per year). Species clusters were determined in the same method as stations. Results of station and species clusters were validated using nonmetric multidimensional scaling (NMDS) ordination. The NMDS algorithm attempts to arrange samples (either stations or areas) such that pairwise distances in the ordination plot match Bray-Curtis similarities; thus, samples closer together in the ordination plot have a more similar species composition than samples farther apart. The final configuration of stations (areas) was determined by minimizing Kruskal's stress statistic (Kruskal 1964), and the number of dimensions for the final ordinations was chosen as the smallest number of dimensions that achieved a stress of no more than 0.2. A stress of 0.1 or lower is considered a good fit (Kruskal 1964) and we defined a stress of less than 0.2 as acceptable. Cluster groups were superimposed on NMDS plots to check for agreement. Once the station clusters were defined, similarity percentages (SIMPER) were calculated to determine the species that typify each cluster by determining the percent contribution of each species to the similarity making up each spatial cluster.

In order to determine what environmental variables were most correlated with species assemblage structure, a Spearman rank correlation was calculated between the Bray-Curtis coefficients and the Euclidean distance of every possible combination of normalized environmental variables (BEST procedure). The significance of this statistic was evaluated using 999 permutations. A preliminary BEST analysis was performed that included bottom depth, latitude, longitude, near-surface temperature, near-surface salinity, near-surface sigma-T, near bottom-temperature, near-bottom salinity, near-bottom sigma-T and mixed layer depth as environmental variables. A subsequent analysis was conducted omitting near-surface and near bottom sigma-T. All techniques were done using PRIMER 7, version 7.0.9 (Clarke and Gorley, 2015).

4. Results

Species composition

A total of 906 eggs comprising five taxa in two families and 1,057 larval and juvenile fishes comprising at least 31 taxa representing 11 families were collected during the study period (Table 1). Taxonomic richness and numbers of eggs and larvae collected were lower in 2013 than 2012. The families Stichaeidae (Pricklebacks) and Pleuronectidae (flatfishes) were represented by the greatest number of taxa (6 and 7, respectively) followed by Liparidae (snailfishes) (4), Gadidae (cods), Cottidae (sculpins), and Agonidae (poachers)(3 each). *Limanda* spp. (probably *Limanda aspera*, yellowfin sole) were the most abundant eggs followed by

Hippoglossoides robustus (Bering flounder). *Limanda aspera* was the most abundant larval fish caught followed by *H. robustus*, *Boreogadus saida* (Arctic cod), and *Mallotus villosus* (capelin).

Species accounts – Eggs

Eggs of *Limanda* spp. , probably *L. aspera*, were found in high concentrations along the north shore of Seward Peninsula and also near Point Hope and Cape Lisburne in both 2012 and 2013 with greater abundances collected in 2012 (Figs. 2a and b).

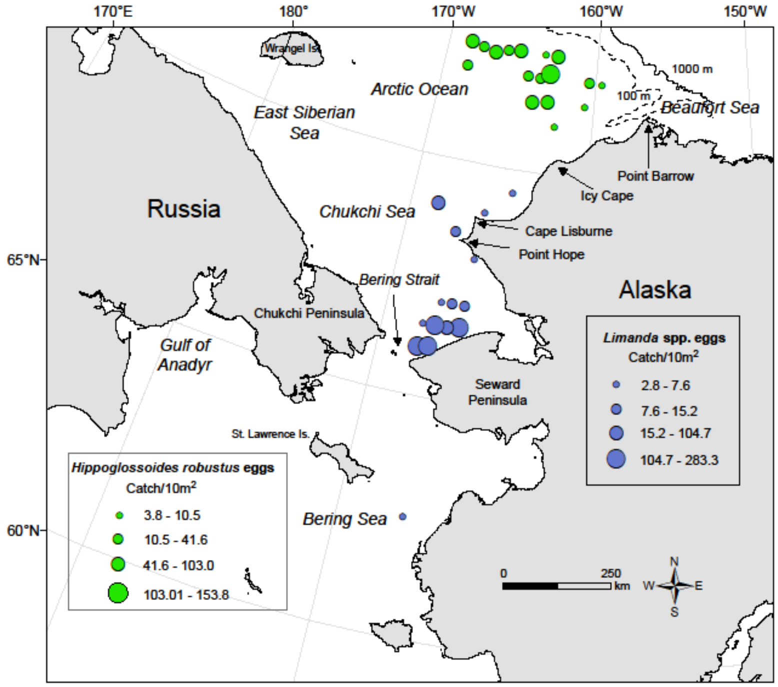

Fig. 2a. Abundance and distribution of *Limanda* spp. and *Hippoglossoides robustus* eggs 2012.

Table 1. Numbers of fish eggs, larvae, and juveniles collected in bongo tows from the Chukchi and Northern Bering Seas (NBS) during 2012 and 2013 Arctic Eis surveys.

			Chukchi			**NBS**			**Chukchi**			**NBS**				
			7 August-9 September 2012 (*n* =100 stations)			10-24 September 2012 (*n* =38 stations)			7 August-8 September 2013 (*n* =100 stations)			7 August, 10-24 September 2013 (*n* =43 stations)			Totals	
Family	**Scientific Name**	**Common Name**	Eggs	Larvae	Juveniles	Eggs	Larvae	Juveniles	Eggs	Larvae	Juveniles	Eggs	Larvae	Juveniles	Eggs	Larvae + Juveniles
Clupeidae	*Clupea pallasi*	Pacific herring					2									2
Osmeridae	*Mallotus villosus*	capelin		22			16			7			3			48
Gadidae		unidentified cods								1						1
	Boreogadus saida	Arctic cod		9	4					22	15					50
	Eleginus gracilis	saffron cod		1						1	5					7
	Gadus chalcogrammus	walleye pollock		1		25		1		2		1	1		26	5
Gasterosteidae	*Pungitius pungitius*	ninespine stickleback						1								1
Hexagrammidae	*Hexagrammos stelleri*	whitespotted greenling											1			1
Cottidae	*Gymnocanthus tricuspis*	Arctic staghorn sculpin		2						6						8
	Hemilepidotus papilio	butterfly sculpin					3									3
	Icelus spatula	spatulate sculpin		1												1
Agonidae	*Aspidophoroides monopterygius*	alligatorfish		1												1
	Aspidophoroides olrikii	Arctic alligatorfish		2						1						3
	Podothecus veternus	veteran poacher								1						1
Liparidae	*Liparis* spp.	unidentified snailfish		3						2						5
	Liparis fabricii	gelatinous seasnail		1						2						3
	Liparis gibbus [1]	variegated snailfish		13						7						20
	Liparis tunicatus	kelp snailfish		3			1			11						15
Stichaeidae		unidentified pricklebacks		1												1
	Acantholumpenus mackayi	blackline prickleback					1									**1**
	Eumesogrammus praecisus	fourline snakeblenny		7						1						8
	Anisarchus medius	stout eelbleny		1						2						3
	Leptoclinus maculatus	daubed shanny		2						3						5
	Lumpenus fabricii	slender eelblenny		1						1						2
	Stichaeus punctatus	Arctic shanny		17						19						36
Ammodytidae	*Ammodytes hexapterus*	Arctic sand lance		4						13			1			18
Pleuronectidae		unidentified flounders	6						1				2		7	2
	Hippoglossoides robustus	Bering flounder	156	66			7		3	10			1		159	84
	Lepidopsetta polyxystra	northern rock sole		1												1
	Limanda spp.	unidentified *Limanda*	370						333			10	1		713	**1**
	Limanda aspera	yellowfin sole		76		1	321			36			221		1	654
	Limanda proboscidea	longhead dab		15									4			19
	Limanda sakhalinensis	Sakhalin sole		9						1						10
	Pleuronectes quadrituberculatus	Alaska plaice		5						1						6
		total number of taxa	3	25	1	2	7	2	3	21	2	2	8	0	5	31
		total number of individuals	532	264	4	26	351	2	337	150	30	11	235	0	906	1057

[1] Could possibly include *Liparis bathyarcticus* . Both species occur in this region and are morphologically similar as adults. Larvae of *L. bathyarcticus* have not been described.

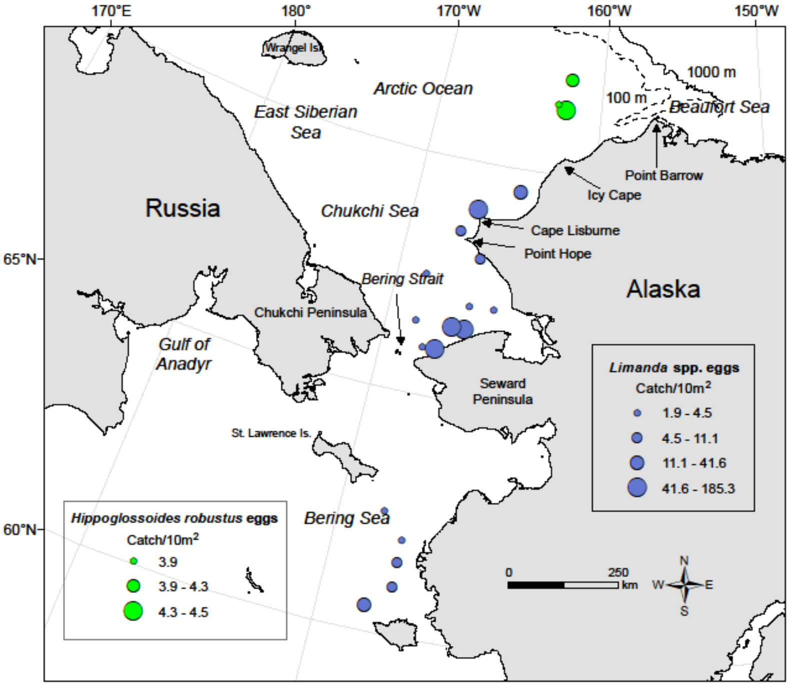

Fig. 2b. Abundance and distribution of *Limanda* spp. and *Hippoglossoides robustus* eggs 2013.

Species accounts – Larvae

Limanda aspera larvae were the most abundant species collected overall in both the Chukchi Sea and NBS and more individuals were caught in 2012 than 2013 (Figs. 3a and b).

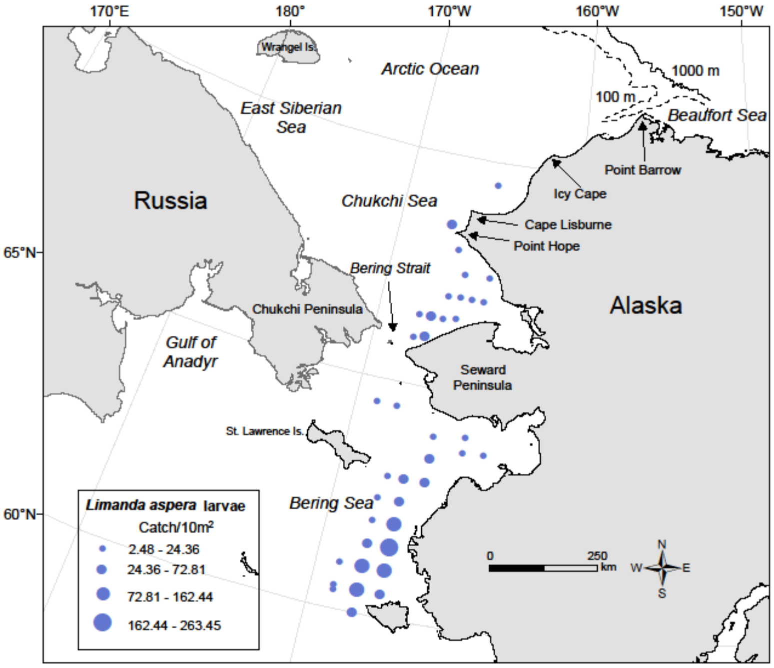

Fig. 3a. Abundance and distribution of *Limanda aspera* larvae 2012.

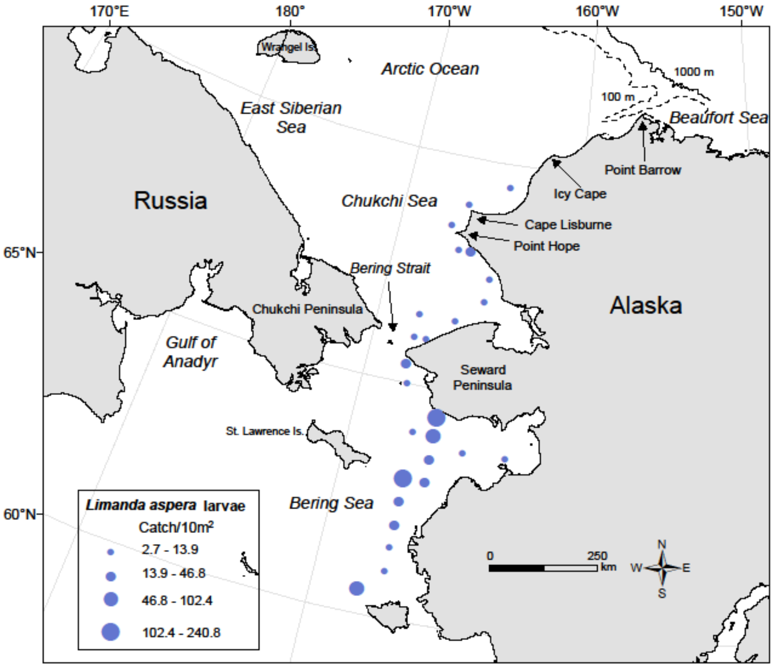

Fig. 3b. Abundance and distribution of *Limanda aspera* larvae 2013.

Larvae of *Hippoglossoides robustus* were the second most abundant species overall considering 2012 and 2013 combined (Table 1) but were more abundant and distributed over a larger geographic area in 2012 than 2013 (Figs. 4a and b). Several other species including *Ammodytes hexapterus* (Arctic sand lance), *Stichaeus punctatus* (Arctic Shanny) and *Boreogadus saida* (Arctic cod) were caught in higher numbers in 2013 than *H. robustus* (Table 1). In both years *H. robustus* larvae were found in highest abundances around Seward Peninsula and north of Icy Cape.

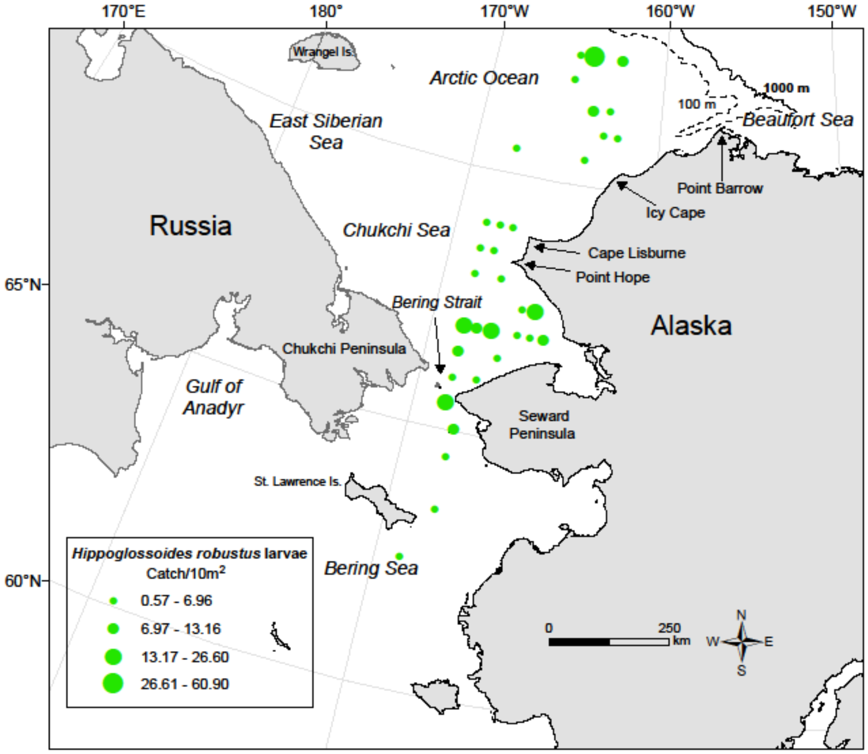

Fig. 4a. Abundance and distribution of *Hippoglossoides robustus* larvae 2012.

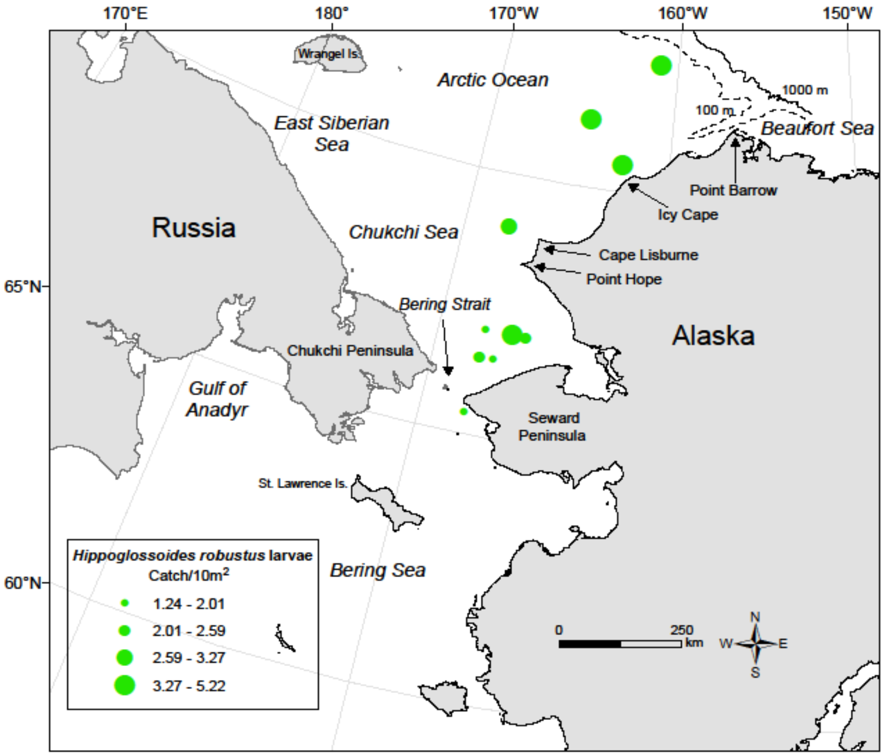

Fig. 4b. Abundance and distribution of *Hippoglossoides robustus* larvae 2013.

Boreogadus saida (Arctic cod), are an important forage fish in the diets of seabirds, marine mammals, and larger fish (Logerwell et al. 2015). In 2013 *B. saida* larvae and juveniles were more abundant than in 2012 but were distributed similarly in the northeastern Chukchi Sea near the ice edge in both years (Figs. 5a and b). Analysis of lengths determined that there was no significant difference in the mean lengths of larvae and juveniles caught in 2012 and 2013 (t-test: p=0.63; KS test: p=0.71).

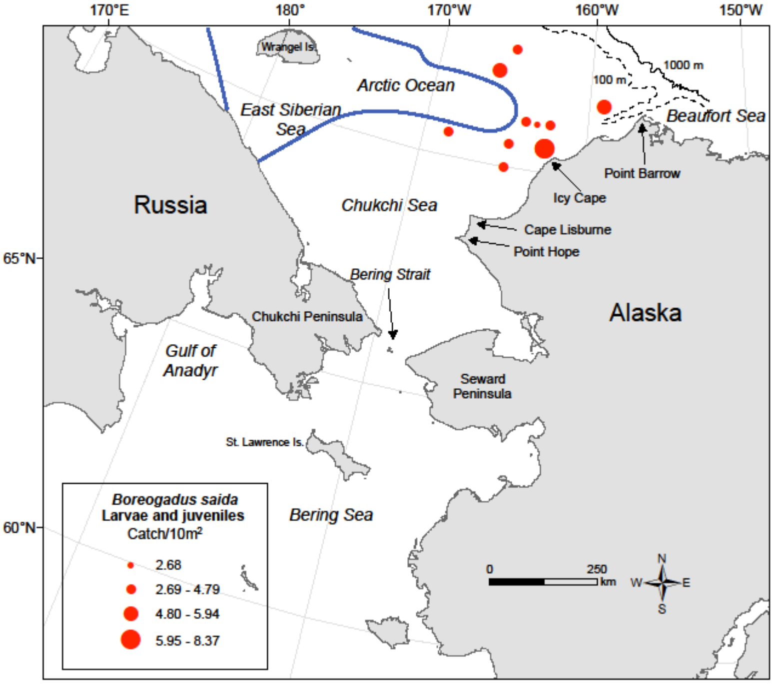

Fig. 5a. Abundance and distribution of *Boreogadus saida* larvae and juveniles 2012. Blue line indicates approximate position of ice edge 15 August 2012.

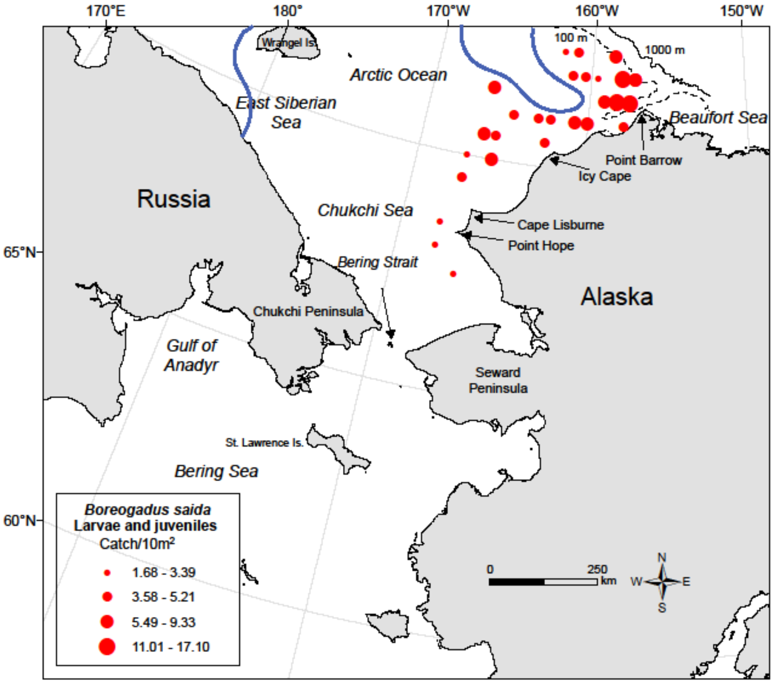

Fig. 5b. Abundance and distribution of *Boreogadus saida* larvae and juveniles 2013. Blue line indicates approximate position of ice edge 15 August 2013.

Mallotus villosus (capelin) are also an important forage fish in the diets of seabirds, marine mammals, and larger fish (Logerwell et al. 2015). Larvae of *M. villosus* were more abundant and widely distributed in 2012 than 2013 (Figs. 6a and b.). In both years they were present along the north shore of the Seward Peninsula but in 2012 there were more in the NBS southeast of St. Lawrence Island along the west coast of Alaska.

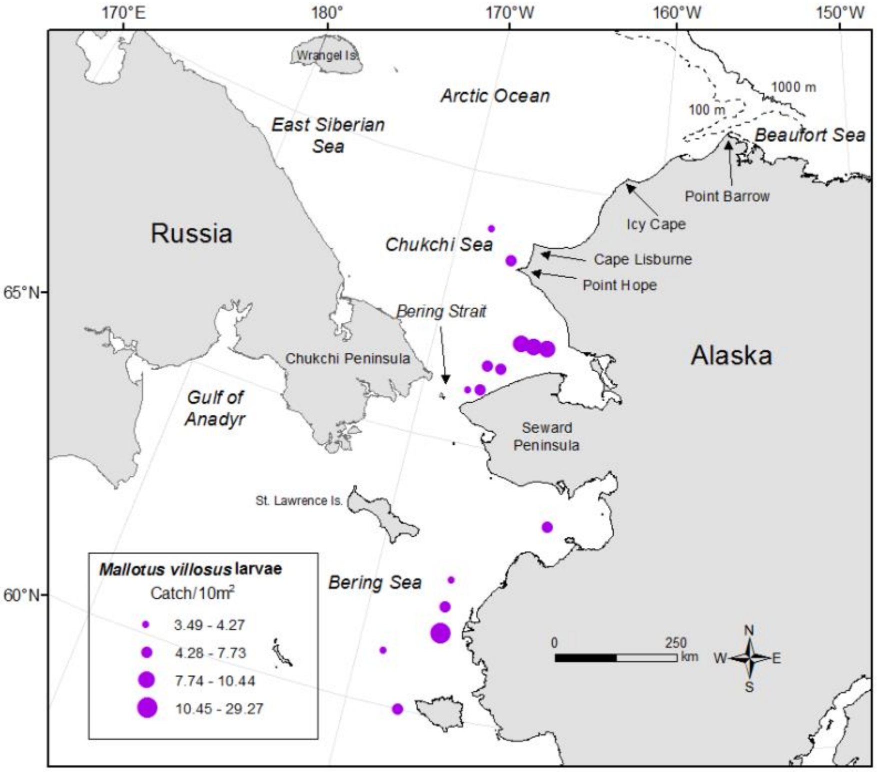

Fig. 6a. Abundance and distribution of *Mallotus villosus* larvae 2012.

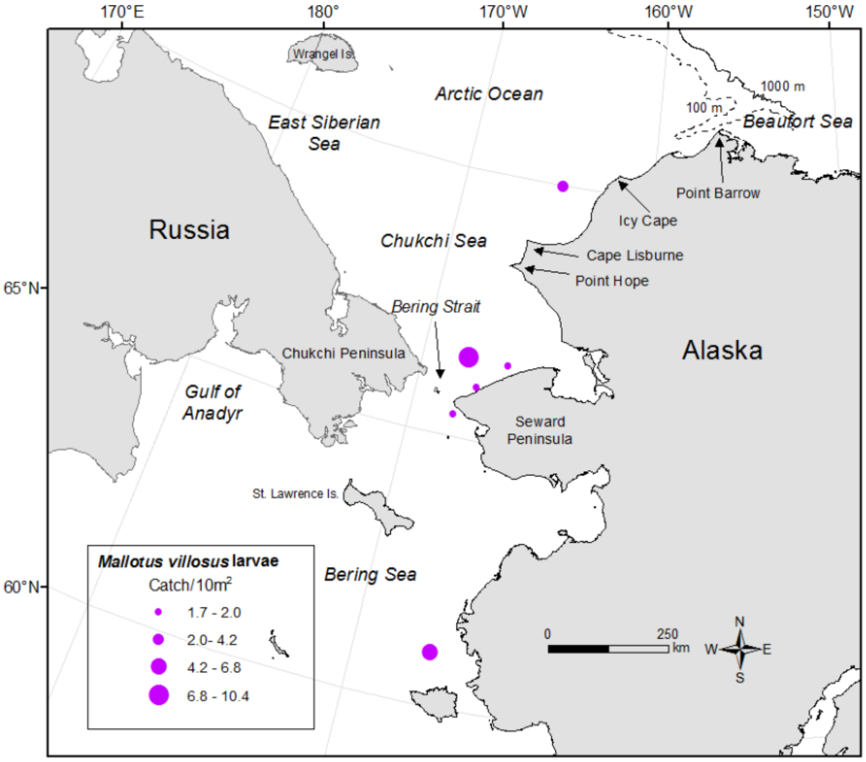

Fig. 6b. Abundance and distribution of *Mallotus villosus* larvae 2013.

Species assemblages

The multispecies assemblage approaches permitted community-level and species-specific gradients to be described across the study area. Cluster and SIMPER analyses showed *L. aspera* to be the dominant component of a southern, nearshore assemblage strongly associated with the northward moving Alaska Coastal Current (ACC) characterized by relatively warm-low salinity water in both 2012 and 2013 (groups 3a, b, and c 2012, group 4 2013)(Figs 7a and b; Tables 2 and 3). *Boreogadus saida* larvae dominated a more northern assemblage in close proximity to the ice edge and were more abundant in 2013 than 2012 (Groups 1 and 5 2012, 5a and b 2013).

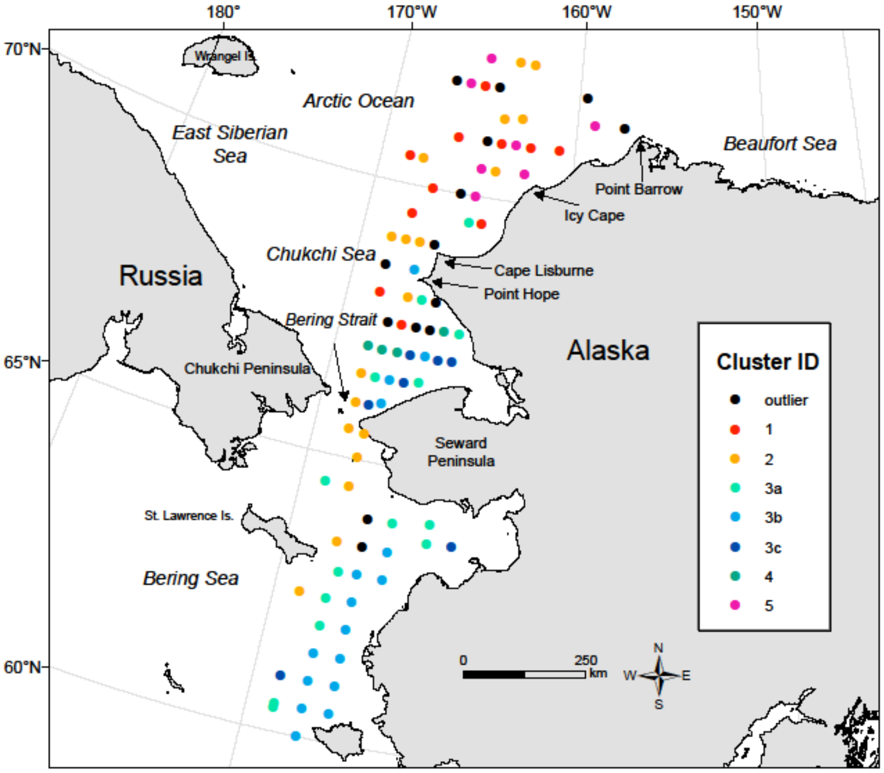

Fig. 7a. Station groupings from cluster analysis 2012.

Table 2. Results of SIMPER analysis for 2012 larval and juvenile fish clusters. Definitions of abbreviations: Cluster % Sim is the average % similarity over all pairs of stations for that cluster group. **Ave Abund** is the average transformed abundance. **% Contrib** is the percent contribution to the overall within group similarity. **%Cum** is the cumulative percent contribution to the overall within group similarity.

Cluster ID	Cluster %Sim	Species	Ave Abund	%Contrib.	% Cum.
Group 1	24.69	*Stichaeus punctatus*	1.53	78.2	78.2
		Boreogadus saida	0.52	8.71	86.91
		Hippoglossoides robustus	0.54	8.35	95.26
Group 2	31.95	*Hippoglossoides robustus*	1.87	92.78	92.78
Group 3a	33.1	*Limanda aspera*	3.11	96.16	96.16
Group 3b	56.92	*Limanda aspera*	6.85	90.88	90.88
Group 3c	46.9	*Limanda aspera*	4.02	67.11	67.11
		Mallotus villosus	1.47	13.08	80.19
		Liparis gibbus	1.4	12.58	92.77
Group 4	54.48	*Hippoglossoides robustus*	4.28	60.29	60.29
		Limanda sakhalinensis	2.28	21.08	81.37
		Limanda proboscidea	1.3	13.4	94.77
Group 5	28.08	*Hippoglossoides robustus*	1.66	59.38	59.38
		Stichaeus punctatus	0.88	29.92	89.29
		Boreogadus saida	0.57	10.71	100
Outliers (x)	7.55	*Limanda proboscidea*	0.59	36.68	36.68
		Limanda aspera	0.78	17.58	54.26
		Hippoglossoides robustus	0.48	14.8	69.06
		Boreogadus saida	0.34	14.19	83.24
		Eumesogrammus praecisus	0.37	9.55	92.8

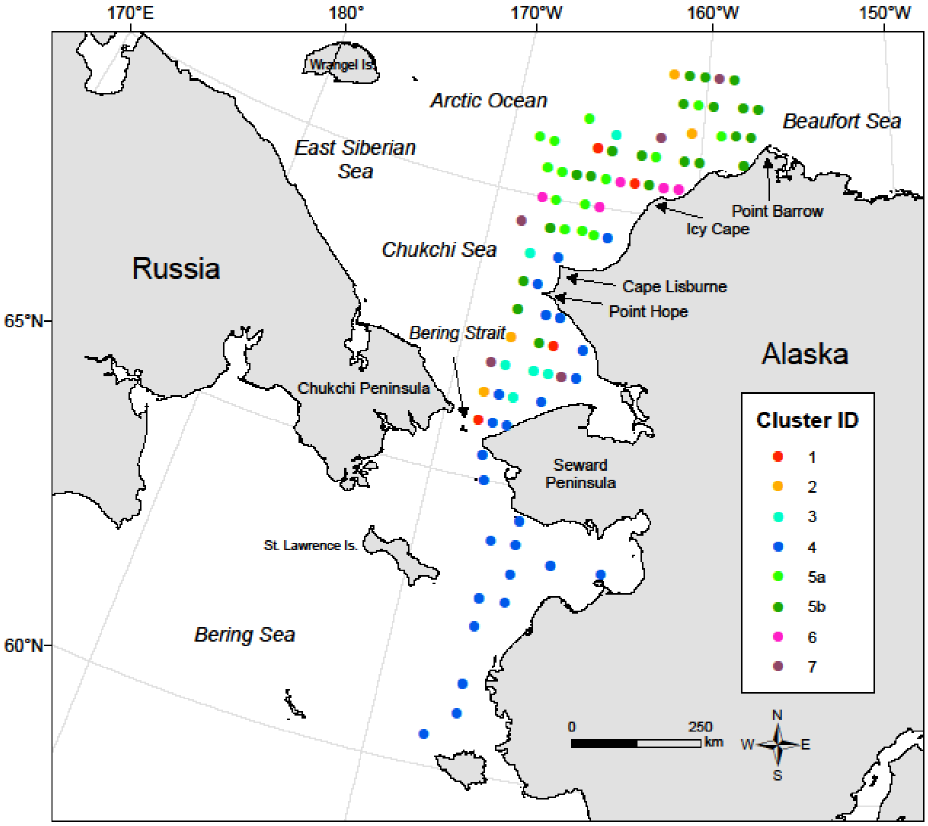

Fig. 7b. Station groupings from cluster analysis 2013.

Table 3. Results of SIMPER analysis for 2013 larval and juvenile fish clusters. Definitions of abbreviations: Cluster % Sim is the average % similarity over all pairs of stations for that cluster group. **Ave Abund** is the average transformed abundance. **% Contrib** is the percent contribution to the overall within group similarity. **%Cum** is the cumulative percent contribution to the overall within group similarity.

Cluster ID	**Cluster %Sim**	**Species**	**Ave Abund**	**%Contrib.**	**% Cum.**
Group 1	90.43	*Liparis tunicatus*	1.9	100	100
Group 2	59.1	*Liparis gibbus*	1.52	100	100
Group 3	52.38	*Hippoglossoides robustus*	1.73	100	100
Group 4	55.23	*Limanda aspera*	4.86	97.87	97.87
Group 5a	41.03	*Stichaeus punctatus*	1.71	68.46	68.46
		Boreogadus saida	1	24.91	93.38
Group 5b	49.19	*Boreogadus saida*	2.36	92.36	92.36
Group 6	40.82	*Gymnocanthus tricuspis*	1.71	87.93	87.93
		Lumpenus medius	0.81	12.07	100
Outliers	28.23	*Ammodytes hexapterus*	1.06	58.21	58.21
		Liparis fabricii	0.9	22.6	80.81
		Eleginus gracilis	0.84	19.19	100

Influences of the physical environment

The preliminary BEST analysis included bottom depth, latitude, longitude, near-surface temperature, near-surface salinity, near-surface sigma-T, near bottom-temperature, near-bottom salinity, near-bottom sigma-T and mixed layer depth as environmental variables. It was determined that there were correlations of sigma-T greater than 0.9 or less than -0.9 with temperature and salinity so additional analyses were conducted with sigma-T omitted. The subsequent analyses determined that latitude and near surface temperature were the environmental variables most correlated with taxonomic composition in 2012 and that bottom depth, latitude, longitude and near-bottom depth temperature were the strongest correlations in 2013 (Table 4).

Table 4. Environmental factors most correlated with taxonomic composition for each year of the study as determined by BEST analysis.

	Year	
Environmental factors	2012	2013
Bottom depth		**X**
Latitude	**X**	**X**
Longitude		**X**
Near-surface temp.	**X**	
Near-surface salinity		
Near-bottom temp.		**X**
Near-bottom salinity		
Mixed layer depth		
Spearman rank correlation	0.362 p=0.01	0.391 p=0.01

5. Discussion

Distribution of Ichthyoplankton

Collections of pelagic fish eggs identified potential locations of spawning centers for yellowfin sole (represented as *Limanda* spp. eggs) nearshore of the Seward Peninsula and *H. robustus* to the west and offshore from Point Barrow in 2012. Similar but less pronounced trends in egg distribution were observed in 2013. The close proximity of high concentrations of eggs for both taxa suggests that they were recently spawned and that minimal advection and/or diffusion had occurred. An investigation of the developmental stages of these eggs could further confirm this. For example, if it were determined the eggs are all in early stages of development, this would indicate that they were recently spawned.

Larvae of the forage fish species *M. villosus* and *A. hexapterus* were present in relatively high abundances in 2012 and 2013 respectively. Adults of both species typically occur nearshore but have different spawning behaviors and habitats. Pacific sand lance (*Ammodytes personatus*) spawn in late winter through early to mid- spring in most areas of the Gulf of Alaska and southeastern Bering Sea. Eggs are buried in sand and mud by females typically in bays and protected waters. We suspect *A. hexapterus* to have similar reproductive behavior but with perhaps a slight temporal difference in Arctic waters. In contrast, *M. villosus* spawn on beaches and deposit their eggs in interstitial spaces between small gravel during summer through fall (June-October). Distribution of *M. villosus* larvae in 2012 was similar to that seen for *Limanda aspera* with relatively high concentrations north and south of Seward Peninsula in outer Kotzebue and Norton Sounds. These two embayments appear to be potential nursery areas for *M. villosus*, *A. hexapterus* (not mapped)*, L. aspera*, and perhaps *H. robustus*.

Physical environment

The localized concentrations of eggs of both *Limanda* spp. and *H. robustus* eggs observed suggest the presence of aggregations of spawning adults on the bottom in those immediate areas. Bottom water at the centers of *Limanda* spp. and Bering flounder egg distribution were Alaska Coastal Water (ACW) in depths about 19-35 m and Bering Sea Shelf Water or Chukchi Sea Winter Water respectively (BSSW or CSWW) in depths around 39-55 m. The average water column temperature varied between 2012 and 2013 and was generally warmer throughout the Chukchi Sea both near the surface and bottom in 2012 than 2013. However, surface and near- bottom ACW (8.79, 9.16 °C) and bottom CSWW (-0.92 °C) were warmer in 2013 than 2012 (8.17, 8.35 °C ACW, -1.3 °C CSWW) (Danielson et al. 2016).

Sea ice southward extent and position in mid-August was similar in 2012 and 2013 but concentration was greater in 2013 (Figs. 8a and 8b) (Wood et al. 2015). This increased sea ice concentration and the expanded area of melt water (MW) was most likely the factor influencing the observed increase in abundance and wider geographic distribution of *B saida* in 2013.

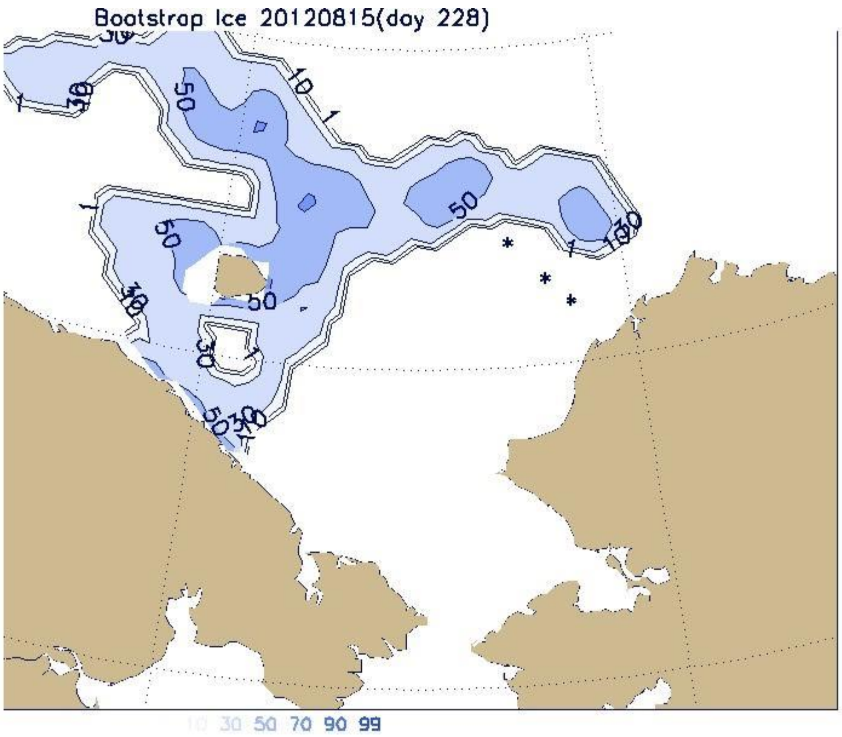

Fig. 8a.   Sea ice extent and concentration 15 August 2012.   Darkness of blue shade indicates greater % sea ice cover and concentration.   Asterix* indicates mooring locations.

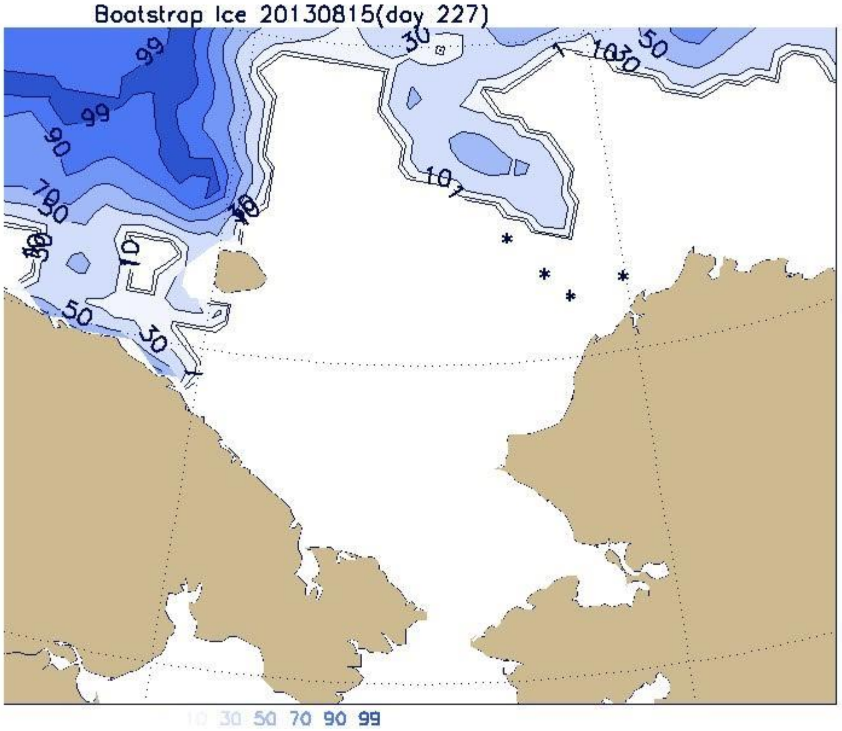

Fig. 8b. Sea ice extent and coverage 15 August 2013. Darkness of blue shade indicates greater % sea ice cover and concentration.   Asterix* indicates mooring locations.

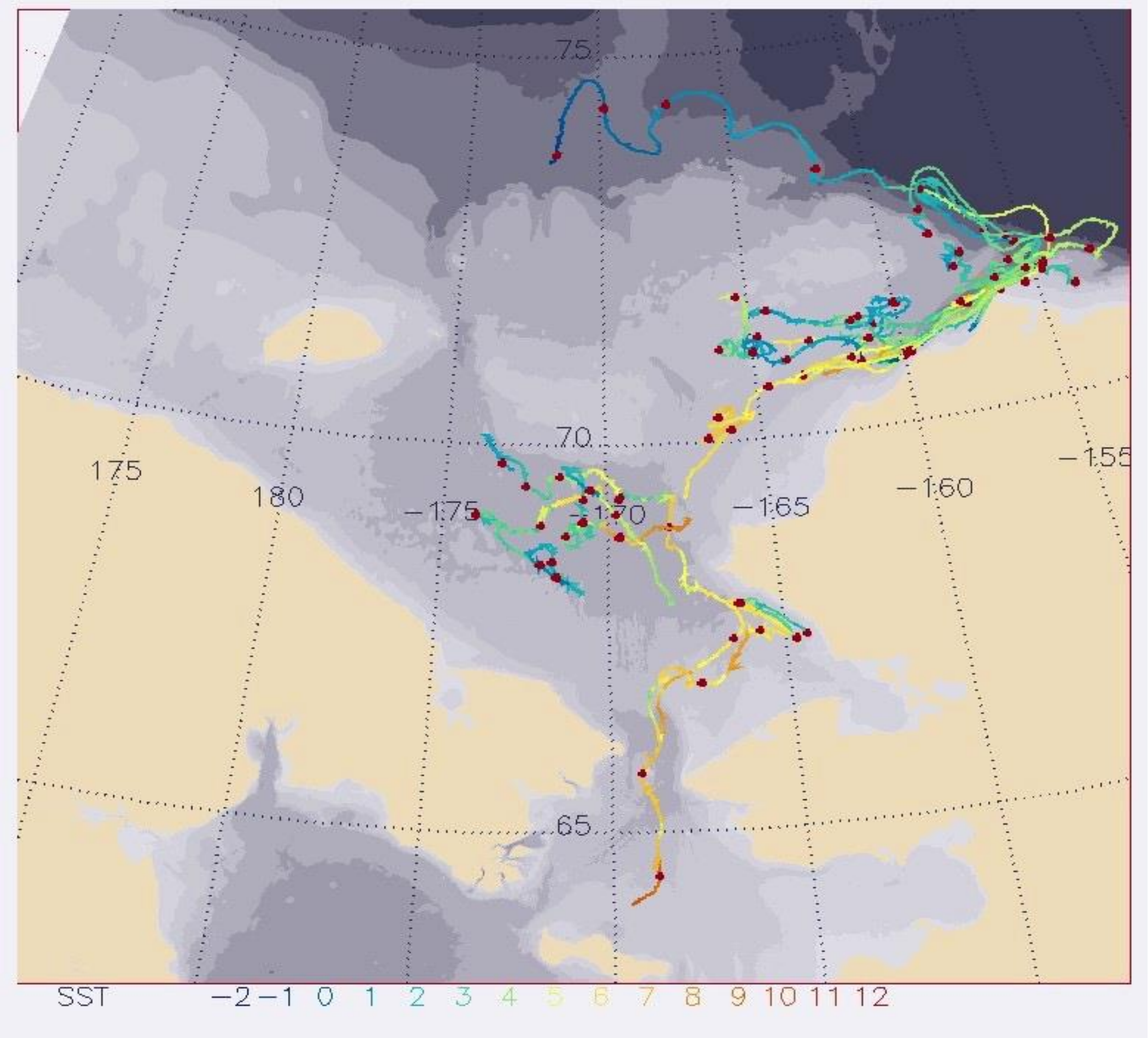

Fig. 9a. Trajectories of Chukchi Sea drifters (12) deployed in 2012.

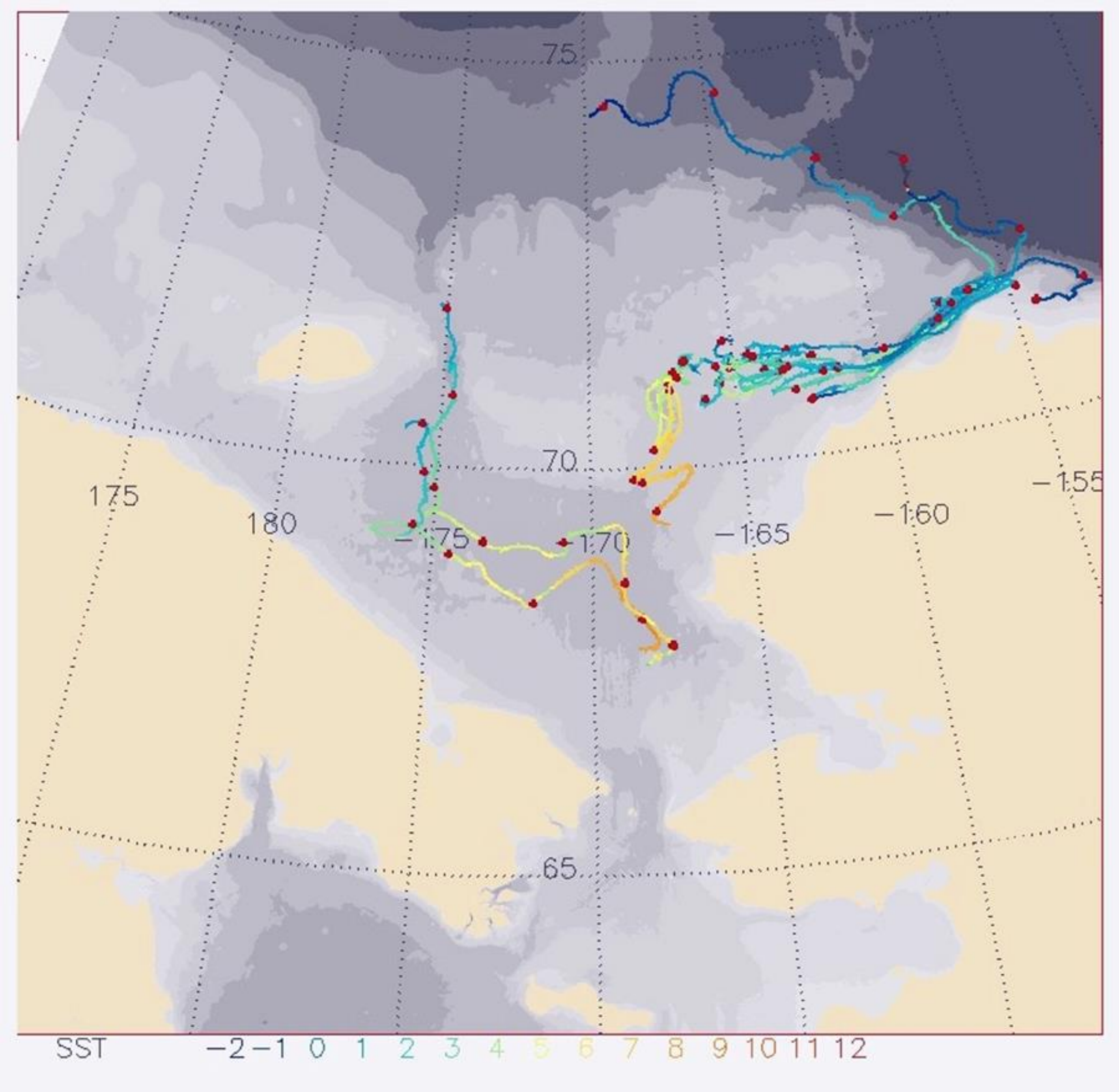

Fig. 9b Trajectories of Chukchi Sea drifters (12) deployed in 2013.

Chukchi Sea drifters deployed in 2012 showed greater advection via Barrow Canyon into the Beaufort Gyre and generally followed previously described Chukchi Sea current patterns (Danielson et al. 2016; Fig 9a). Satellite-tracked drifters deployed in 2013 showed reduced flow into in the Beaufort Gyre and greater retention on shelf in the Alaska Coastal Current (Fig 9b).

The distributions of eggs and larvae of each taxa suggest both **allochthonous** and autochthonous sources of larvae as both species were collected south of the centers of egg production in the Chukchi Sea (Figs 2 a, 3, 4) and transport in both years was clearly northward as evidenced by drifter trajectories (Figs. 9a and b). Adult *L. aspera* of spawning age (4+) have been collected in nearshore areas in the NBS south of Bering Strait during AFSC groundfish surveys (AFSC, unpubl. data) potentially providing a source of eggs and larvae south of Bering strait for transport into the Chukchi Sea.

These patterns in the distribution of eggs and larvae reported here are somewhat different than those observed in other studies mostly because the survey areas were different. In the RUSALCA surveys (2004, 2009, 2012) (Norcross et al. 2010; Busby et al. in prep.) *B. saida* larvae and juveniles were caught mostly near Bering Strait and the Chukchi Peninsula while Arctic Eis cruises found *B. saida* in the eastern Chukchi Sea. Similarly, eggs of *H. robustus* were caught, sometimes in high abundances, near Wrangel Island on RUSALCA surveys while eggs of this species were abundant during 2012 Arctic Eis surveys in the Eastern Chukchi Sea, (Figs. 2a and 2b), however, the survey areas were very different. Similar distributions of *L. aspera* and *H. robustus* larvae in the vicinity of Point hope and Cape Lisburne were seen in both survey programs. The influence of circulation patterns and other physical drivers on the distributions of fish during all life history stages in the Chukchi Sea is currently being investigated by researchers at the AFSC and University of Alaska.

6. Acknowledgements

The authors thank the crew of the *F/V Bristol Explore*r for their efforts and dedication to this project, Arctic Eis Lead Investigator Franz Muter and Project Coordinator Jared Weems. Kimberly Bahl (AFSC) served as data manager. Alexei Pinchuk (UAF) and Wess Strasburger (AFSC) provided assistance throughout. Ann Matarese (AFSC) reviewed an early version of the manuscript and provided numerous helpful comments. Sigrid Salo (PMEL) provided sea ice data and maps.

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Appendix C.

A comparison between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing crops in the northern Bering and Chukchi Seas

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December 9, 2015

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

ACC	Alaskan Coastal Current
ACW	Alaskan Coastal Water
ADFG	Alaska Department of Fish and Game
AFSC	Alaska Fisheries Science Center
Arctic Eis	Arctic Ecosystem Integrated Survey
AtlW	Atlantic Water
AW	Anadyr Water
BOEM	Bureau of Ocean Energy Management
BSSW	Bering Shelf Summer Water
BCSW	Bering-Chukchi Summer Water
BCWW	Bering-Chukchi Winter Water
BSWW	Bering Shelf Winter Water
CIAP	Coastal Impact Assistance Program
CSSW	Chukchi Shelf Winter Water
GPS	Global Positioning System
HFR	High-Frequency Radar
MW	Melt Water
NASA	National Aeronautics and Space Administration
NOAA	National Oceanic and Atmospheric Administration
NSIDC	National Snow and Ice Data Center
PMEL	Pacific Marine Environmental Laboratory
SFOS	School of Fisheries and Ocean Sciences
UAF	University of Alaska Fairbanks
USFWS	US Fish and Wildlife Service
WW	Winter Water

List of Oral and Poster Presentations

Danielson, S., Eisner, L., Ladd, C. Northern Bering and Chukchi Sea Physics, Nutrients, Chlorophyll of Late Summer 2012 and 2013, oral presentation, Arctic Eis meeting, Juneau, AK, June 17-19, 2014.

Eisner, L., Danielson, S., Ladd, C. 2015. Northern Bering and Eastern Chukchi Sea Physics, Nutrients, and Chlorophyll in late summer 2012 and 2013, poster presentation, Polar Marine Science meeting (Gordon Conference), Lucca Italy, March 15-20, 2015.

Martini, K., Stabeno, P., Ladd, C., Winsor, P., Weingartner, T., Mordy, C. Eisner, L. 2015. Dependence of subsurface chlorophyll maxima on seasonal water masses in the Chukchi Sea, poster presentation, Polar Marine Science meeting (Gordon Conference), Lucca Italy, March 15-20, 2015.

Eisner, L. and Farley, E. 2015. The Potential Impact of Loss of Sea Ice on Alaska's Arctic Marine Ecosystems, oral presentation, 6th Symposium on the Impacts of an Ice-Diminishing Arctic on Naval and Maritime Operations, co-hosted by the U.S. National Ice Center (NIC) and the U.S. Arctic Research Commission (USARC), July 14-16, 2015, Washington, DC. This presentation included Arctic Eis oceanography, zooplankton and fisheries data.

Proposed Objectives and Study Chronology

OBJECTIVES

The overall goal of the Arctic Eis study is to contribute to a comprehensive assessment of the oceanography, lower trophic levels, crab, and fish communities of the eastern Chukchi Sea shelf and evaluate results relative to earlier studies in the same area and relative to similar studies in adjacent regions. Specific objectives that relate to oceanography include: Objective 1) Document and characterize the oceanography and the abundance and distribution of pelagic species (surface and midwater) at multiple trophic levels from plankton to fish in the Chukchi Sea lease area during the open water season; Objective 6) Provide a comparison of these communities with that of prior studies in the Chukchi Sea, as well as adjacent regions (Beaufort and Bering Seas), and relate species distributions and abundances to oceanographic water masses; Objective 7) Provide a geodatabase including base maps and attribute tables of marine fish and lower trophic communities. Objective 8) Facilitate collaboration (through a data sharing protocol) for an integrated ecosystem analysis with other researchers including State of Alaska, BOEM, NSF, NOAA, NPRB, and international industry research in the Chukchi Sea and recommendations of USARC.

We believe that we have full filled these objectives by collecting and providing quality oceanographic data to other investigators in a timely easy accessible format, offering assistance with data interpretations throughout the project, and summarizing key findings in poster and oral presentations, quarterly reports and peer reviewed manuscripts.

OCEANOGRAPHIC DATA COLLECTION

In 2012 and 2013, oceanographic data were collected by scientists from the NOAA AFSC Ecosystem Monitoring and Assessment program (EMA) and University of Alaska Fairbanks (UAF). Data were collected at each trawl station in the north Bering and Chukchi seas and at oceanographic stations spaced at 15 nm intervals along transects in the Chukchi Sea. Vertical profiles of salinity, temperature, chlorophyll a fluorescence, light attenuation (beam c), photosynthetic available radiation (PAR) and dissolved oxygen, were obtained from surface to near bottom depths at each trawl station using a conductivity, temperature, and depth meter (CTD) with ancillary sensors (SBE 25 or 9-11 plus CTD, Sea-Bird Electronics, Inc., Bellevue, WA). Only temperature and salinity data were obtained at oceanography stations (FastCat or SBE 19+ CTD). Continuous along-track measurements of surface temperature and salinity were collected using a thermosalinograph (SBE-45). Water samples for nutrients (N, P, Si), chlorophyll a (Chla, total and size fractionated) were collected at the surface and below the pycnocline using 5-L Niskin bottles. Salinity and oxygen samples to calibrate the CTD were collected intermittently. A flooding incident onboard the charter vessel in 2013, led to loss Chla samples for the northern Being Sea in 2013, therefore, these data are missing from our final dataset.

LABORATORY ANALYSIS

Water samples for dissolved inorganic nutrients (phosphate, silicic acid, nitrate, nitrite and ammonium) were filtered through 0.45 µm cellulose acetate filters, frozen at -80 °C on board ship, and analyzed at a shore-based facility within 6-8 months of collection, using colorimetric protocols (Gordon et al., 1994). Chla samples were filtered through Whatman GF/F filters (nominal pore size 0.7 µm) to estimate total Chla, and through polycarbonate filters (pore size 10 µm) to estimate large-size fraction Chla. Filters were stored frozen (-80°C) and analyzed within 6 months with a Turner Designs (TD-700) bench top fluorometer following standard methods (Parsons et al., 1984).

DATA ANALYSIS, DATABASE LOCATION

CTD data were processed within 6 months of collection by Pacific Marine Environmental Laboratory (PMEL) using standard Sea Bird Electronics processing routines. All CTD, nutrient and Chla data were checked for errors prior to upload on the Arctic Eis AOOS portal (as Excel and net cdf files and as maps), for use by other investigators. All data were available prior to the June 2014 Arctic Eis meeting. Data were analyzed and mapped using Matlab and ArcMap (ArcGIS), and statistical analysis were conducted in SYSTAT for more in depth data synthesis (for oceanography manuscripts) by scientists from UAF, AFSC EMA and PMEL.

SUBMISSION OF MANUSCRIPTS

Deep Sea Res. II Arctic Eis special issue (accepted pending minor revision): Danielson, S., Eisner, L., Ladd, C., Weingartner, T., Mordy, C. *In review*. A comparison between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing crops in the northern Bering and Chukchi Seas.

Journal of Geophysical Res. (accepted pending minor revision): Martini, K., Stabeno, P., Ladd, C., Winsor, P., Weingartner, T., Mordy, C., Eisner, L. *In review*. Dependence of subsurface chlorophyll on seasonal water masses in the Chukchi Sea. Some of the Chukchi Sea oceanography, nutrient and chlorophyll a Arctic Eis data were included in this manuscript.

1. Abstract

Survey data from the northern Bering and Chukchi sea continental shelves in August-September 2012 and 2013 reveal inter-annual differences in the spatial structure of water masses along with statistically significant differences in thermohaline properties, chemical properties, and phytoplankton communities. We find that the near-bottom Bering-Chukchi Summer Water (BCSW) water mass was more saline in 2012 and Alaskan Coastal Waters (ACW) were warmer in 2013. Both of these water masses carried higher nutrient concentrations in 2012, supporting a larger chlorophyll *a* standing crop biomass that was comprised primarily of small (<10 µm) size class phytoplankton. The location of phytoplankton biomass concentrations and their size compositions reveal linkages between the wind fields, seafloor topography, water masses, and the pelagic production. We speculate that the decrease in salinity and nutrients from 2012 to 2013 may have been related to an observed decrease in net Bering Strait transport from 2011 to 2012 (Woodgate et al., submitted). The horizontal structure of the shelf water masses, including the strength and location of stratification and fronts, respectively, differed in part because of the August regional wind field, which was more energetic in 2012 but was more persistent in direction in 2013. ACW were found all along the coast from Nunivak Island to Point Barrow in 2012, but in response to the persistent wind of 2013 ACW was not found north of Ledyard Bay. Instead, the 2013 NE Chukchi shelf was flooded with cold and fresh waters derived from ice melt waters (MW) that resided above cold and salty Bering-Chukchi Winter Waters (BCWW). Similarly, in the northern Bering Sea, low-salinity coastal waters from western Alaska were driven offshore to a greater extent in 2013, while in 2012 they were found more confined to shore and more prominently extended northward through Bering Strait. The water mass distributions together with the winds and limited surface current data suggest that the NE Chukchi Alaskan Coastal Current (ACC) was shut down for a

time in August and September 2013. Our results have implications for the fate of fresh water, heat, and pelagic production on the Bering-Chukchi shelves.

2. Introduction

The changing climate and diminishing sea ice impart a cascade of effects upon the sub-arctic and arctic marine ecosystem including species range alterations (e.g. Mueter and Litzow, 2008; Logerwell et al., 2015) and potentially increased access for human activities such as tourism, industrial development, and commercial fishing (Moran and Farrell, 2011; NRC, 2014). Consequently, periodic surveys to document the state of the ecosystem are required to maintain an up-to-date understanding and inform current management and policy decisions. The Arctic Ecosystem Integrated Survey (Arctic Eis) program represents a multi-disciplinary approach to fulfilling such information needs through oceanography, plankton, fisheries, and seabird/marine mammal surveys coupled with a variety of discipline-specific process studies. In the context of the flow field, ice cover, and atmospheric conditions, this manuscript describes physical, chemical, and phytoplankton observations conducted as part of the August-September 2012 and 2013 Arctic Eis ship-based surveys. Our goal is a better understanding of how the currents, ice, and atmosphere affect this region's physical hydrography, macronutrients, and phytoplankton standing stock in August and September. Our observations and analyses will provide a physical and chemical backdrop for the Arctic Eis study and other marine ecosystem studies in conducted in the northern Bering and Chukchi Seas in 2012-2013.

2.1. Oceanographic setting

The northern Bering and Chukchi Sea continental shelf waters and the regional marine ecosystem are all dominated by the influence of the northward-flowing Bering Strait flow field (Fig. 1). This transport is driven by a seasonally fluctuating Pacific-Arctic pressure head (Stigebrandt, 1984; Aagaard et al., 2006) that transmits ~ 1.0-1.2 Sv (1 Sv = 10^6 m^3 s^{-1}) during summer and ~0.5-0.6 Sv during winter months (Woodgate et al., 2005a). The flow field is strongly steered by the coastlines and the seafloor bathymetry on these two expansive (~ 800 km wide) continental shelves. The Bering Strait waters are routed across the Chukchi shelf along three principal conduits: Herald Valley in the west, Barrow Canyon in the east and the Central Channel across the mid-shelf, although wind driven and other fluctuations modify or at times even reverse these flows (Roach et al., 1995; Winsor and Chapman, 2004; Weingartner et al., 2005; Woodgate et al., 2005b; Spall, 2007).

Flow field fluctuations are driven directly by local wind stress (Aagaard et al., 1985), in addition to the remotely driven influences of propagating shelf waves and changing Ekman suction over the North Pacific sub-arctic gyre that alters the Pacific-Arctic pressure head (Danielson et al., 2014). The Bering Strait flow reverses with regularity during winter months, but rarely for more than a week or two at a time (Roach et al., 1995). Other non-steady currents are driven by baroclinic jets associated with the fresh coastal water (Gawarkiewicz et al., 1994; Weingartner et al., 1999), dense polynya water (Danielson et al., 2006) and marginal ice zone (MIZ) meltwater fronts (Lu et al., in revision), and the high frequency tidal and inertial motions . Tidal currents near St. Lawrence Island can exceed 20 cm s^{-1} (Danielson and Kowalik, 2005), but they are much weaker across the Chukchi Sea, where they exceed 5 cm s^{-1} only in Kotzebue Sound and near Wrangel Island (Danielson, 1996). In summer, the Alaskan Coastal Current (ACC) is a low-salinity and warm flow associated with coastal runoff and solar heating of the shallow and turbid nearshore zone (Coachman et al., 1975). All of these fluctuating currents are locally important to the region's biology via their roles in advecting nutrients, mixing subsurface nutrients into the euphotic zone, aggregating prey along convergent fronts, and dispersing passively drifting eggs and larvae.

The northern Bering Sea provides fresh water, nutrients, and organic matter to the Chukchi Sea through Bering Strait (Walsh et al., 1989). Waters from three distinct origins comprise this flow: Anadyr

Waters (AW), Alaska Coastal Waters (ACW), and Bering Shelf Waters (BSW) (Coachman et al., 1975). Typically found along the Siberian coast and the western portion of Bering Strait, AW is relatively saline, cold, and nutrient-rich (Sambrotto et al., 1984). Limited observations (Overland et al. 1996), numerical modeling (Kinder et al., 1986; Overland and Roach, 1987; Clement et al. 2005; Danielson et al. 2012a), and the tracing of water mass characteristics (Coachman et al., 1975) identify the upper slope of the Bering Sea basin as the probable source for AW. The Anadyr Current circumscribes the Gulf of Anadyr in a clockwise fashion, carrying AW to Anadyr Strait, Chirikov Basin, Bering Strait, and thence to the Chukchi Sea. Along the Alaskan coast, relatively low-salinity waters carry the markings of terrestrial discharge (Coachman et al., 1975; Iken et al., 2010) from the Yukon River, the Kuskokwim River, and other numerous smaller drainage basins. Bering shelf water is comprised of a mixture of slope and coastal waters.

The multi-month journey of Pacific-origin waters into the Arctic dictates that the seasonally varying influences of atmosphere-ocean heat fluxes significantly modify these waters en route. In the oceanic heat loss phase of the year (approximately October through April), much of the water on these shallow (< 50 m) shelves cools to and remains near the freezing point from late fall to spring (e.g. Woodgate et al., 2005a,b). Pacific Winter Waters represent an important source for feeding the cold halocline of the Arctic Ocean (Aagaard and Carmack, 1981). The characteristic salinity signature of the AW, BSW and ACW may even be removed through the influence of brine-induced salinization in leads and polynyas in winter and through the influence of sea-ice melt and river discharges in summer. In the oceanic heat gain phase of the year the atmosphere is a net source of heat to the ocean and heat is carried into the arctic by the Bering Strait throughflow. The location and timing of the various heat contributions determines whether it is available to melt ice, influence fall freeze-up, or is subducted into the interior (Shimada et al., 2006; Woodgate et al., 2010; Timmermans et al., 2014).

Critically important to the biology of the northern Bering and southern Chukchi seas is the delivery of high levels of nutrients (e.g., $NO_3 > 10$ uM) to Chirikov Basin, a highly productive region of the shelf (250–300 g C m-2 y^{-1}) (Sambrotto et al. 1984; Grebmeier et al. 1988; Springer 1988; Walsh et al. 1989) that lies ~500 km from the nearest continental slope and deep-water nutrient reservoir. Despite the shallow depths and large transit distance, the AW nutrient flux into Chirikov Basin is maintained by the persistent Pacific-Arctic pressure head (Stigebrandt, 1984) rather than the intermittently persistent wind-forced coastal upwelling that drives the majority of the world's most productive shelf ecosystems (Mann and Lazier, 1991). Flow rates and nutrient fluxes are particularly elevated throughout the long summer season when the Bering Strait transport is at its annual maximum (Woodgate et al., 2005a), winds are weak and stratification strong so flow reversals in Bering Strait are infrequent (Coachman, 1993; Danielson et al., 2014). Nearly 24 hours of sunlight is available to support primary production. As AW are first drawn through the narrow Anadyr Strait and then the narrow Bering Strait, nutrients are presumably delivered to the euphotic zone via mixing induced by the high levels of total kinetic energy, eddy kinetic energy and bottom stress that characterize the current field here (Clement et al., 2005).

In contrast, low levels of surface nutrients, chlorophyll *a* (Chl*a*), and phytoplankton productivity (~ 80 g C m^{-2} y^{-1}) are typically observed in ACW after the spring bloom and associated nutrient depletion (Springer and McRoy, 1993). Farther north in stratified areas of the Chukchi Sea, late summer and early fall surface nutrient depletion and a shallow pycnocline can lead to formation of subsurface Chl*a* maxima with peak values more than an order of magnitude greater than the near-surface concentrations (Cota, 1996; Cotispoti, 2005; Hill and Cota, 2005; Martini et al., in prep). Furthermore, melting sea ice and snow pack through late spring and summer months expose shelf waters to sufficient insolation to fuel new production, even in the presence of ice cover, and both water column and sympagic blooms can commence prior to full ice retreat (Arrigo et al., 2014). Phytoplankton community composition and phytoplankton biomass concentrations also vary among waters masses, with large chain-forming diatoms typically observed within high Chl*a* regions and smaller taxa such as phytoflagellates observed in low nutrient waters outside of the Anadyr plume region (Springer and McRoy 1993).

Against this backdrop of elevated nutrient fluxes, uptake rates and productivity, the study region as a whole is characterized by strong pelagic-benthic coupling resulting from water column production, which often exceeds grazing capacity (Grebmeier et al., 1988) and in turn supports foraging of upper trophic level organisms including seabirds (Hunt and Harrison, 1990), grey whales (Coyle et al., 2007) and walrus (Jay et al, 2012; Jay et al., 2014). Thriving epibenthic and infaunal communities populate nearshore regions, influenced by ACW, such as Kotzebue Sound and Norton Sound (Feder and Jewett, 1981; Feder et al., 2007) and farther offshore where BSW and AW dominate (Feder et al., 2007; Grebmeier et al. 1989; Iken et al., 2010). There exists a series of regional benthic "hotspots" where the deposition fields support benthic communities having biomass that regularly exceeds 15 g m^{-2} (Grebmeier et al., 2015)

Because long-lived benthic organisms are conveniently observable integrators of shifting environmental conditions and top-down feeding pressures, the hotspots represent valuable monitoring sites for detecting the biological impacts of change over time over a range of Pacific sector latitudes (Grebmeier et al., 2006a; Iken et al., 2010). Repeat sampling of these hotspots is the foundation of the international Distributed Biological Observatory (DBO) monitoring program (Grebmeier et al., 2010;

Grebmeier et al., 2015). Within (or near to) the Arctic Eis survey grid, the DBO program includes five monitoring regions: SW of St. Lawrence Island (DBO 1), in Chirikov Basin (DBO 2), in the southern Chukchi Sea southwest of Point Hope (DBO 3), near the southern side of Hanna Shoal (DBO 4) and Barrow Canyon (DBO 5). Consequently, studies that attempt to understand benthic hotspot changes over time need also an understanding of the controls that mediate nutrient availability, pelagic productivity, and other bottom-up drivers.

While numerous oceanographic observations have been collected in portions of this region during the open water season and some even in ice cover, the Arctic Eis survey is perhaps the first set of comprehensive physics-to-fish surveys covering such a large expanse of the northern Bering-Chukchi shelves (U.S. waters only) between Nunivak Island in the central Bering Sea and Barrow Canyon in the NE Chukchi Sea with such a tightly and regularly spaced set of stations. Hence, the data offer an unusual opportunity to examine inter-annual and spatial variations within this region. We characterize horizontal and vertical variations of the thermohaline, macronutrient and Chl*a* distributions, their year-to-year differences, and their co-variability. We show that some of the notable features captured by our measurements can be ascribed to the influence of ice melt, wind forcing, and oceanic circulation.

2.2. Paper organization

Section 2 describes the data collections, model sources, and data handling methods. Results are presented in Section 3, with Sections 3.1-3.3 defining the various water masses, showing their spatial distributions, and examining their spatial and temporal variability, respectively. Sections 3.4 and 3.5 examine the nutrient and phytoplankton data. A discussion of results is in Section 4 and a summary of our findings is in Section 5.

3. Data and Methods

3.1. CTD data and bottle samples

Arctic Eis oceanographic data were collected at stations spaced 28 and 55 km apart, depending on location, over a survey grid that spanned the US northeastern Bering Sea and Chukchi Sea shelves (157-170 °W, 60-72 °N, Fig. 1). Sampling occurred from 7 August – 24 September in both 2012 and 2013, with a similar order of station occupations in both years. Sampling began in Bering Strait on 7 August, progressing northward toward the Chukchi shelf break along zonal transects until 8 September 2012 and

6 September 2013. Sampling recommenced in Bering Strait on 10 September in both years, whereupon the survey vessel worked its way southward to 60 °N during the last two weeks of the cruise.

At the primary stations spaced every 55 km, conductivity-temperature-depth (CTD) measurements were collected with a Sea-bird (SBE) 911 or SBE 25 CTD equipped with a Wetlabs Wet-Star fluorometer to estimate in vivo Chl*a*. A SBE 49 or SBE 19+ CTD towed obliquely with a bongo net for zooplankton sample collection was deployed to obtain hydrographic data at higher spatial resolution (between primary stations) along longitudinal transects in the Chukchi Sea. At the primary stations, water samples for nutrients and total Chl*a* were collected at ~10 m intervals and size-fractionated Chla at two of these depths (10 m and 30 m) during the upcast with Niskin bottles attached to the CTD.

Water samples for dissolved inorganic nutrients (phosphate, silicic acid, nitrate, nitrite and ammonium) were filtered through 0.45 µm cellulose acetate filters, frozen at -80 °C on board ship, and analyzed at a shore-based facility. Measurements were made using automated continuous flow analysis with a segmented flow and colorimetric detection. Standardization and analysis procedures specified by Gordon et al. (1994) were closely followed including calibration of labware, preparation of primary and secondary standards, and corrections for blanks and refractive index. Protocols of Gordon et al. (1994) were used for analysis of phosphate, silicic acid, nitrate and nitrite. Ammonium was measured using an indophenol blue method modified from Mantoura and Woodward (1983). Nutrient samples were filtered through 0.45 µm filters, frozen at -80 °C on board ship and analyzed for dissolved phosphate, silicic acid, nitrate, nitrite, and ammonium at a shore-based facility using colorometric methods (Gordon et al., 1994).

Chl*a* samples were filtered through Whatman GF/F filters (nominal pore size 0.7 µm) to estimate total Chl*a*, and through polycarbonate filters (pore size 10 µm) to estimate large-size fraction Chl*a*. Filters were stored frozen (-80°C) and analyzed within 6 months with a Turner Designs (TD-700) bench top fluorometer following standard methods (Parsons et al., 1984). In vivo fluorescence data, calibrated with discrete Chl*a* samples by fluorometer and year were used to calculate water column integrated Chl*a*. The integrated >10 µm (large) size-fractionated Chl*a* was similarly estimated by multiplying the total integrated Chl*a* from calibrated in vivo fluorescence data by the mean large-size fraction ratio (>10 µm Chl*a* /total Chl*a*) from discrete samples. The integrated <10 µm (small) size-fractionated Chl*a* was estimated by subtraction of the large-size fraction from the total integrated Chl*a*. We used in vivo Chl*a* data for our integrations since discrete Chl*a* samples for a subset of stations in 2013 were accidentally destroyed during a flooding incident onboard-ship; in addition, discrete size-fractionated Chl*a* did not provide sufficient vertical resolution for accurate water column integrations.

Statistical comparisons were conducted to determine significant interannual differences in surface and deep nutrients and integrated chlorophyll for each water mass classification. Surface nutrients were evaluated by surface water mass, deep nutrients by deep water mass, and integrated chlorophyll by each combination of surface and deep water mass found in our survey area. All data were natural log transformed prior to statistical analysis using one-way ANOVAs in SYSTAT.

3.2. Ocean Currents

Ocean circulation observations in the NE Chukchi Sea in 2012 and 2013 included measurements of surface currents via land-based high frequency radar (HFR) stations, surface currents via satellite-tracked drifters, and subsurface currents via taut-wire oceanographic moorings. We used a selection of these data to characterize the flow field in the northernmost portion of the Arctic Eis survey.

CODAR, Inc. long-range (5 MHz) Seasonde HFR stations were deployed at Barrow, Wainwright, and Pt. Lay. HFR data grids were processed on an hourly basis, but diurnal ionospheric activity at this latitude resulted in reduced data coverage for a portion of each day. Because of this, the HFR data were binned into daily averages. HFR processing for these data are described in Weingartner et al. (2013). Data were collected from all three sites through August and September 2012. Equipment difficulties in

2013 resulted in a week of missing data from Barrow and delayed Point Lay data collection until 28 August.

Pacific Gyre MicroStar satellite-tracked surface drifters were programmed to collect hourly or half-hourly Global Position System (GPS) fixes. The MicroStars employ a cross-shaped sail tethered 1 m below the surface. Data were screened for GPS quality and indications of missing drogues, although none of the drifters incorporated a drogue sensor. Other deployments of MicroStar drifters that did incorporate drogue sensors suggest that drogue loss can become a problem after 2 or 3 months. For this paper we present data only from within the first month after deployment and we assume that drogue loss during this time is minimal. Drifter data examined herein include 36 drifter tracks in 2012 and 52 drifters in 2013.

A mooring was deployed at site BC2 (70.9 °N, 159.9 °W)(Fig. 1) for both 2012 and 2013, although the battery died prior to recovery in both years, truncating the record before the Arctic Eis surveys. Nevertheless, the mooring data from the months leading up to the survey reveals aspects of the flow field and its influence on preconditioning the shelf waters sampled during August and September. The BC2 mooring provides a record of the flows up and down Barrow Canyon (Weingartner et al., 2013b).

3.3. Meteorological data

A moored meteorological buoy was deployed seasonally offshore from Pt. Lay in both 2012 and 2013 near 166.1 °W, 70.0 °N. The Pt. Lay mooring was deployed on August 10th in 2012 and on August 1st in 2013 and recorded into October in both years. Measurement parameters include air temperature, water temperature, solar radiation, and atmospheric pressure. A second buoy, named the Klondike buoy, was deployed near 165.3 °W, 70.9 °N and measured significant wave height and direction from August 21 into October in both years. Hourly observations were transmitted in real time to UAF and converted to engineering units using factory calibration coefficients.

Nominally hourly weather conditions (wind speed and direction, air temperature, relative humidity, atmospheric pressure, sky cover) recorded at the Barrow airport were obtained from the National Climate Data Center (http://www.ncdc.noaa.gov/). All data were error-checked for sensor spikes, stuck readings and other obviously erroneous data. These data are part of the long-term weather record at Barrow, which extends back to 1920 for temperature and sea level pressure and back to 1936 for winds.

3.4. Passive microwave sea ice concentrations

Satellite-based sea ice concentration data from 1979-2014 were downloaded from the National Snow and Ice Data Center (NSIDC) archive of the Goddard Space Flight Center NASA team dataset (http://nsidc.org/data/docs/daac/nsidc0051_gsfc_seaice.gd.html). These data were collected on the Nimbus-7, DMSP-8, -F11, -F13, and -F17 satellites and reported on a nominally 25 km grid (Cavalieri et al., 1996). Data were collected after July 1987 on a daily basis, while data before this were collected every other day. We linearly interpolated the earlier records to daily intervals.

3.5. Streamflow

Quality-controlled river discharge records for 2012 and 2013 were obtained from the USGS on-line database for the Yukon River Pilot Station monitoring site located at 61°56’04”N, 162°52’50”W (http://waterdata.usgs.gov/nwis/inventory?agency_code=USGS&site_no=15565447). These data required no additional processing.

4. Results

Although the two surveys are not synoptic, the success of the Arctic Eis program in occupying the same stations with nearly identical day of year timing in the two field efforts provides a remarkably consistent dataset for inter-annual comparison. Sections 3.1-3.3 describe the 2012 and 2013 similarities and differences in the regional atmospheric, ice, and circulation fields. The physical and chemical hydrography and the Chl*a* biomass are described in 3.4-3.6.

4.1. Sea Ice

The range of satellite-observed daily ice concentrations for two 17-year intervals, 1979-1996 and 1997-2014, along with the envelope that contains the overlap in range are shown in Fig. 2a. This depiction ignores regional spatial heterogeneity (Frey et al., 2015) but emphasizes extreme events that push the regional ranges to new daily highs and lows. May-November tends to contain mostly ice concentration minima during 1997-2014 and mostly maxima during the earlier period (1979-1996), revealing the tendency for earlier retreat and delayed onset in recent years (Stroeve et al., 2011). The lack of ice between spring and fall during the latter period is highlighted.

The length of time to transition from ice-covered to ice free conditions in the spring and then from ice-free to ice-covered conditions in the fall is potentially important physically and biologically. Temporal trends in the transition length for the study region are shown in Fig. 2b, with recent years showing a spring transition that occurs nearly 30 days more quickly and a fall transition that occurs nearly 40 days more quickly. The trends in each case are significant at the 99% level ($p < 0.001$), with $r^2 = 0.30$ and 0.29 for spring and fall, respectively.

Fig. 2a also shows that although 2012 and 2013 each exhibited multiple instances of daily record high ice concentration in winter, these anomalies did not persist into the following summers. Presumably, the ability for the system to shift so rapidly reflects the loss of ice mass through net ablation and thinning of the ice pack (Kwok and Rothrock, 2009). While ice concentrations in April and May were generally higher than average in both 2012 and 2013, both years displayed concentrations well below normal by the end of June. The passive microwave satellites reported ice-free waters by mid August in both years (Fig. 2a). As a caution to interpretation, however, the Arctic Eis survey vessel did encounter appreciable ice in the northern portion of the study grid that kept the vessel from working at a number of planned stations (compare 2012 and 2013 panels in Fig. 1 for locations of stations sampled north of

70 °N). In 2013, ice was found consistently at locations on the northern shelf that were more than about 200 km from shore. In August 2012, ice was near Hanna Shoal, including a very large piece (tens of km^2 in area) of thick ice that grounded atop of Hanna Shoal during the winter. The tendency for passive microwave satellites to under-estimate ice cover in regions of sparse and wet ice (Polashenski et al., 2012) thus mandates an appreciation of this platform's limitations and a nuanced interpretation of its data.

4.2. Atmospheric conditions

Average monthly sea level pressure patterns (Fig. 3) reveal strongly contrasting wind fields in the two field years, particularly in August. In August 2012, low pressure was observed over the northwestern Chukchi Sea leading to southwesterly (winds from the southwest) flow over our study area. By September 2012, a low was positioned over western Alaska and the southeastern Bering Sea, leading to northeasterly winds over the Chukchi Sea. In 2013, zonally elongated low pressure patterns were present over the Bering Sea (August) and Gulf of Alaska (September), promoting more zonal easterly flow over the Chukchi. These broad directional patterns were also observed at the surface in Barrow, manifesting as differences in wind direction steadiness. For example, station PABR recorded 100 hourly observations (~4 days in total) of winds blowing into the SW sector between 180 °T and 270 °T during August 2012, whereas in August 2013 the winds blew into this sector for 383 hours (more than half of the month). PABR recorded 306 hourly observations of winds blowing into the SW sector in September 2012 while September 2013 recorded 377 observations.

In addition to differences in wind direction, the August 2012 mean wind speed (WS) recorded at Barrow was 1 m s^{-1} higher and with larger standard deviation (σ) than August 2013 (WS_{AUG12} = 5.52 m s^{-1}, σ_{AUG12} = 2.55 m s^{-1}; WS_{AUG13} = = 4.56 m s^{-1}, σ_{AUG13} = 1.99 m s^{-1}), reflected in longer durations of strong winds (2012 recorded 379 hourly observations of wind speed >= 5 m s^{-1}, while August 2013 recorded only 223). Like the wind directions, September 2012 and September 2013 wind speeds were quite similar to each other (WS_{SEP12} = 5.23 m s^{-1}, σ_{SEP12} = 2.54 m s^{-1}; WS_{SEP13} = 5.56 m s^{-1}, σ_{SEP13} = 2.58 m s^{-1}).

The Pt. Lay surface meteorological buoy shows that August 2013 winds were directed more to the west and south, carrying cool air temperatures above warmer sea surface temperatures (Fig. 4). There was more incident solar radiation in August 2013 (fewer clouds), while 2012 had deeper dips in the recorded atmospheric pressure record. Over the August 21 to September 30 interval, the Klondike mooring recorded more large (> 3 m) swells in 2012, which were present for about 15% more of the time in this year. In accordance with the inter-annual differences in wind direction observed by the mooring and at station PABR, the dominant wave direction in 2013 favored wave propagation from the ENE octant, whereas the waves in 2012 were more evenly distributed from the NNW, NNE and ENE octants.

4.3. Currents

The pronounced differences observed in the wind field were reflected in the oceanic response of near-surface currents as measured by surface 1-m drogued drifters and the HFR, despite spatial and temporal data gaps that hinder interpretation of both sets of measurements.

On average, surface velocities in August 2012 as measured by the HFR (Fig. 5) exhibited a strong ACC in the vicinity of Barrow Canyon with northeastward flow over the entire region. There was particularly strong eastward flow in the region bounded by the coast, 162 °W, and 71.5 °N. In September 2012, when northeasterly winds prevailed the mean flow reversed to the southwest, but was generally weak. The mean August 2013 HFR record (biased by missing data) indicated a weak ACC flowing to the northeast and northwestward flow over Hanna Shoal. September 2013 winds reversed the flow along the coast and waters over the shelf offshore of Barrow Canyon flowed toward the northwest.

In 2012, drifters deployed offshore near 70.5 °N, 164 °W progressed toward the Alaskan coast between 11 August and 30 August (Fig. 6). Drifters deployed close to shore (< 15 km from shore) were caught in the coastal flow and accelerated eastward into Barrow Canyon. On August 30 and 31, upwelling-favorable winds reversed the shelf flow and many drifters moved westward for about a week, after which the currents reverted to their initial direction and drifters close to Barrow Canyon were swept into the ACC. Upon reaching the slope region, drifters that moved down Barrow Canyon either turned to the northwest, turned east onto the Beaufort Sea shelf, or moved off the shelf and into the basin. In contrast, the 2013 drifters primarily headed to the west and the south and none of the 2013 drifters left the shelf via Barrow Canyon in August or September. Many of the 2013 drifters wound up beaching on the Chukchi's Siberian coastline.

Currents earlier in the year preceding the Arctic Eis cruises also exhibited contrasting flow regimes that likely influenced the winter and spring hydrographic conditions at least on the NE Chukchi shelf. Mooring BC2 located near the head of Barrow Canyon recorded no net flow in the along-canyon direction (not shown) for the 4-month interval January-April 2012. In contrast, from the last week of December 2012 through mid-March 2013 the flow was nearly continuously *up-canyon*. Associated with this flow reversal at times was, at times, an extensive coastal polynya that was captured by the passive microwave satellite as an ice concentration minimum that extended from Point Barrow southward past

Point Hope and over 100 km offshore. In both years, flow between the start of May and mid-July was primarily down-canyon, i.e., toward the basin.

4.4. Physical hydrography

In this section, we examine CTD data in order to further characterize the physical environment within the 2012 and 2013 surveys by defining the water masses, describing their spatial distributions, and contrasting features of interest within each year.

4.4.1. Water Mass Identification

Examining all 1-db averaged T/S measurements from the two cruises, we subjectively parsed the data into five bounding boxes (Fig. 7 and Table 1) that encompass all observed water types, including eight distinct water masses: Alaskan Coastal Water (ACW), Anadyr Water (AW), Bering Sea Summer Water (BSSW), Bering Sea Winter Water (BSWW), Chukchi Sea Summer Water (CSSW), Chukchi Sea Winter Water (CSWW), and Atlantic Water (AtlW). On the Bering shelf, BSWW is commonly referred to as “cold pool” water (e.g., Takenouti and Ohtani, 1974), although an upper temperature bound for cold pool waters is often taken at 2 °C (e.g., Stabeno et al., 2002). For the purposes of this study, we often refer to aggregate water masses that encompass the AW/BSSW/CSSW and BSWW/CSWW water types as Bering-Chukchi Summer Waters (BCSW) and Bering-Chukchi Winter Waters (BSWW), respectively.

In some instances we do need to distinguish between the constituent water masses that comprise the BCSW and BCWW aggregates because of different locations, time histories, and the different roles that they play in the ecosystem. For example, BSWW and CSWW are both cold remnants of the previous winter’s heat loss but at summer’s end they lie hundreds of kilometers to either side of Bering Strait. Similarly, AW, BSSW and CSSW are indistinguishable here based on their T/S properties alone. AW are generally known as the saline nutrient-rich waters delivered across the Gulf of Anadyr to Bering Strait (Coachman et al., 1975). BSSW and CSSW can achieve the same T-S properties as AW through the cycles of freezing, brine rejection, and then summer warming, but they lack the important slope-derived AW nutrient load.

For water masses named by one end member only (e.g., MW and AtlW), we caution that interpretation of habitat or other features based on the names alone can be misleading. For example, the influence of Atlantic Waters (AtlW) is identified by the tightly clustered line of points that trends away from the near-freezing winter waters for salinities greater than about 33.5. Of course, all points lying along such a mixing line would have contributions from both the CSWW and AtlW end members, but the relative fractions vary inversely with distance along the mixing line and waters with salinity closer to 33.5 are comprised of more CSWW than AtlW.

4.4.2 Water mass distributions

Because the two cruises occupied most stations on nearly the same year-day, inter-annual differences in water mass extents reflect year-to-year differences in the forcing and/or circulation. Distributions of the water masses in each year are mapped in Fig. 8. Fig. 9 shows maps of averaged near-surface (0-10 m) and near-bottom (within 5 m of each CTD cast’s deepest depth) temperatures and salinities. Fig. 10 includes maps of surface-to-bottom density differences to show the average water column stratification and the magnitude of the horizontal density gradient to show the location of near-surface and near-seafloor fronts.

The one station having AtlW was located at the mouth of Barrow Canyon at an upper slope station that was occupied in 2013 but not in 2012. The maximum CTD depth recorded in 2012 was 88 m, while in 2013 the CTD reached 274 m at the station with AtlW.

ACW were observed close to shore from Nunivak Island to Point Barrow in 2012 but in 2013 only as far north as Ledyard Bay. These data support the drifter and HFR suggestions (Section 3.2) of an ACC that was mostly absent from the NE Chukchi Sea during the 2013 cruise. It appears that the ACW was able to round C. Lisburne but not progress appreciably farther along the coast in 2013. Examination of satellite imagery suggests that Ledyard Bay is often the site of a recirculation cell where a portion of the ACC flow stalls, while the Point Hope and Cape Lisburne promontories and associated bathymetry commonly deflect some of the ACC offshore. Farther south in the Bering Sea, ACW spread at least 100 km farther offshore from the Yukon-Kuskokwim Delta in 2013, occupying most of the surface mixed layer. Together these observations show strongly contrasting ACW behaviors and pathways during the two Arctic Eis surveys in both the southern and northern portions of the survey.

The BCSW range of properties were found at most stations, with exceptions at some coastal stations having only ACW and at some stations occupied instead by only MW and WW in the very northernmost portion of the survey grid. Although ACW was absent from the northwest Alaskan coast in 2013, CSSW was located at half a dozen stations adjacent to the coast between Point Lay and Barrow. Along with the greater penetration of ACW into the northern Chukchi Sea in 2012, the northern edge of the CSSW was farther north in 2012 than in 2013. Even in 2012, however, relatively few stations with CSSW were found near Hanna Shoal, a known area of flow stagnation (Martin and Drucker, 1997). Instead, particularly in 2013, we observed MW overlying BCWW near Hanna Shoal. Between St. Lawrence and Nunivak Islands, the presence of ACW and BSWW in layers of at least 10 m thick each (Fig. 8) mostly displaced or precluded any BSSW here in 2013, which occupied only a 1-3 m thick layer at eight stations (and could have been the result of mixing between the upper and lower layers). No BSSW was observed in Norton Sound in 2012 although we did observe it at three stations along the north shore of the Sound in 2013. Comparison of the BCSW properties shows that the 2013 salinities in the northern Chukchi Sea were appreciably less saline than in 2012 (despite the large and long-lived 2013 mid-winter polynya). The primary mixing line about which most data points are clustered (through the BCSW box in Fig. 7 that runs between the ACW and BCWW boxes) shows a salinity offset of about -0.5 in the 2013 data.

MW were confined solely to the northern and northeastern Chukchi shelf. In 2012 they were located mostly offshore, while in 2013 they extended all the way to the NW Alaskan coast, occupying stations at which we might have expected ACW instead. Sea ice prevented access to the farthest northwest corner of the planned survey grid in 2013 but based on the maps shown in Fig. 8, we may infer that CTDs at these missed stations would have found MW and CSWW, and possibly a contribution from CSSW. The theta-S diagrams shown in Fig. 7 show a much larger number of MW observations in 2013 relative to 2012. Along with ACW in Norton Sound, MW over Hanna Shoal contributed to the strongest levels of vertical stratification observed in the survey (Figure 10).

CSWW were confined to the northeast Chukchi Sea but with a somewhat greater lateral extent (50-150 km) to the south and west than the MW. In the Bering Sea, we found BSWW at seven stations south of St. Lawrence Island in 2013 and at one station in Chirikov Basin in 2012. Along with the 2012/2013 differences in salinities and currents noted above, these data also suggest that the northern Bering and Chukchi shelf of 2013 may have experienced less (or different) flushing between winter's end and the cruise than during the same time period in the prior year. A striking example is seen in Fig. 7 between the sigma-theta 26 and 27 isopycnals, in which we see considerably denser waters on the northern Chukchi shelf in 2012. This stands in contrast to the extended upcanyon flow observed at mooring BC2 in the middle of the 2013 winter, from which we might have expected that the low ice concentrations would have promoted greater polynya activity and shelf densification. We do observe more CSWW data points within the 2013 BCWW box, but the salinity is lower on average.

At a number of stations north of 70 °N we found MW, CSWW and CSSW all present in the same water column in both years. MW is always the least dense water mass of the three and CSWW typically underlies CSSW. These intrapycnocline occurrences of BCSW between the other two water masses may be the result of subducting BCSW as described by Lu et al. (in press).

4.4.3 Descriptive physical hydrography

In the northern Bering Sea south of St. Lawrence Island and in Norton Sound, surface waters were warmer (by ~2 °C) and near-bottom salinities were fresher (by ~ 0.5) in 2013 than in 2012 (Fig. 9). Near bottom temperatures in 2013 were warmer inside the ACW front and cooler offshore, including the seven stations at which BSWW was observed. Although the station spacing did not well resolve the frontal structure, year-to-year differences in the horizontal density gradients suggest differences in the location and strength of the ACC jet (Fig 10). South of

St. Lawrence Island we find primarily ACW characteristics lying above BSWW (Figure 8); the front near the seafloor primarily separates these two water masses without BSSW between.

Vertical stratification was weak in both years in Chirikov basin, just north (downstream) of Anadyr Strait (Fig. 10). Chirikov Basin was somewhat fresher during the 2013 survey both at the surface and at depth, although temperatures were similar to those of 2012 (Fig. 9). This area is strongly influenced by the Anadyr Water flowing past the western side of St. Lawrence Island and multiple processes may have contributed to the observed differences (e.g., water pathways, degree of topographic or wind-induced mixing, flow rates and bottom friction). The lower salinities in 2013 are consistent with an offshore transport of coastal waters that would conform to the winds associated with the sea level pressure patterns shown in Fig. 3. On the other hand, the salinity difference stands in contrast to the greater 2013 net Bering Strait annually averaged (Woodgate et al., submitted), which might have suggested a greater flow of the more saline AW.

Coastal waters were appreciably warmer in 2013 between Nunivak Island and Ledyard Bay (Fig. 9). However, salinities just north of Bering Strait were much fresher in 2012 than in 2013 both near the surface and near the bottom except for at the stations along the US-Russia Convention Line. These data suggest that the Yukon discharge was mostly trapped in Norton Sound or was spread to the west and south in 2013, while the runoff was able to leak out of Norton Sound and along the eastern shore of Bering Strait into the Chukchi Sea in 2012.

Waters in Norton Sound were very fresh ($19 < S < 30$) in both years even below the surface mixed layer, reflecting the local influence of the massive freshwater input from the Yukon River (~ 200 $km^3 yr^{-1}$ on average (Aagaard et al., 2006)) and the long local residence time suggested by a very few oceanographic drifters deployed in coastal waters on the Bering shelf (T. Weingartner, pers. comm.; also see www.ims.uaf.edu/drifters/). Peak Yukon River discharge measured at Pilot Station occurs in June, and then slowly tapers off through October. Using recent and historical USGS streamflow data from Pilot Station, we found that June 2013 exhibited one of the highest discharges on record for this month, 20,100 $m^3 s^{-1}$, 25% higher than the mean climatology of 16,200 $m^3 s^{-1}$ (σ = 3,240 $m^3 s^{-1}$). The 2012 discharge (17,700 $m^3 s^{-1}$) was also higher than the June climatology but within one standard deviation of the mean. Both the 2012 and 2013 total discharges were within one standard deviation of the climatological discharge for July – August.

The warm and fresh signature of the ACW follows the Alaskan coast from Norton Sound to Bering Strait and north toward Barrow Canyon. In 2012, near surface temperatures and salinities clearly show the influence of this current all the way to Barrow Canyon (Fig. 9) and the surface and bottom fronts were coincident with each other (Fig. 10). In 2013, the warm water appears to pool and spread offshore at ~70°N (Ledyard Bay), a cold and salty (both surface and bottom) mass of water resides near the shoreline north and east of Icy Cape, and the surface and bottom fronts were not coincident. Northeastward transport calculated from moorings deployed off of Icy Cape was much weaker than average during August 2013 while August 2012 transport was closer to a 5-year climatology (Stabeno, et al., in prep). The CSWW and MW near to the coast in 2013 is consistent with coastal upwelling of subsurface waters due to offshore Ekman transport and/or upwelling of cold waters from deeper in Barrow Canyon.

Relative to 2013, saltier waters were found in near-bottom waters across much of the 2012 survey (Fig. 9 and Table 2). A widespread change of salinity could be due to greater fraction of AW occupying Chirikov Basin, greater ice production and shelf water salinization during the previous winter, a reduced influence of melt water mixed over the water column, or less lateral exchange with fresh coastal waters. To the extent that higher salinity waters carry higher dissolved nutrient loads, there exists potential for these two years to support contrasting levels of biological production. In Section 3.5 we examine the nutrient data.

4.5. Nutrient hydrography

Macronutrient distributions exhibited year-to-year differences in both the surface (Fig. 11 and Table 2) and near-bottom (Fig. 12 and Table 3) layers.

In 2012, surface nitrate was low to moderate (< 4 µM) except at five stations in Chirikov Basin, where concentrations reached as high as 20 µM (Fig. 10). Surface nitrate concentrations of 1-4 µM (near and slightly above limiting levels for phytoplankton growth) were observed at eleven stations within 200 km (both north and south) of Bering Strait. Surface silicate (SiO_4) was generally higher inshore than offshore (4-24 µM inshore and 0-8 offshore), although the highest value (38 µM) was observed just south of Bering Strait at the station that also had highest surface nitrate. Silicate-enriched surface waters (> 15 µM) were found in Norton Sound, Bering Strait, and in-between these areas. Surface phosphate was generally lower in the Chukchi Sea and higher in the northern Bering Sea, while the reverse was true for surface ammonium. Ammonium is a reduced and preferential nitrogen source for phytoplankton growth (Dortch, 1990), and in 2012, near-surface ammonium concentrations > 1 µM were common from just south of Bering Strait to the northernmost stations in the Chukchi Sea.

At near bottom depths, higher nitrate levels were observed in the colder, higher salinity BCWW and BCSW water masses, relative to the generally (but not exclusively) nitrate-deplete shallower stations near the coast (Figs. 8, 12). Near-bottom nitrate concentrations exceeding 10 µM were observed at a total of 12 stations in 2012, and these were located in Chirikov Basin, Bering Strait, offshore of Point Hope, and along the northern edge of the 2012 survey. Near-bottom $Si0_4$ was also elevated at these stations, as well as at the northernmost sites that also contained high near-bottom nitrate concentrations. With some exceptions, near-bottom ammonium was relatively high (> 1 µM) in the Chukchi Sea and Chirikov Basin and relatively low (0-1 µM) in Norton Sound and south of St

Lawrence Island. Similarly, the highest near-bottom phosphate (> 1 µM) were located in Chirikov Basin and the Chukchi Sea.

Despite a few similarities, in 2013 the nutrient fields did not closely resemble those in 2012 and many of the differences align with the different water mass distributions described above (Figs. 9 -12; Tables 2 and 3). Surface nitrate was very low (< 2 µM) in 2013 at all but two stations in Chirikov Basin at 64.5 °N and one at the head of Barrow Canyon at 70.5 °N. Surface silicate ranged from 0.2 to 30 µM with the highest values observed in Norton Sound. Surface ammonium was low (< 2 µM) at all stations except for the nearest-to-shore station at 70.5 °N at the head of Barrow Canyon. Surface phosphate was also elevated (> 1 µM) at this Barrow Canyon station relative to those nearby, and at one station in Chirikov Basin. High near-bottom nitrate (>10 µM) was seen in the colder, higher salinity water masses (Chirikov Basin, southwest of Point Hope, and the northernmost region near Hanna Shoal and Barrow Canyon). The high NO_3 values found here in the CSWW were also associated with relatively elevated levels of NH_4, SiO_4, and PO_4. Bottom silicate was highest in Norton Sound in 2013, at one station in Chirikov Basin with AW, and at the same northernmost stations with high bottom nitrate.

For the 38 Chukchi Sea stations sampled in both years, no systematic difference was found in the integrated nitrate concentrations but relative to 2013, 2012 had significantly more water column ammonium, phosphate, and silicate (significant at the 99%, 90%, and 99% levels, respectively) (Tables 2 and 3; Fig. 13). This result is consistent with the 2012 higher salinities described above in Section 3.4. Nutrient limitation of phytoplankton growth in near-surface waters may have been considerably more widespread in 2013 than in 2012 because more stations had non-limiting levels of NO_3, NH_4 and SiO_3 in 2012 (Fig. 11).

Interannual comparisons indicate that nutrient concentrations also varied significantly between years within water mass classifications. Surface NH_4 and PO_4 were significantly higher in 2012 for all three surface water mass classifications MW, BCSW, ACW (Table 2). In addition, SiO_4 was higher in MW and BCSW, and NO_3 was higher in MW. Bottom nutrients (PO_4, SiO_4, NO_3, NH_4, NO_2) and bottom salinity were significantly higher in 2012 than in 2013 in the BCSW (Table 3), due to differing inputs of the constituent water masses (AW, BSSW, CSSW). There were also more stations having BCSW near the seafloor in 2012 than in 2013 (Fig. 7). Bottom NH_4 was significantly higher in ACW in 2012 (Table 3). In the next section, we will show that these variations in the nutrient loads were also associated with detectable changes in the phytoplankton.

4.6. Chlorophyll *a*

In 2012, near-surface Chl*a* from discrete samples (Fig. 14) was highest (5-14 mg m^{-3}) at Chirikov Basin stations with high nitrate and silicate concentrations (Fig. 10). Fig. 13 also shows moderate (1-2 mg m^{-3}) 2012 Chl*a* levels across most of the northern Bering Sea, in a plume emanating northward toward Point Hope from Bering Strait, and at coastal stations located northeast of Cape Lisburne. Relatively high (2-12 mg m^{-3}) subsurface Chl*a* at 20 or 30 m depth was seen at some offshore locations near Point Hope, between 70 °N and 72 °N over Hanna Shoal, and at two stations along 71°N (data not shown). Integrated Chl*a* was highest (> 100 mg m^{-2}) in Chirikov Basin, Bering Strait, one station southwest of Point Hope and two stations over Hanna Shoal (Fig. 15). Relatively high integrated Chla (50-100 mg m^{-2}) was found at several other stations in Chirikov Basin and Hope Basin. Low integrated Chl*a* (< 25 mg m-2) levels were present offshore between 68 and 72.5 °N where three of these stations had very low Chl*a* (< 10 mg m^{-2}).

In 2013, similar to 2012, discrete Chl*a* near the surface was elevated in the DBO-3 region (Fig. 14). Discrete sample Chl*a* data were not available south of Bering Strait in this year; however Chla from calibrated in vivo fluorescence measurements (data not shown) indicated high surface Chl*a* in Chirikov Basin at stations with relatively high surface nutrients and high integrated Chl*a*. Subsurface chlorophyll maxima were observed at ~ 25-30 m depths over Hanna Shoal (data not shown) in locations with integrated Chl*a* of 26-50 mg m^{-2}. Chirikov Basin and SW of Point Hope encompass DBO transects with a documented history of high primary production, phytoplankton standing crop, and benthic biomass (Grebmeier et al., 2015). Relatively high integrated Chl*a* was also seen offshore in the southern part of the survey grid (Fig. 15). The lowest Chl*a* (< 10 mg m^{-3}) was observed offshore at 70 to 71.5 °N and at several near-shore stations south of 71 °N.

For stations occupied in both years, the average integrated Chl*a* was significantly lower in 2013 than in 2012 ($p < 0.05$) (Fig. 15). In particular, there was significantly lower integrated Chl*a* in 2013 at stations with ACW throughout the water column or at stations with ACW overlying BCSW (Table 4). For both years combined, there was significantly more integrated Chl*a* at stations having the BCSW bottom water mass than ACW or CWW ($p = 0.020$).

Small phytoplankton made up the majority of the Chl*a* biomass in the Chukchi Sea in 2012, comprising at least 70% of the biomass at two-thirds (43/61) of the stations. In contrast, in 2013 fewer than half (24/54) of the stations had more than 70% small phytoplankton. Integrated large fraction Chl*a* was very low (< 10 mg m^{-3}) at most stations north of 69 °N in 2012, whereas low to moderate large integrated Chl*a* (11-25 mg m^{-3}) was seen near Hanna Shoal in 2013; note that large and small Chl*a* concentrations were similar. While BCSW covered much more of the NE Chukchi shelf in 2012, 2013 was a year with more extensive pools of MW and nutrient-rich CSWW. The percent large size phytoplankton (>10 µm/total Chl*a*) were highest (> 50% large) offshore of Kotzebue Sound (DBO3 region) in both years, suggesting that large taxa, such as diatoms or dinoflagellates, may make up a greater portion of the total Chl*a* at this location, and particularly in 2013.

In contrast to a Chukchi shelf system dominated by small phytoplankton in 2012, large phytoplankton dominated at about half of the Bering Sea stations (particularly near Nunivak Island), even though the Bering Sea stations were occupied after those in the Chukchi Sea. Low to moderate concentrations were found in both large and small fractions at most Bering Sea nearshore (ACW) stations.

Taking the observations of Section 3.6 together, our interpretation is that year-to-year differences in the location, magnitude and composition of the phytoplankton community can be partially attributed to water mass distributions and their associated nutrient loads. However, the classical assumptions that larger phytoplankton would be associated with higher nutrient levels and higher biomass do not hold in these two years.

5. Discussion

The character of the currents, air-sea interactions, and water properties on the Chukchi shelf depends on wind velocity and wind persistence (e.g., Weingartner et al., 2005; Woodgate et al., 2005b). While August 2012 had stronger winds than August 2013, the latter were more directionally polarized, with nearly half the month experiencing wind that blew toward the south and southwest. In response, ACW was not found north of Ledyard Bay in the 2013 Arctic Eis survey. The 2013 winds forced surface waters and satellite-tracked drifters westward and likely promoted a several week period of upwelling in Barrow Canyon.

The ramifications of temporarily redirecting the more typical coastal flow pathway for multiple weeks at a time are not clear, but there exists potential for both physical and biological consequences (see, for example, papers in this volume by Marsh et al., Pinchuk and Eisner, and Sigler et al.). Deposition of shelf-origin organic matter feeds benthic hotspots near Hanna Shoal and Barrow Canyon, and reorganization of the shelf flow also suggests that a different, and quite possibly lesser flux of carbon would have been deposited. However, one region's loss may be another region's gain. If the Bering Strait throughflow is uncoupled from winds that locally reverse the Barrow Canyon flow (an assumption that likely fails at least on occasion) then it would appear that a greater fraction of the Bering Strait throughflow was probably directed northwestward along the Siberian Shelf toward Herald Canyon and possibly Long Strait in 2013 (e.g., Luchin and Panteleev, 2014).

We found that interannual differences in the BCSW salinities were associated with statistically significant differences in nutrient loads, Chl*a* biomass and phytoplankton community composition. The higher nutrient concentrations and larger number of stations with bottom water mass BCSW could both have contributed to the overall higher Chl*a* biomass in 2012. Not all differences were associated with the BCSW, however. The more extensive spatial range of low levels of integrated Chl*a* in nearshore waters in 2013 were associated with reduced nutrient (ammonium and phosphate) concentrations in ACW in this year (Tables 2 and 3). Higher ammonium concentration in 2012 than in 2013 in all surface water masses, in ACW and BCSW bottom waters suggest more nutrient regeneration and regenerated production in 2012. The dominance of smaller phytoplankton in 2012 also suggests the possibility of a more important microbial loop in this year. It appears likely that all of these observed differences propagated farther up the food chain: Pinchuk and Eisner (this volume) show differences that extend to the zooplankton as well.

The location of phytoplankton concentrations and their size compositions reveal some consistent linkages between the wind fields, seafloor topography, water masses, and the pelagic production. The higher concentrations of large phytoplankton near Hanna shoal in 2013 suggests that spatial variations in phytoplankton community composition between years were related to the different lateral extent of the CSWW and MW distributions. A subsurface Chl*a* maximum was detected over Hanna shoal and southwest of Point Hope in both years (compare Figs. 14 and 15, whereas the bloom in Chirikov Basin was near the surface; surface nutrients were available in the weakly stratified Chirikov Basin but not elsewhere. It is possible that the Bering Sea phytoplankton were part of a fall bloom driven by the September low-pressure systems and associated winds (Figs. 3 and 4), taking advantage of new nutrients introduced from below the mixed layer depth.

The annual average volume flux through Bering Strait exhibited an increase in northward transport of ~ 50% from 2001 (0.7 Sv) to 2013 (1.1 Sv) (Woodgate et al. 2012, Woodgate et al. submitted), and this increase corresponds to changes in heat and freshwater fluxes through the strait and implications for nutrient fluxes (Woodgate et al., 2012). Annual mean transports through Bering Strait during our two study years, 2012 and 2013, were at opposite extremes of the range with very low (~0.7 Sv) and then high (~1.1 Sv) transport, respectively (Woodgate et al. submitted). Another high transport year was 2011, with an estimated flux nearly the same as that in 2013 (Woodgate et al. submitted). We assume that a stronger Bering Strait flow represents a higher nutrient flux and that waters on the Chukchi shelf have a correspondingly smaller residence time. Although the 2012 to 2013 decrease in nutrients is not clearly consistent with an increase in flow between these two years, the decrease in flow from 2011 to 2012 could be consistent if the near-bottom nutrients at the end of summer on the Chukchi shelf are a function of the previous year's Bering Strait transport. Might near-bottom nutrient concentrations found at summer's end be related to the bulk flushing of the shelf in the previous year? The annual (January-December) integration period is likely not the proper time frame to consider, but we expect that a fuller analysis of the Bering Strait mooring data would be no more conclusive given the small number of observations (N=2) that we have for comparison.

The Yukon discharge was either mostly trapped within Norton Sound or was spread to the west and south in 2013, and in 2012 this fresh water was able to leak out of Norton Sound and along the eastern shore of Bering Strait. These distributions conform to inter-annual differences in the wind field (Fig. 3) and the expected influence of Ekman transport (Danielson et al., 2014) and suggest that the two years at least began the fall with very different distributions of the terrestrial fresh water and associated lithogenic matter. Norton Sound has an average depth of ~40 m and surface area of ~$3x10^4$ km^2. For an estimated average summer salinity decrease of 2, there would be approximately 80 km^3 of excess fresh water stored in the Sound, or about 40% of the annual total Yukon discharge. Hence, some significant fraction of the Yukon's spring and summer discharge likely remains on the Bering shelf by early fall. Sufficient winds can subsequently drive this freshwater westward (Danielson et al., 2006; Danielson et al., 2012) and possibly even off the shelf, where it would be effectively lost to the Arctic. The Yukon is generally considered an Arctic River (Peterson et al., 2002) with all of its discharge feeding Bering Strait but a wind-mediated redistribution of the coastal plume could impart a small (~ 5% of the annual Bering Strait fresh water flux, Aagaard and Carmack, 1989) but possibly not negligible fresh water variability to the Bering Strait throughflow.

The data from 2012 and 2013 reveal dramatic differences between the two years in the thermohaline properties and the spatial structure of the water masses, and there exists considerable prior information to help put these changes in a more extended temporal context. We know that 2012 had a below-average Bering Strait transport and that 2013 was near the observed maximum (Woodgate et al., submitted), so these two years may represent near-opposite extremes from the perspective of Pacific-Arctic fluxes. It might seem that the shelf system of 2013 may have more closely resembled the shelf of three decades ago, with the broader extent of CSWW and extensive cold ice melt in the NE Chukchi, but the 2013 ice field was not nearly as extensive as was normally found in the 1970s and 1980s; even 2013 nearly set a record for the lateness in freezeup for the study region. Upwelling is a potential source for new production both in the summer and fall (Pickart et al., 2013; Arrigo et al., 2014), so despite the extensive ice melt and cold temperatures we believe that the 2013 summer is not a good analogue for cold conditions in past decades.

As shown in Fig. 2, the length in days of the seasonal transition is rapidly decreasing in both spring and fall, so processes that depend on the presence of melting ice or partial ice cover have less time to manifest. These could include functions such as under-ice phytoplankton blooms (e.g. Arrigo et al., 2014), or ice as a platform for moving walrus (Jay et al. 2010). Eventually the system may reach a new persistent balance rather than one of progressive change, because the seasonal transition can eventually only decrease so far.

6. Summary

The data provided an unusual glimpse into the late summer temporal and spatial variability in the water mass structure and characteristics, nutrient fields, and phytoplankton community on the northern Bering and Chukchi shelves. We find that the wind field influenced water mass distributions across the entire study region and it was likely responsible for at least a partial shut-down of the ACC in 2013 on the NE Chukchi shelf that was associated with extensive MW and CSWW and relatively large size phytoplankton. Higher salinities in 2012 subsurface BCSW were associated with higher nutrient concentrations and a higher overall phytoplankton standing crop biomass that was dominated by small size phytoplankton. Nutrient and phytoplankton distributions were both affected by water mass location and structure, which in turn reflected the influence of geographic location, currents and winds. The observed and inferred flow field differences suggest a different fate for pelagic production and the waters flowing north through Bering Strait in these two contrasting summers.

7. Acknowledgements

We thank the captain and crew of the Bering Explorer, and all of the Arctic Eis scientists who helped carry this program forward, particularly Franz Mueter and Jared Weems for keeping us all on track. Thanks to BOEM program managers Cathy Coon (Arctic Eis) and Warren Horowitz (NE Chukchi circulation studies). Thanks to Rachel Potter for processing the HFR data, to Elizabeth Dobbins for processing the surface drifter data, and to Eric Wisegarver and Peter Proctor for nutrient analysis. Microstar 1-m drogue surface drifter data deployed at the nearshore locations in 2012 and 2013 were supported by the North Slope Borough-Shell Baseline Studies Program. The offshore deployments and HFR data collections were supported by BOEM under contract M12AC00008. This publication was partially funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement NA10OAR4320148, and is PMEL contribution number 4363, contribution EcoFOCI-0845 to NOAA's Ecosystems and Fisheries-Oceanography, and JISAO contribution number 2446. Arctic Eis was funded under grants including the Coastal Impact Assistance Program (AKDNR/USFWS), the University of Alaska Fairbanks 10-CIAP-010, and F12AF00188, Bureau of Ocean Energy Management and the University of Alaska Fairbanks M12AC00009.

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Table 1. Water mass temperature and salinity bounds and defining characteristics. Abbreviations include ACW = Alaskan coastal water, AtlW = Atlantic Water, AW = Anadyr Water, BSSW = Bering Shelf Summer Water, BCSW = Bering-Chukchi Summer Water, BCWW = Bering-Chukchi Winter Water, BSWW = Bering Shelf Winter Water, CSSW = Chukchi Shelf Summer Water, and CSWW = Chukchi Shelf Winter Water.

Water Mass	Temperature Limits	Salinity Limits	Characteristics
ACW	7 < T < 12	20 < S < 32	The warmest and freshest waters observed in the Arctic Eis surveys. Influenced by the fresh coastal discharges from Alaskan rivers and the ability for incident solar radiation to exert a proportionally larger warming in shallow, turbid water columns.
BSWW **CSWW**	-2 < T < 0	30 < S < 33.5	Cold waters remnant from the previous winter's cooling, ice formation, and brine rejection. Together, these water masses comprise the **BCWW**.
AW **BSSW** **CSSW**	0 < T < 7	30 < S < 33.5	Waters of intermediate temperature and salinity that have warmed since the previous winter or that have advected into the study domain from the Bering Sea continental slope and through the Gulf of Anadyr. Together, these water masses comprise the **BCSW**.
MW	-2 < T < 7	25 < S < 30	Relatively cool and fresh waters influenced by sea ice melt. Can directly mix with summer shelf waters, coastal waters, or winter waters.
AtlW	-2 < T < 1	33.5 < S < 35	Relatively saline waters that originate in the North Atlantic and typically reside at depths below the Arctic Ocean's cold halocline. This water mass is characterized by a subsurface temperature maximum at about 300-600 m.

Table 2. Mean surface T, S, nutrients (µM) by surface water mass (WM Surface) and year. Water mass abbreviations as in Table 1. On way ANOVA used for comparisons between years for each water mass for natural log transformed nutrient data and untransformed T and S. * indicates significantly higher (P< 0.05) in that year.

year	WM Surface	T	S	PO_4	SiO_4	NO_3	NO_2	NH_4	N
2012	MW	2.74	29.27*	0.52*	8.93*	0.72*	0.01	0.54*	12
2013	MW	1.78	27.93	0.35	3.41	0.04	0.01	0.12	16
2012	BCSW	5.33	31.16	0.54*	7.25*	1.27	0.03	0.58*	44
2013	BCSW	4.87	31.36	0.43	5.12	1.26	0.04	0.38	25
2012	ACW	8.17	29.77	0.48*	8.92	0.13	0.02	0.54*	40
2013	ACW	8.79*	29.64	0.39	7.77	0.27	0.02	0.22	52

Table 3. Mean near-bottom T, S, nutrients (µM) by near-bottom water mass (WM Bottom) and year. Water mass abbreviations as in Table 1. One-way ANOVA used for comparisons between years for each water mass for natural log transformed nutrient data and untransformed T and S. * indicates significantly higher (P< 0.05) in that year.

year	WM Bottom	T	S	PO_4	SiO_4	NO_3	NO_2	NH_4	N
2012	BSWW	-0.07	32.38	1.34*	12.53	11.26	0.14	1.66	1
2013	BSWW	-0.61	31.38	0.93	12.30	2.30	0.08	1.31	6
2012	CSWW	-0.92*	32.96*	1.56	21.86	7.36	0.14	3.11	17
2013	CSWW	-1.30	32.59	1.37	20.53	7.07	0.13	2.47	24
2012	BCSW	3.47	32.03*	0.94*	12.72*	3.10*	0.08*	2.06*	54
2013	BCSW	4.01	31.48	0.66	8.72	1.81	0.06	1.22	44
2012	ACW	8.35	29.90	0.57	9.48	0.20	0.04	1.08*	25
2013	ACW	9.16*	29.78	0.52	12.84	0.23	0.03	0.33	18

Table 4. Mean integrated Chla (IntChla, mg m^{-2}) by water mass (WM) structure and year. Water masses as defined in Table 1. One-way ANOVA used for comparisons between years within each water mass combination for natural log transformed integrated Chla data. * indicates significantly higher ($P < 0.05$) in that year.

Year	**WM Surface**	**WM Bottom**	**IntChla**	**N**
2012	MW	CSWW	43.88	17
2013	MW	CSWW	24.60	16
2012	MW	BCSW	31.34	2
2013	MW	BCSW	N/A	0
2012	BCSW	BSWW	39.57	1
2013	BCSW	BSWW	N/A	0
2012	BCSW	CSWW	18.51	9
2013	BCSW	CSWW	14.17	8
2012	BCSW	BCSW	61.94	37
2013	BCSW	BCSW	102.29	18
2012	ACW	BSWW	N/A	0
2013	ACW	BSWW	32.53	6
2012	ACW	BCSW	33.90*	15
2013	ACW	BCSW	16.82	28
2012	ACW	ACW	32.56*	25
2013	ACW	ACW	15.88	18

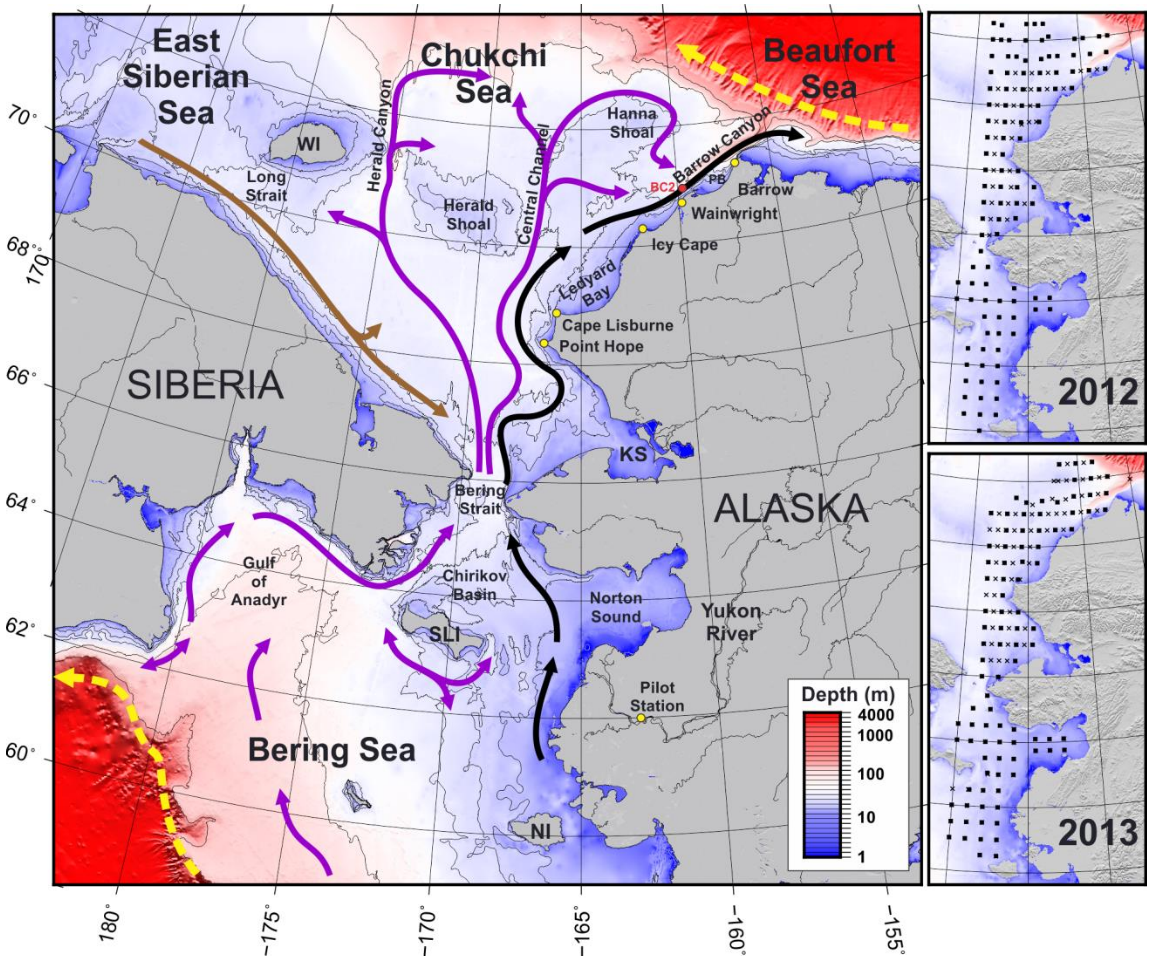

Figure 1. Study region map with bathymetric depths (200, 80, 45, 35, and 25 m isobaths), place names and typical flow pathways. Abbreviations include NI = Nunivak Island, SLI = St. Lawrence Island, WI = Wrangel Island, KS = Kotzebue Sound, PB = Peard Bay. Mean flow pathways are color coded to denote current systems and/or typical water mass pathways: Yellow = Bering Slope Current and Beaufort Gyre; Black = Alaskan Coastal Current; Brown = Siberian Coastal Current; Purple = pathways of Bering shelf, Anadyr, and Chukchi shelf waters. Panels on the right hand side show the Arctic Eis station locations for 2012 and 2013. Full CTD hydrographic, nutrient and phytoplankton sampling occurred at stations with squares, while only CTD sampling occurred at stations marked with an “x”. Mooring BC2 location is marked with a red circle.

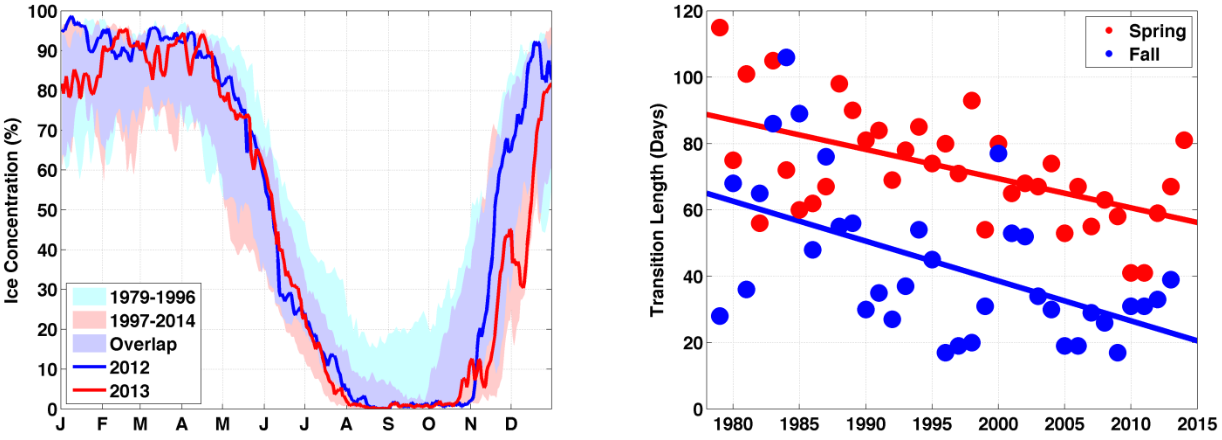

Figure 2a (left panel). Sea ice concentrations over the region 60-72 °N and 170-157 °W for 1979-2014, showing the envelope of daily ice concentration ranges for first (blue, 1979-1996) and second (red, 1997-2014) halves of the period of record and the region of overlap between the two periods (purple). Daily ice concentrations for 2012 and 2013 are shown in red and blue, respectively. **Figure 2b** (right panel) Number of days for the same region to transform from ice-covered (> 80%) to ice-free (< 20%) conditions in the spring/summer (red), and vice-versa in the fall/winter (blue). Spring $r^2 = 0.30$ and fall $r^2 = 0.29$ and $p < 0.001$ for both.

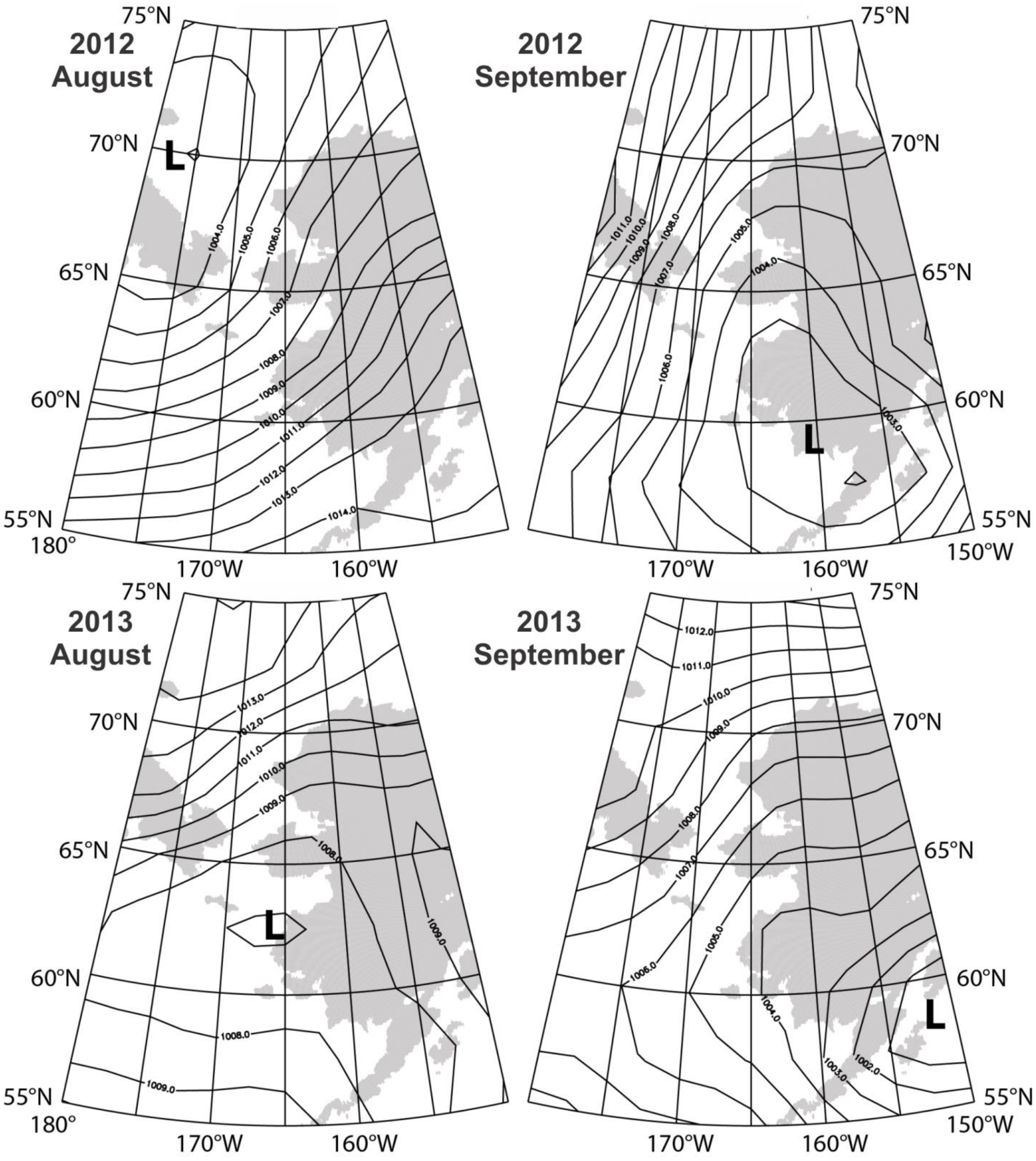

Figure 3. Monthly average sea level pressure contours (mbars) for August (left) and September (right) in 2012 (top) and 2013 (bottom) from the NCEP-NCAR Reanalysis.

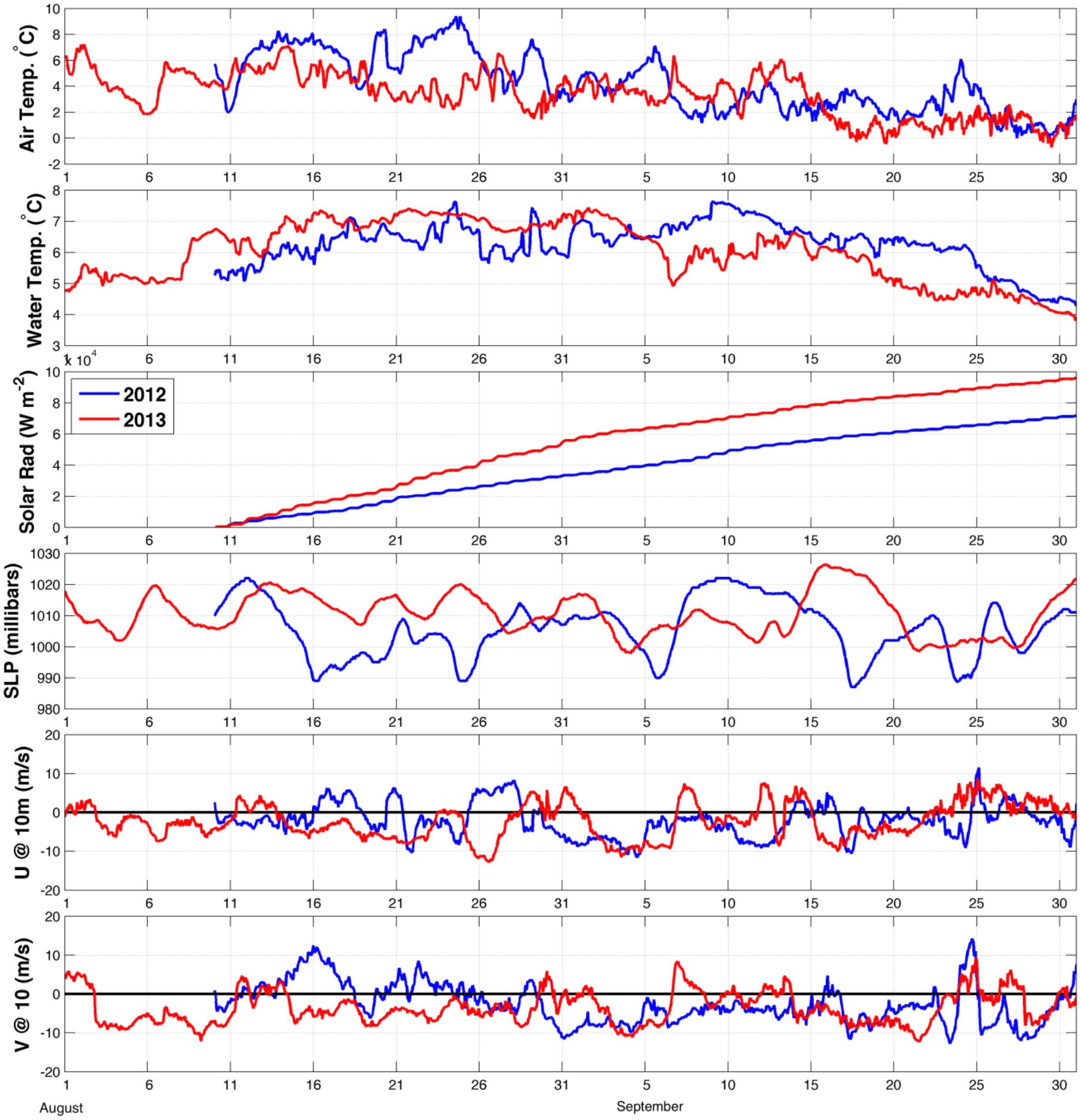

Figure 4. Meteorological measurements from a surface buoy deployed offshore of Pt. Lay in 2012 (blue) and 2013 (red). From top to bottom, panels depict: 2 m air temperature (°C), 1 m depth water temperature (°C), integrated solar radiation (W m^{-2}), sea level pressure (mbar), and the east (U, m s^{-1}) and north (V m s^{-1}) components of the wind. In both years the Arctic Eis cruise operated in the Chukchi Sea from 10 August through the first week of September, working from south to north.

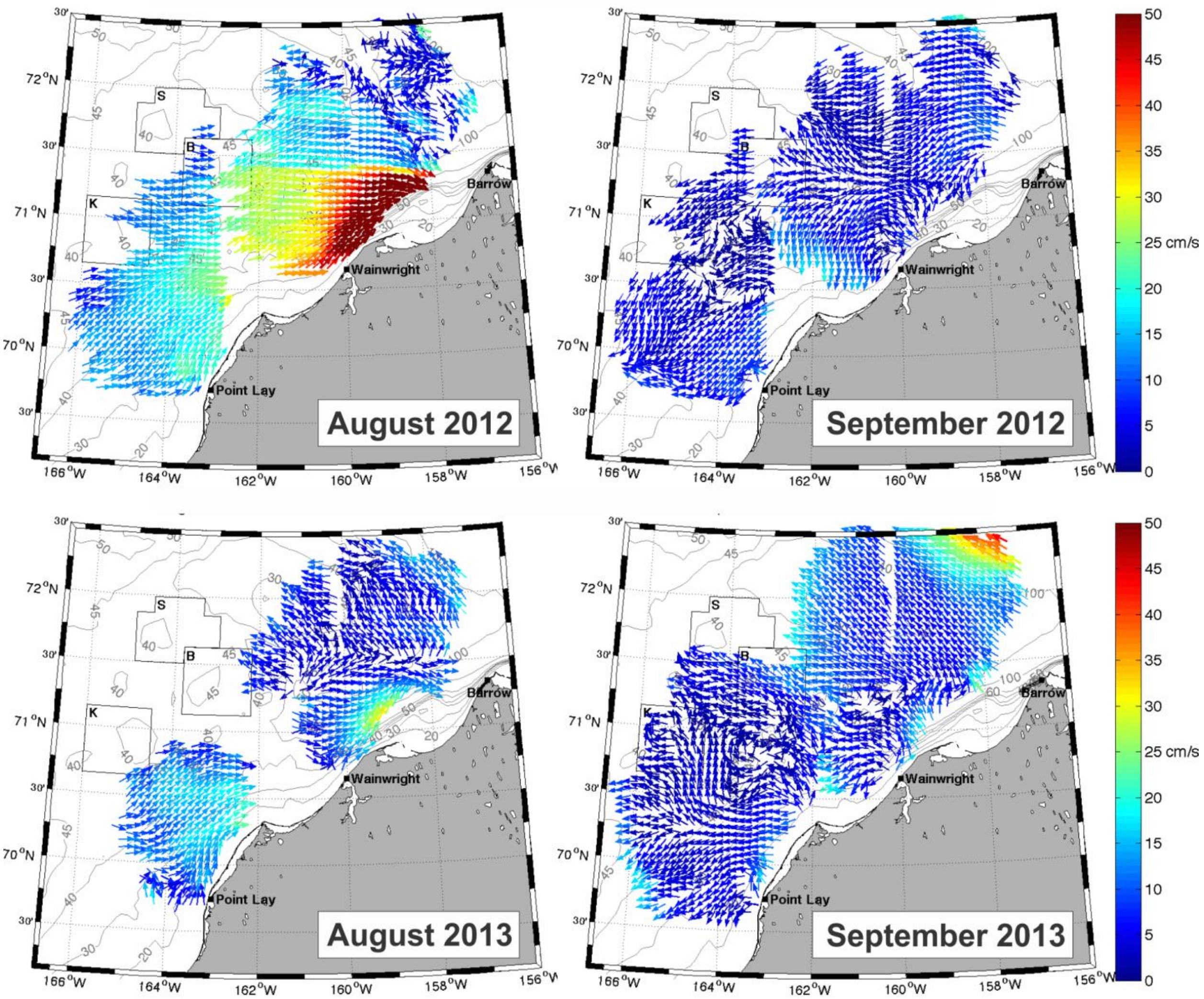

Figure 5. Mean monthly surface currents as measured by HFR installations at Point Lay, Wainwright, and Barrow in August and September 2012 and 2013. Note that incomplete coverage severely biases August 2013 due to missing data.

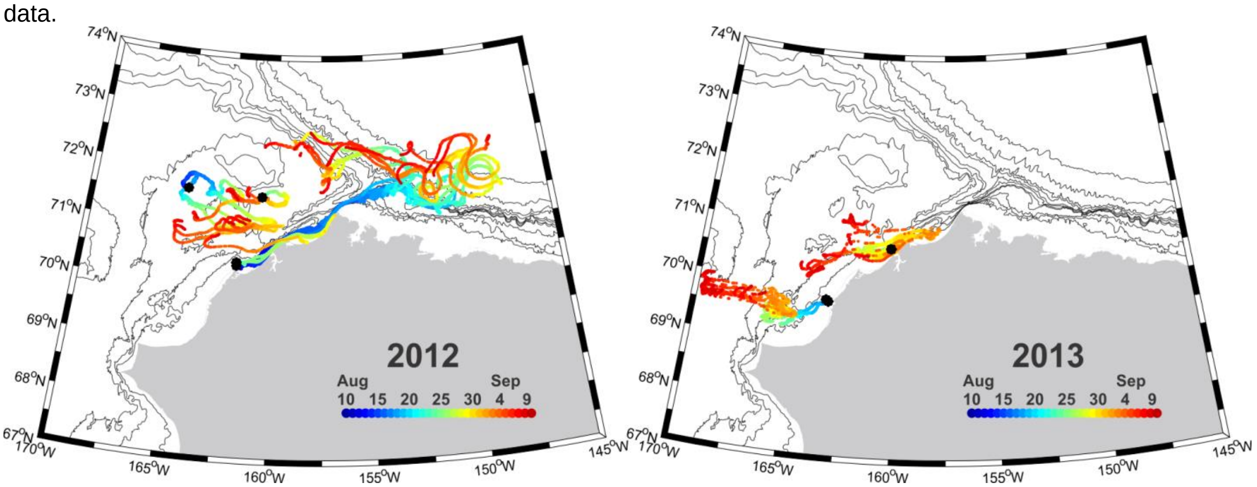

Figure 6. Surface (1-m) drogued satellite-tracked drifters deployed over 10-24 August 2012 (left) and 17-24 August 2013 (right). Color denotes the date of each location fix. Black dots locate the deployment sites.

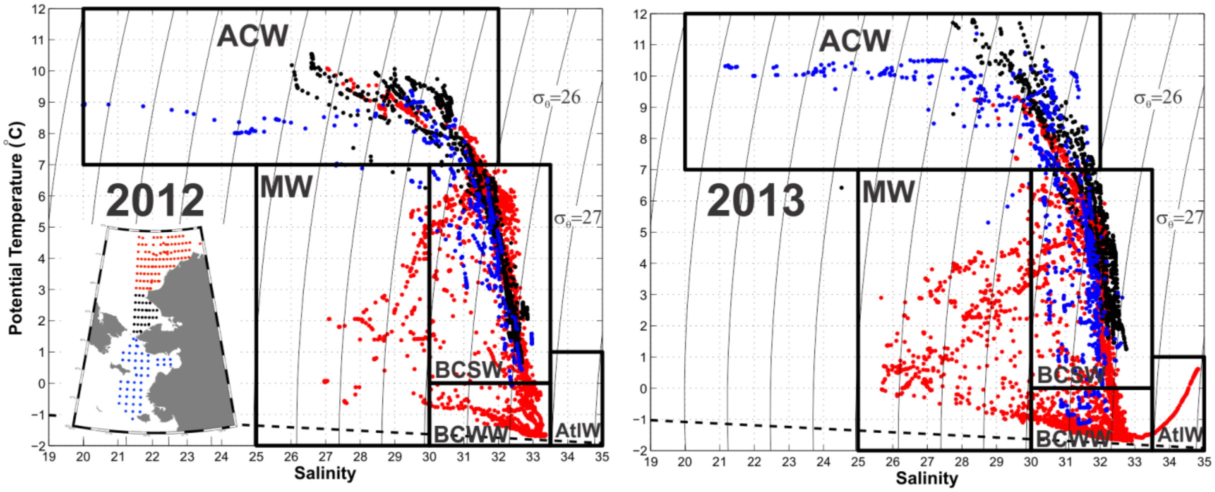

Figure 7. Theta-S diagrams for 2012 (left) and 2013 (right). Contours show sigma-theta isolines with a contour interval of 1 kg m^{-3}. Data points are colored (see inset) by region: northern Chukchi shelf are red, southern Chukchi shelf are black and northern Bering shelf are blue. See Table 1 for water mass abbreviation definitions.

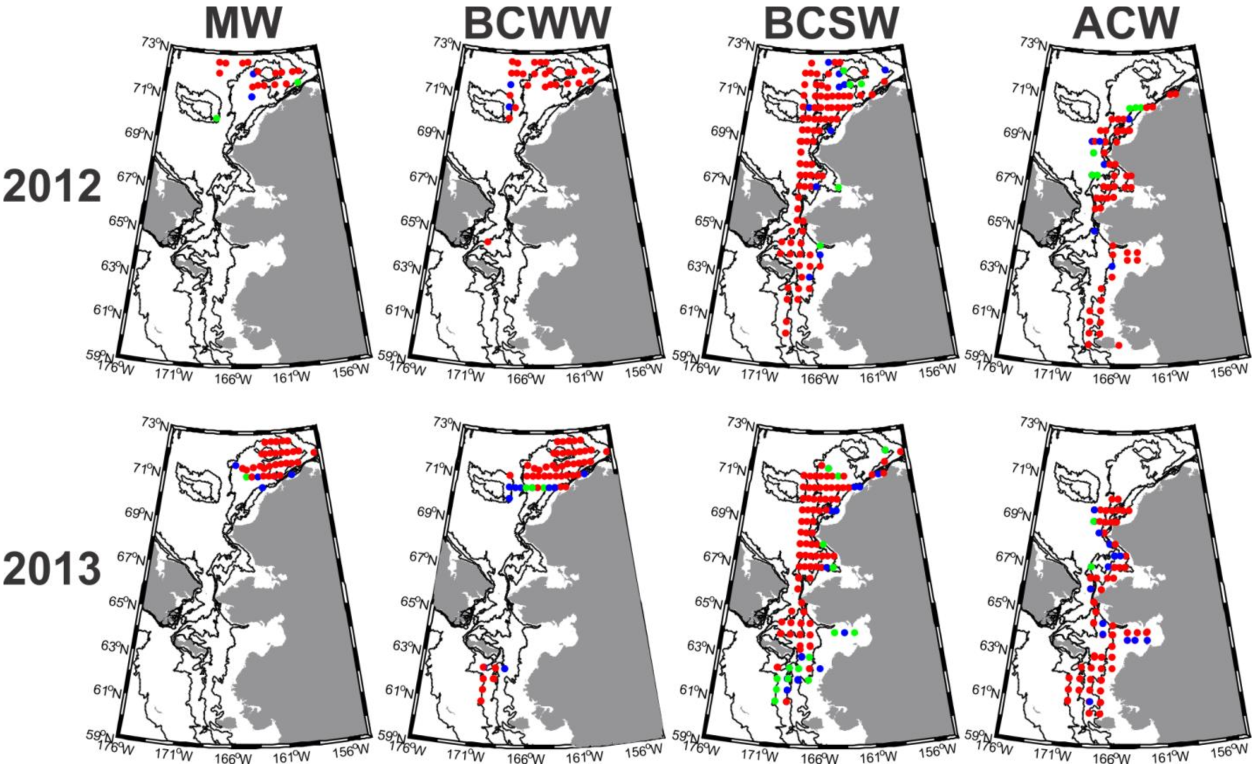

Figure 8. Distribution of water masses in 2012 (top row) and 2013 (bottom row). Colors denote the number of 1-dbar averaged data points found in each water column profile: 1-2 (green), 3-10 (blue) and more than 10 (red). No marker

is displayed at stations that did not observe the corresponding water mass. See Table 1 for water mass abbreviation definitions. AtlW was found only at the easternmost station, near Point Barrow, in 2013.

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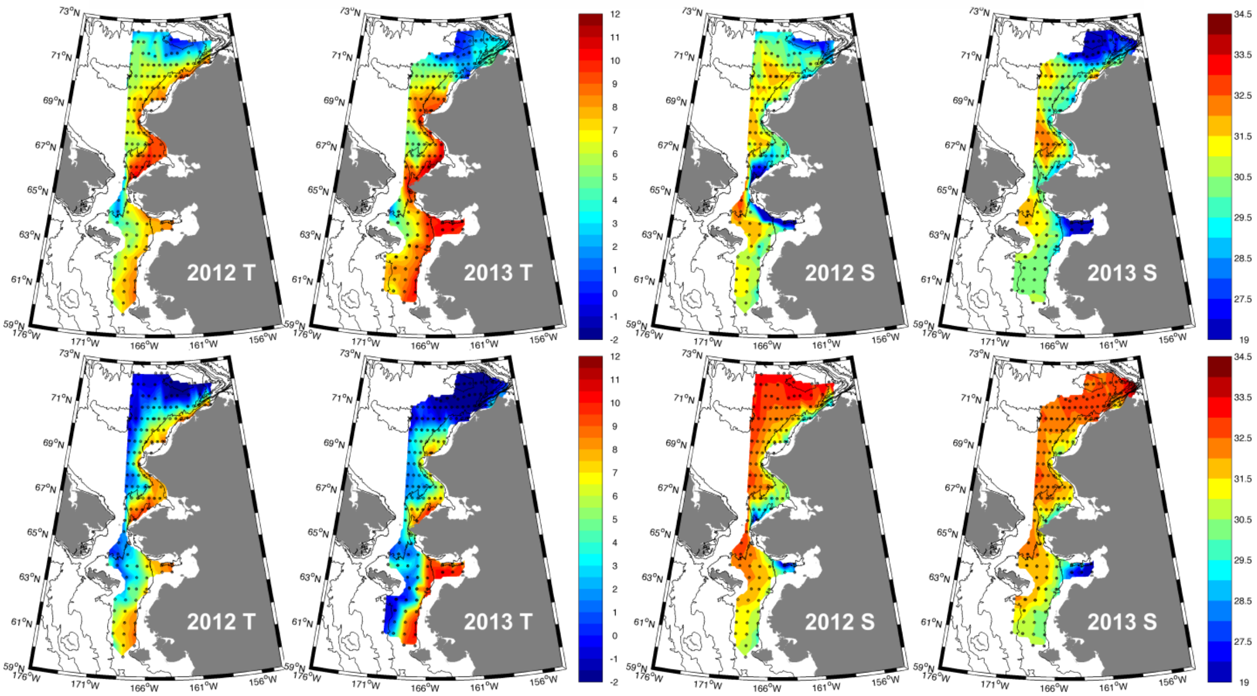

Figure 9. Temperature (left four panels) and salinity (right four panels) near within 10 m of the surface (top row) and near the seafloor, within 5 m of CTD cast deepest measurement (bottom row), for 2012 and 2013.

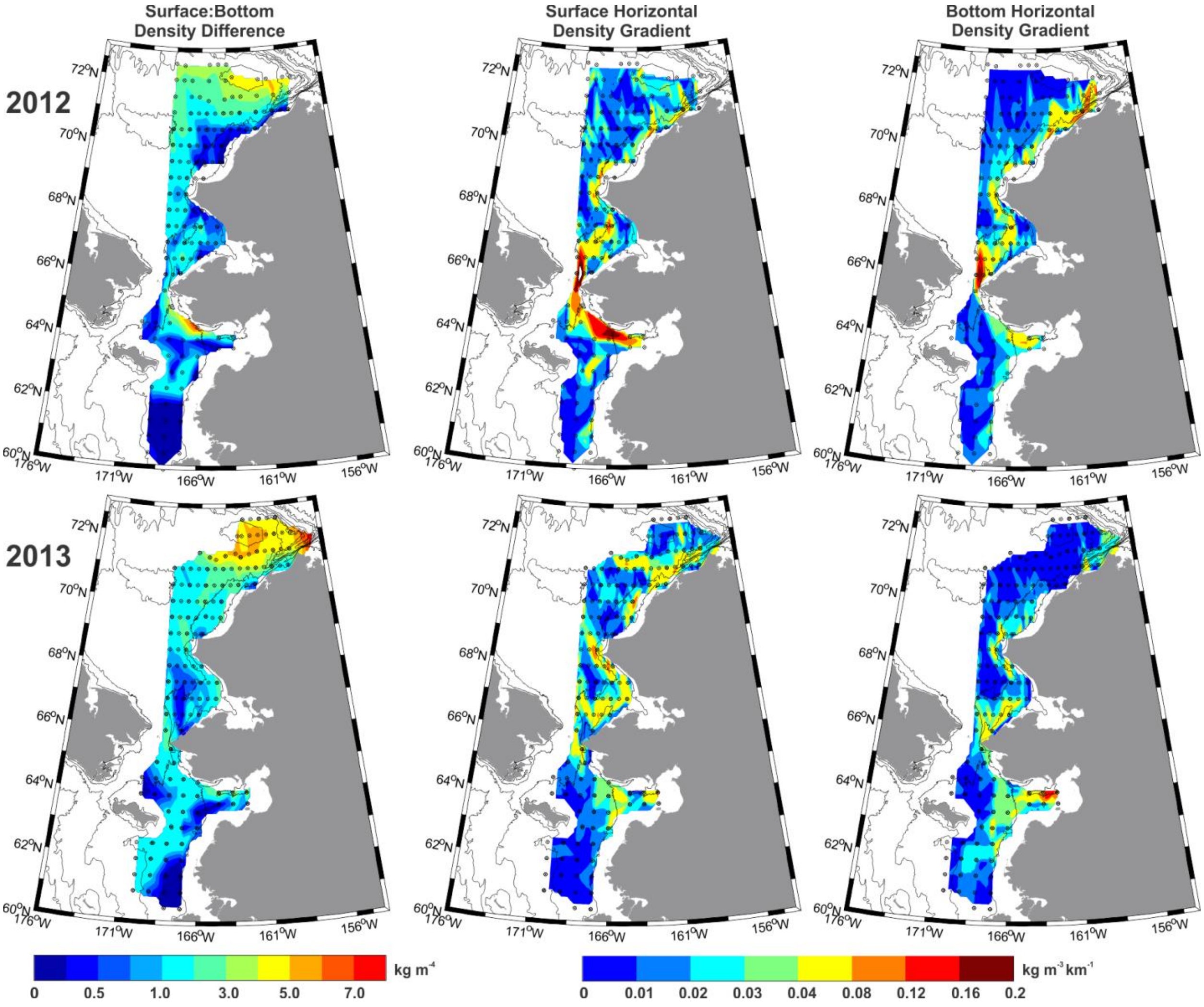

Figure 10. Stratification and fronts in 2012 (top) and 2013 (bottom). Left column shows the difference between the near-surface and near bottom water density. Middle column shows the magnitude of the near-surface horizontal density gradient and the right column shows the magnitude of the near-bottom horizontal density gradient.

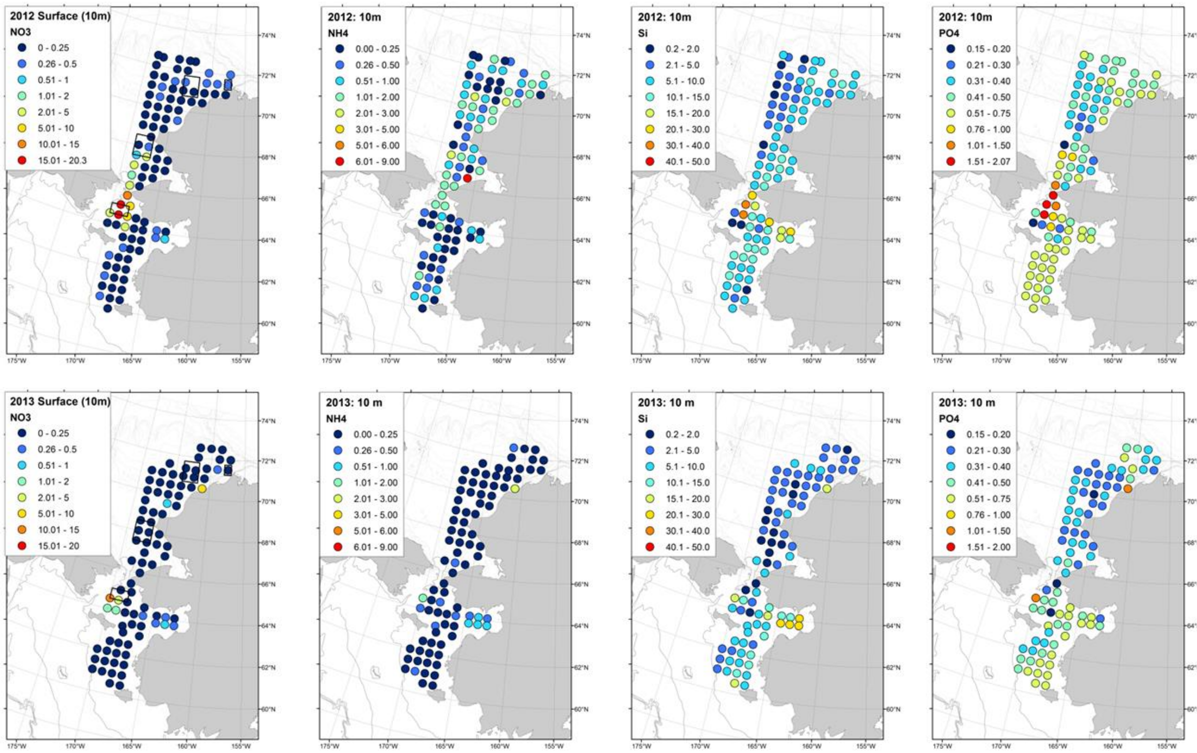

Figure 11. Nutrient concentrations close to the surface (10 m) for 2012 (top row) and 2013 (bottom row). From left to right, the panels show NO_3, NH_4, SiO_4, and PO_4. Black boxes in nitrate plots denote benthic hotspot regions DBO-2 in Chirikov Basin and DBO-3 offshore of Point Hope, DB4 near Hanna Shoal, and DB5 at Barrow Canyon.

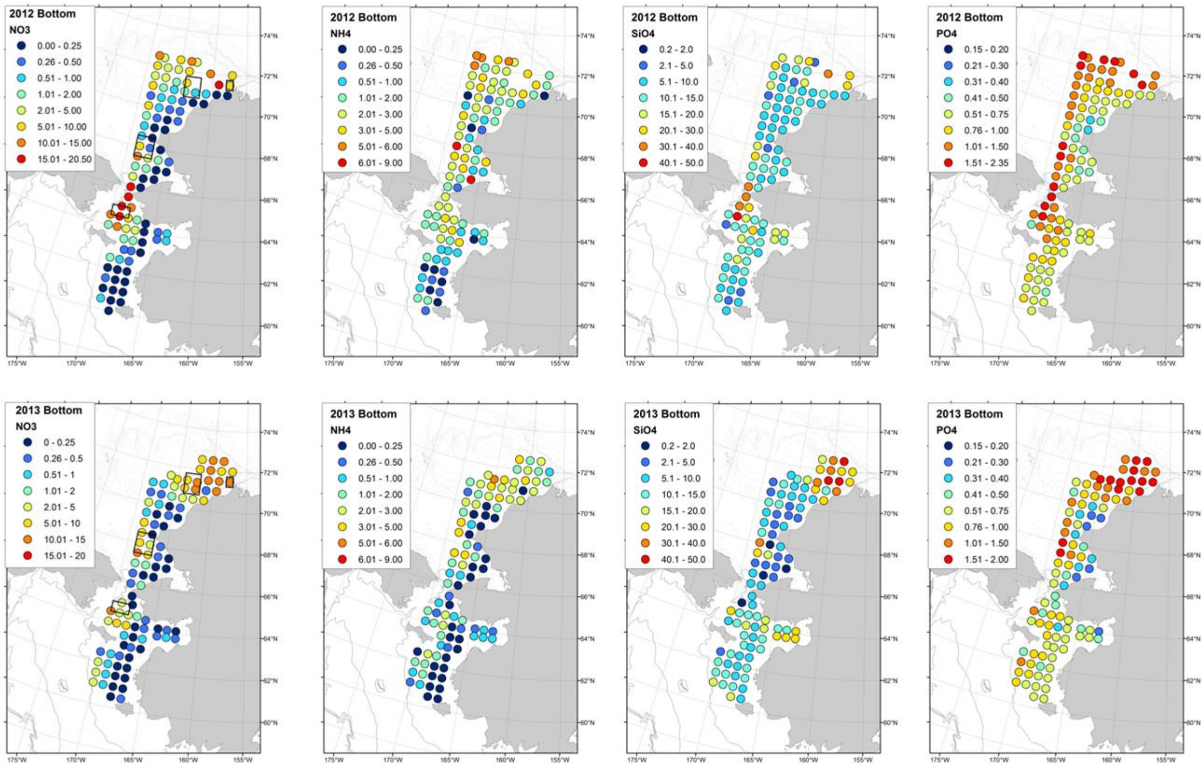

Figure 12. As in Figure 11, but for nutrients close to the seafloor.

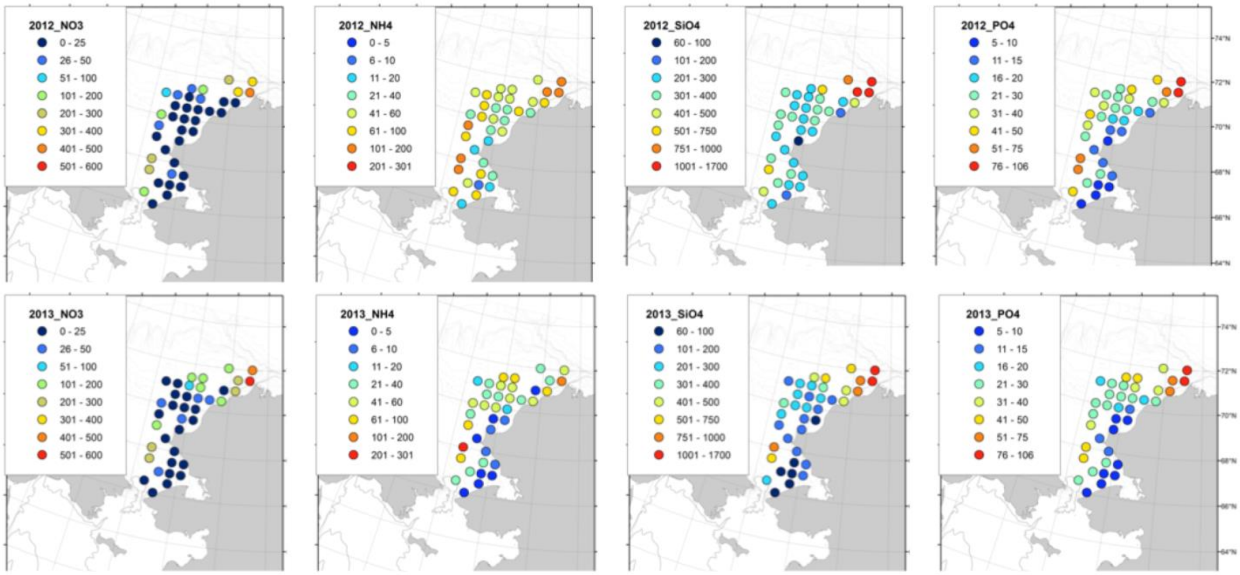

Figure 13. Nutrient standing stocks, integrated through the water column for Chukchi Sea only at stations sampled in both 2012 (top row) and 2013 (bottom row). From left to right, the panels show NO_3, NH_4, SiO_4, and PO_4.

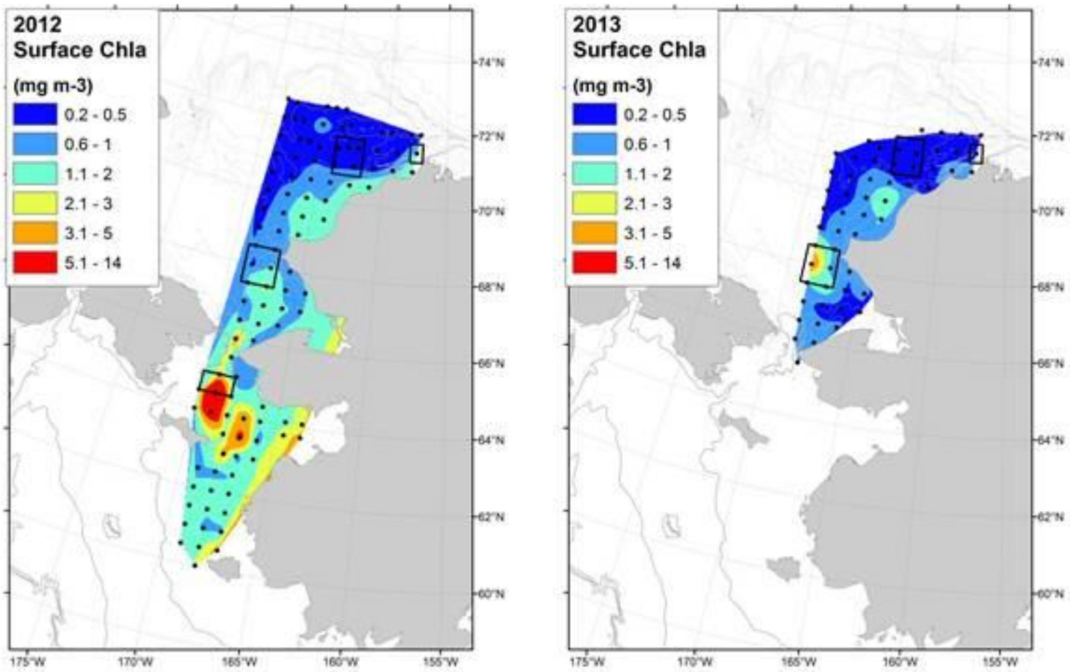

Figure 14. Surface chlorophyll a (mg m^{-3}) from discrete samples for 2012 (left) and 2013 (right). Black boxes denote benthic hotspot regions DBO-2 in Chirikov Basin and DBO-3 offshore of Point Hope, DB4 near Hanna Shoal, and DB5 at Barrow Canyon.

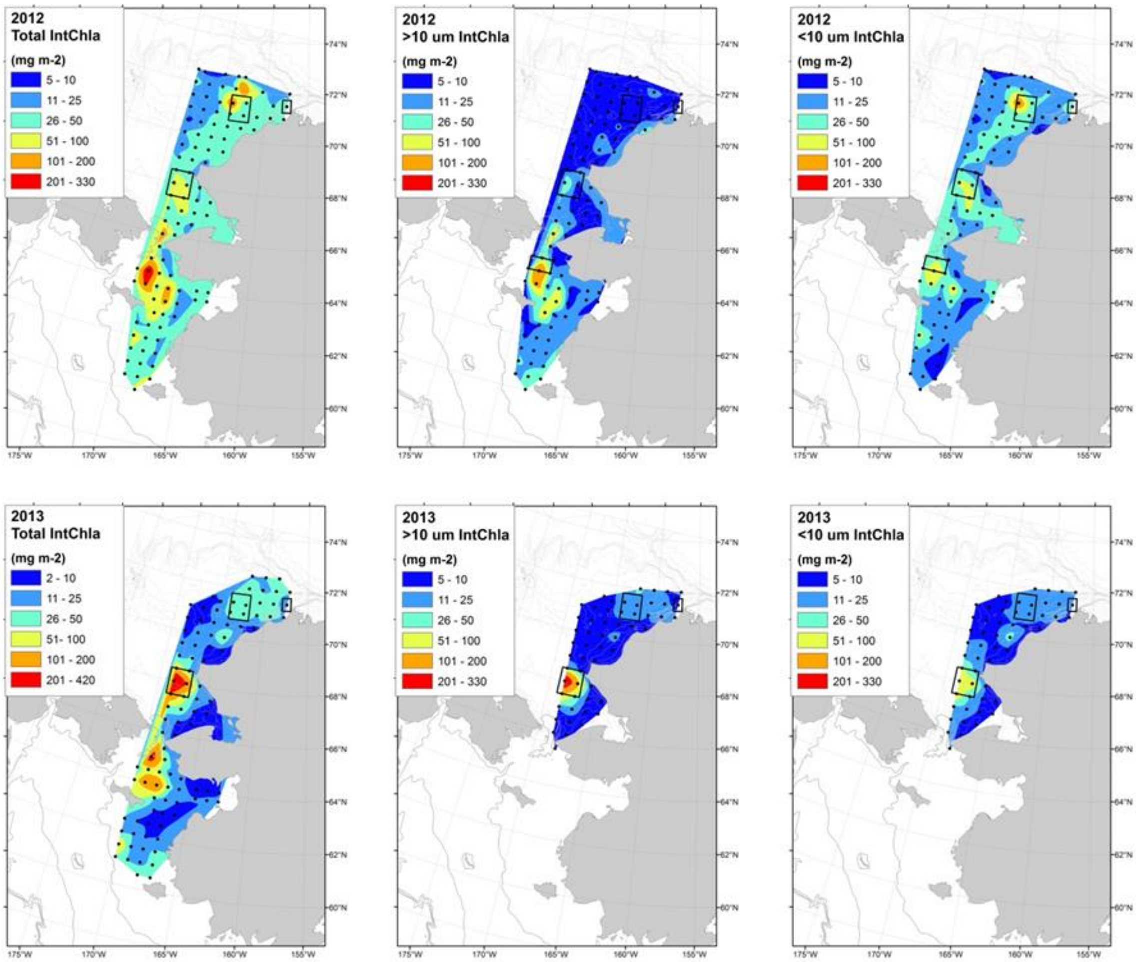

Figure 15. Total, large fraction (> 10 µm) and small fraction (<10 µm) water column integrated chlorophyll a (mg Chl*a* m^{-2}) for 2012 (left) and 2013 (right). No size fraction data exist south of Bering Strait in 2013. Black boxes denote benthic hotspot regions DBO-2 in Chirikov Basin, DBO-3 offshore of Point Hope, DBO-4 near Hanna Shoal, and DB5 at Barrow Canyon.

Appendix D.

Species and Size Selectivity of Two Midwater Trawls used in an Acoustic Survey of the Alaska Arctic

Authors
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Christopher D. Wilson

December 12, 2015

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

List of Oral and Poster Presentations

Species and size selectivity of two midwater trawls used in a survey of the Alaska Arctic. Presented as an Oral presentation by Alex De Robertis at the Joint Session of the ICES-FAO Working Group on Fishing Technology and Fish Behaviour (WGFTFB) and the Working Group on Fisheries Acoustics Science and Technology (WGFAST) – (JFATB). May 5th, 2014 New Bedford, Massachusetts

Proposed Objectives and Study Chronology

Acoustic-trawl (AT) survey methods are widely used to estimate the abundance and distribution of pelagic organisms. This technique relies on estimates of size and species composition from trawl catches along with estimates of the acoustic properties of these animals to convert measurements of acoustic backscatter into animal abundance. However, trawls are selective samplers, and if the catch does not represent the size and species composition of the animals in the acoustic beam the resulting abundance estimates will be biased. We conducted an experiment to quantify trawl selectivity for species encountered and trawls used during the Arctic EIS survey. The pelagic assemblage in this environment was dominated by small young-of-the-year (age-0) fishes and jellyfish, which may be poorly retained in trawls. A large midwater trawl (Cantrawl) and a smaller midwater trawl (modified Marinovich) were used during the survey. The Marinovich was equipped with 8 small-mesh recapture nets which were used to estimate the probability that an individual that enters the trawl is retained. In addition, paired hauls were made with the Cantrawl and Marinovich to estimate the difference in selectivity between the two trawls. A statistical model was developed to combine the catches of the recapture nets and the paired hauls to estimate the length-dependent selectivity of the trawls for the most abundant species (e.g., age-0 fishes and jellyfish). The analysis indicated that there was substantial size and species selectivity: although the modified Marinovich generally had a higher catch per unit effort, many of the animals encountered in this environment were poorly retained by both trawls. The observed size and species selectivity of the trawls were used to correct the Acoustic-trawl survey estimates for the biases introduced in the trawl capture process.

This work has been published in Deep Sea Research II:

De Robertis, A., Taylor, K., Williams, K., Wilson, C.D., 2015. Species and size selectivity of two midwater trawls used in an acoustic survey of the Alaskan Arctic. Deep Sea Research II http://dx.doi.org/10.1016/j.dsr2.2015.11.014.

1. Abstract:

Acoustic-trawl (AT) survey methods are widely used to estimate the abundance and distribution of pelagic organisms. This technique relies on estimates of size and species composition from trawl catches along with estimates of the acoustic properties of these animals to convert measurements of acoustic backscatter into animal abundance. However, trawls are selective samplers, and if the catch does not represent the size and species composition of the animals in the acoustic beam the resulting abundance estimates will be biased. We conducted an experiment to quantify trawl selectivity for species encountered during an AT survey of the Alaska Arctic. The pelagic assemblage in this environment was dominated by small young-of-the-year (age-0) fishes and jellyfish, which may be poorly retained in trawls. A large midwater trawl (Cantrawl) and a smaller midwater trawl (modified Marinovich) were used during the survey. The Marinovich was equipped with 8 small-mesh recapture nets which were used to estimate the probability that an individual that enters the trawl is retained. In addition, paired hauls were made with the Cantrawl and Marinovich to estimate the difference in selectivity between the two trawls. A statistical model was developed to combine the catches of the recapture nets and the paired hauls to estimate the length-dependent selectivity of the trawls for the most abundant species (e.g., age-0 fishes and jellyfish). The analysis indicated that there was substantial size and species selectivity: although the modified Marinovich generally had a higher catch per unit effort, many of the animals encountered in this environment were poorly retained by both trawls. The observed size and species selectivity of the trawls can be used to select appropriate nets for sampling pelagic fishes, and correct survey estimates for the biases introduced in the trawl capture process.

2. Introduction

Acoustic-trawl (AT) survey methodology relies on trawl sampling to estimate the species and size composition of sound-scattering organisms. The catches from survey trawls are used to convert observations of volume backscattering into animal abundance (Simmonds and MacLennan, 2005). However, fishing gear is selective (i.e. there are size and species differences in the probability of capture), and the trawl catch is likely to have a different size and species composition than the population in the volume sampled (MacLennan, 1992, Wileman et al., 1996, Bethke et al., 1999). If the trawl gear is size or species selective this can cause substantial biases in AT abundance estimates (Nakashima 1990, Bethke et al., 1999, Williams, 2013). Biases in trawl-based species or size composition introduce errors in all size or species classes in AT surveys. This occurs because the acoustic measurement detects backscatter from all species (and sizes) present in the acoustic beam, and this echo energy is converted to species abundance based on the acoustic scattering expected from the animals retained in the trawl (Bethke et al., 2010). For example, in the case of a mixture of strong and weak sound scattering organisms, underestimates in the proportion of the strong scatterers due to net selectivity will result in comparatively large overestimates of the weakly scattering organisms, as a larger proportion of the observed backscatter is allocated to the weakly scattering organisms in the calculation of animal abundance from acoustic backscatter (e.g. McClatchie and Coombs, 2005).

Trawls used in commercial fishing are species and size selective, and there has been considerable interest in quantifying and altering the selectivity of trawls to reduce unwanted bycatch (reviewed in MacLennan 1992, Wileman et al., 1996). However, the size and species selectivity of survey trawls is commonly assumed to be negligible (i.e. catchability is constant across species and size classes), and trawl catches are often used to estimate fish abundance with no correction for trawl selectivity. Trawls capture fish primarily by exploiting herding behavior (Wardle, 1984, 1993), and the probability of retention in the trawl is often strongly size and species dependent (Nakashima, 1990, Wardle, 1993, Williams et al., 2011). When fish aggregations are dominated by a single species, and size classes are spatially segregated, trawl selectivity may have relatively minor impacts on acoustic estimates of abundance. However, in many environments, fish occur in aggregations of mixed species and sizes, and the species and size compositions of acoustic scatterers are inferred from trawl samples. The assumption of negligible selectivity is likely to be untenable in these mixed species or size class situations, and trawl selectivity is likely to introduce large biases into AT survey results. For example, Williams (2013) found that accounting for trawl selectivity in an area of mixed age aggregations of walleye pollock resulted in large underestimates of the poorly retained juvenile pollock and comparatively small changes in the biomass of adults.

This study was a part of a large-scale baseline survey of the Arctic Ecosystem integrated survey (Arctic Eis) of the eastern Alaska Chukchi Sea in 2012 and 2013. A large midwater trawl (Cantrawl) was used for the AT survey in 2012 to estimate the abundance and distribution of near-surface and midwater fishes. The trawl had been used in earlier surface trawl surveys and was used in the 2012 and 2013 surveys to continue that surface trawl survey time series (Farley et al., 2009, Eisner et al., 2013). During the 2012 AT survey, it became clear that the fish assemblage in the eastern Chukchi Sea was dominated by small and/or juvenile fishes which were likely to be poorly retained by the Cantrawl. During the 2013 survey, a smaller modified midwater herring trawl (hereafter mod-Marinovich) was used to target acoustically observed fish aggregations, as it was expected to be better at retaining the small size classes of fishes present in the survey area in 2012.

This work aims to quantify the size and species selectivity of the two trawls used in the Arctic Eis AT surveys. The information is necessary to correct the trawl-based estimates of species and size composition used to convert acoustic backscatter to species abundances so that accurate and comparable estimates of animal density are generated from the two surveys. A two-part experiment was conducted in 2013 in which 1) the mod-Marinovich was equipped with small-mesh recapture nets to capture fishes that escaped from the trawl, and 2) a series of paired trawls with the Cantrawl and mod-Marinovich were conducted during the survey. The results of these fishing trials are analyzed jointly in a model framework to estimate the size-dependent selectivity of the trawls for the abundant species.

3. Methods

3.1 Trawl sampling

A series of hauls with the mod-Marinovich trawl equipped with small-mesh recapture nets to capture fish exiting out the trawl meshes, as well as back-to-back trawl hauls with the mod-Marinovich and a large Cantrawl 400/601 rope trawl were conducted as part of an interdisciplinary survey of the Chukchi Sea. These midwater trawl hauls were conducted aboard the F/V *Bristol Explorer*, a chartered 55 m commercial stern trawler during an AT survey conducted between 7 August and 11 September 2013 (Fig. 1). Both nets were fished with 5 m^2 alloy doors at a vessel speed of ~ 2 $m\ s^{-1}$ during daylight hours. The trawl opening during fishing (measured after the doors had spread the net and the net depth was stable) was observed with a Wesmar trawl sonar attached to the headrope, and the depth of the trawl was measured with Seabird SBE-39 temperature and pressure recorders attached to the headrope.

The Cantrawl is ~198 m long, has a 122 m headrope, and is constructed with ropes at the leading edge of the net followed by meshes reducing from 162 to 1.2 cm stretched length in the codend liner (Farley et al., 2009). The Cantrawl was equipped with floats to keep the headrope near the surface and towed for 30 min at predetermined locations. A trawl vertical opening of 19.7 ± 2.7 m (mean ± SD) and a horizontal opening of 45.8 ± 3.6 m was measured while surface trawling.

The mod-Marinovich herring trawl is ~31 m long, has a 12 m headrope, and is constructed as a symmetrical 4 seam box trawl with meshes reducing from 6.4 cm in the wings to 3.8 cm in the aft panel (Fig. 2). The body of the trawl is constructed from four panels. The aftmost panel was covered by 2 by a 3 mm knotless oval mesh liner. Hereafter, the two forward panels are referred to collectively as the forward section, the remaining unlined panel as the aft section, and the rear lined panel as the codend (Fig. 2). The trawl was modified from the original design to allow it to be fished effectively (i.e. with minimal overspreading of the net) with the same 5 m^2 trawl doors used for the Cantrawl by adding larger wings and fishing it with 55 m bridles. A trawl vertical opening of 5.7 ± 0.6 m (mean ± SD) and a horizontal opening of 8.3 ± 0.9 m was observed while fishing.

The mod-Marinovich was equipped with recapture nets designed to recapture organisms that escape from inside the trawl by exiting through the trawl meshes (e.g. Zijlsta, 1969, Nakashima, 1990, Matsushita et al., 1993, Williams et al., 2011). The trawl was divided into the codend and 8 additional partitions, defined by each trawl side (i.e. top, bottom, left, right), with each side divided into front and aft sections (Fig. 2). Recapture nets were attached to the outside of the trawl at the center of each of the 8 partitions (Fig. 2). The recapture nets were made of the same 2 by 3 mm oval mesh as the mod-Marinovich codend liner, and were constructed with a mouth opening as a rhombus with 1.2 m sides and a 2.6 m long body reducing into a codend. The recapture nets, which were dyed black to minimize their visibility, covered approximately 3.1 % of the trawl surface area: 2.2 % of the meshes in the forward section, and 5.5 % of the meshes in the aft section (Fig. 2).

The mod-Marinovich was fished in 30 hauls in which all 8 recapture nets and the codend were sampled. Although the recapture nets were permanently attached to the mod-Marinovich, they were not sampled on all trawl hauls due to the effort required to sample the catches. On several occasions, catch was lost from one or more nets from inadvertently opened codend(s). Data from these hauls were not used.

A total of 14 paired hauls were conducted when the mod-Marinovich and Cantrawl were fished over a similar trawl path near the surface (Fig. 1). These comparison hauls were conducted by first fishing the Cantrawl and then towing the mod-Marinovich over the reciprocal tow path. During these hauls, the Cantrawl headrope depth averaged 3.2 ± 2.8 m (mean ± SD) and the footrope depth averaged 22.7 ± 2.3 m. The mod-Marinovich, which could not be fished as close to the surface, had an average headrope depth of 15.0 ± 5.1 m and a footrope depth of 20.3 ± 4.9 m during the paired surface hauls.

The catches in the recapture nets on the mod-Marinovich were sampled on 9 of the 14 paired hauls (i.e. 5 paired hauls in which the recapture nets were not sampled are included in the analysis).

Trawl catches were weighed, subsampled if large, and the catch was enumerated and identified to species where possible. Fork lengths of a subsample of up to 50 fishes and bell diameters of up to 50 undamaged jellyfishes were measured to the nearest 1.0 mm using an electronic measuring board (Towler and Williams, 2010). The volume (*V*) sampled by each net was computed by estimating the mouth opening as an ellipse based on the mean horizontal and vertical mouth opening (a, b) observed on each haul with the trawl sonar, and multiplying this by the distance fished ($d;\ V = \pi \cdot a/2 \cdot b/2 \cdot d$). The surface area of the mouth opening of the Cantrawl averaged (± SD) 708 ± 97 m^2, and the mouth opening of the mod-Marinovich was 36 ± 2 m^2, which means that the Cantrawl sampled ~20 times more volume per unit distance towed.

3.2 Description of mod-Marinovich escapement pattern

The catches in the recapture nets were used to describe the rate of escapement in different sections of the mod-Marinovich trawl. The proportion *p* of the individuals of a given species entering the trawl mouth that either escapes from a trawl partition or is captured in the codend was calculated as

$$p_i = \sum_s \left(c_{mar,s,i}/f_{mar,i}\right) / \sum_{s,i} \left(c_{mar,s,i}/f_{mar,i}\right), \qquad (1)$$

where *i* represents the mod-Marinovich trawl partition (i.e. the 8 partitions covered by recapture nets and the codend), *s* represents the trawl station, $c_{mar,s,i}$ represents the number of individuals captured at station *s* in partition *i*, and $f_{mar,i}$ is the fraction of the meshes in trawl partition *i* covered by the 2 by 3 mm oval mesh in the recapture nets and the codend (Fig. 2).

Confidence intervals for p_i were estimated by drawing bootstrap samples with replacement from the recapture net trawl hauls in which the species of interest was captured. In a given realization, a bootstrap sample was assembled by randomly drawing a series of trawl stations *s'* with replacement from the subset of the original series of stations s in which the species was captured (i.e. randomly draw from the subset of hauls where the species was captured as many times as there are hauls where the species was captured). The proportion of fish retained in each trawl section was computed using s' and equation 1. Approximate 95% confidence intervals of p_i were estimated by finding the 2.5 and 97.5% percentiles from 10^5 bootstrap realizations.

We compared the size of fish escaping from different sections of the trawl with the length of those captured in the codend in an analogous manner. For each fish k captured in trawl partition i at station s, the length discrepancy from the mean length of fish in the codend catch was estimated as

$$\Delta l_{k,i,s} = l_{k,i,s} - \overline{l_{s,cod}}\,, \tag{2}$$

where $\overline{l_{h,cod}}$, is the mean length of the fish captured in the codend at station s. The mean difference in length for fish in partition i relative to the codend was computed as

$$\overline{\Delta l_i} = \sum_{k,s} \Delta l_{k,i,s}/n_i\,, \tag{3}$$

where n_i is the total number of fish captured in partition i in all hauls. Approximate confidence intervals for Δl_i were estimated by drawing bootstrap samples with replacement from the recapture net trawl hauls as described above.

3.3 Estimation of trawl selectivity

A statistical analysis was undertaken to estimate the selectivity of the mod-Marinovich and the Cantrawl from the recapture nets and the paired hauls. An analysis framework was developed that allowed the catch data from both the paired trawls and the recapture nets on the mod-Marinovich to be considered simultaneously. The observed catch in the trawl partitions in the mod-Marinovich (codend, 4 aft recapture nets, 4 front recapture nets), and the catch in the Cantrawl codend was fit to a statistical model as follows:

The proportion of the total catch at a given station (i.e. a sampling location) of length class *l* expected in the mod-Marinovich codend can be expressed as

$$p_{mar,l} = r_{mar,l} \cdot \rho_{mar} \ , \qquad (4)$$

where $r_{mar,l}$ is the probability that a fish of length *l* entering the mod-Marinovich is retained in the codend, and ρ_{mar} is the fraction of the total volume sampled at this station by the mod-Marinovich i.e. $\rho_{mar} = V_{mar}/(V_{mar}+V_{can})$, where V_{mar} is the volume sampled by the mod-Marinovich net and V_{can} is the volume sampled by the Cantrawl. $r_{mar,l}$ was modeled as a length-dependent logistic function parameterized in terms of the length at which 50% of fish are retained (L_{50}), and the selection range (*SR*; length in cm between 25% and 75% retention):

$$r_{mar,l} = (1 + \exp^{(\frac{k(L_{50}-l)}{SR})})^{-1} \ , \qquad (5)$$

where *l* is length in cm and $k = 2 \log (3)$ (Millar, 1993). The corresponding probability of escapement at length *l* is $1 - r_{mar,l}$.

The proportions of the total catch of length *l* expected in the mod-Marinovich aft and forward recapture nets are:

$$p_{mar,aft,l} = \left(1 - r_{mar,l}\right) \cdot \rho_{mar} \cdot (1-e) \cdot f_{mar,aft} \ , \qquad (6)$$

$$p_{mar,fwd,l} = \left(1 - r_{mar,l}\right) \cdot \rho_{mar} \cdot e \cdot f_{mar,fwd} \ , \qquad (7)$$

Where *e* is a fitted parameter representing the fraction of the mod-Marinovich escapement occurring in the forward panel, and f_{aft} and f_{fwd} are the fractions of the aft and forward mod-Marinovich sections covered by recapture nets (0.055 and 0.022, respectively – see Fig. 2).

The proportion of the total catch of length class *l* expected in the Cantrawl codend is

$$p_{can,l} = r_{can,l} \cdot (1 - \rho_{mar}) \ , \qquad (8)$$

where $r_{can,l}$ is the probability that a fish entering the Cantrawl mouth is retained in the codend, which has the same logistic form as $r_{mar,l}$.

The total number of fish (U) in the volume sampled by all trawls deployed at each trawl station s (i.e. $V_{mar,s}+V_{can,s}$) can be estimated by dividing the catch of that length class by the expected proportion of animals retained in the trawl partitions i and summing over length classes:

$$U_s = \sum_l \left(\sum_i c_{i,s,l} / \sum_i p_{i,s,l} \right) . \tag{9}$$

Note that this allows for cases where only some trawl partitions were sampled to be included in the analysis (e.g. stations where the Cantrawl was not deployed are handled by setting the volume sampled by the Cantrawl ($V_{can,s}$) and the Cantrawl codend catch ($c_{can,s}$) for that station to zero).

The predicted total catch y in each partition i at each station is estimated as

$$y_{i,s} = p_i \cdot U_s . \tag{10}$$

The size-dependent selectivity in the mod-Marinovich and Cantrawl (r_{mar} and r_{can}) and e, the proportion of the mod-Marinovich escapement in the forward panel were fit by maximizing agreement of the observed (c) and predicted (y) catches over all partitions i (i.e. mod-Marinovich codend, 8 partitions sampled by recapture nets, and the Cantrawl codend) and all stations s by maximizing the following log likelihood function:

$$LL = \sum_s \sum_i \left(c_{i,s} \cdot \ln(y_{i,s}) - y_{i,s} \right) , \tag{11}$$

which assumes that the probability of capture follows a Poisson distribution, similar to the model described by Kirkwood and Walker (1986). Thus, fitting the model for a given species or species group produces maximum likelihood estimates for 5 parameters, two for the logistic function $r_{mar,}$ two for the logistic function $r_{can,}$ and e, the proportion of Marinovich escapement occurring in the front panel, which is not of immediate interest, but must be accounted for in the model.

Interpretation of the selectivity estimates derived by the model depends on the estimate of volumetric abundance of a given organism in the path of both trawls (i.e. U_s in equation 9). This is most easily understood when the volumetric density of the organism estimated from the mod-Marinovich (i.e. catch and escapement combined) exceeds the catch rate in the Cantrawl codend (as is generally the case – see section 3.4). In this situation, a selectivity of 1 corresponds to the case in which all the catch in the mod-Marinovich occurs in the codend (i.e. no catch of this species/size class in the recapture nets, indicating that all individuals entering the net are retained). If the volumetric density estimated from the Cantrawl codend exceeds the density estimated from the Marinovich (i.e. catch and escapement), the Cantrawl is assumed to be fully selective for this species/size class (i.e. selectivity =1). However, in either case, the results can be interpreted in terms of the ratio of the Cantrawl to mod-Marinovich selectivity. The model was fit to catches of the following species groups: Arctic cod (Boreogadus saida), saffron cod (Eleginus gracilis), Pacific sand lance (Ammodytes hexapterus), capelin (Mallotus villosus), all other fishes combined (various species pooled, ~ 23.2 % of catch was larvae), and jellyfishes (86.4% *Cyanea capillata* , 13.4 % *Chrysaora melanaster*). The results for Arctic cod are presented in detail, as this group was abundant and was consistently captured in the survey area. The results for other species groups are summarized.

A bootstrap resampling procedure was employed to evaluate the uncertainty in the parameters of the two logistic functions. For each species group, a bootstrap sample was assembled by establishing the number of cases in which the species was captured in 1) paired hauls 2) paired hauls with Marinovich recapture nets and 3) mod-Marinovich hauls with recapture nets. A bootstrap sample comprised of this number of trawls of each type (i.e. paired, paired with recapture nets, mod-Marinovich with recapture nets) was randomly drawn with replacement from the trawls in which at least 1 individual was caught. The parameters of the selectivity function were fit to the data with the model described above for 10^5 bootstrap samples.

The resulting L_{50} and *SR* parameters were often variable, and were particularly uncertain for species and size ranges where few individuals were captured, as there was little data to constrain the fit in these areas of the curves. We chose to use the 90% confidence intervals of the parameters to characterize variability of the parameter estimates, as in some bootstrapped samples the total catch was low and the tails of the bootstrap parameter estimates were highly skewed. To evaluate the relative performance of these two nets for the size distribution of animals encountered in the survey, the selectivity parameters were used to calculate the average probability (*pc*) that fishes with a size distribution corresponding to that in the environment are retained by the trawl, i.e.

$$\boldsymbol{pc} = \sum_{\boldsymbol{l}} \boldsymbol{r_l} \cdot \boldsymbol{PL_l}\,, \tag{12}$$

where $r(l)$ is as in eq.5, PL_l is the proportion of the population in length class *l* in the environment. *PL* was estimated from the mod-Marinovich hauls equipped with recapture nets, as this accounts for the size distribution of fish that are not retained in the trawl as well as those that are captured,

$$\boldsymbol{PL_l} = \left(\sum_{\boldsymbol{s,i}} \boldsymbol{c_{mar,i,l,s}} / \left(\boldsymbol{f_{mar,i}} \cdot \boldsymbol{v_{mar,s}}\right)\right) / \left(\sum_{\boldsymbol{s,i,l}} \boldsymbol{c_{mar,i,l,s}} / \left(\boldsymbol{f_{mar,i}} \cdot \boldsymbol{v_{mar,s}}\right)\right) \tag{13}$$

where *l* represents length, *i* represents the mod-Marinovich trawl partition (codend, 4 aft recapture nets, 4 forward recapture nets), *s* represents station, $c_{mar,i}$ represents the number of individuals captured in mod-Marinovich partition *i*, and $f_{mar,i}$ is the fraction of the meshes covered by the recapture nets or codend liner in partition *i* (e.g. Fig. 2), and $v_{mar,s}$ is the volume sampled by the mod-Marinovich in at station *s*. The quantity *pc* quantifies the probability that a fish of the size distribution estimated to occur in the environment (*PL*) was captured by the trawl, and is contingent on the assumption that the volumetric density of this organism is reflected by U_s. In addition, the selectivity at size of 4 cm (i.e. l = 4 cm) was computed to allow for comparisons of selectivity across species at common size. The bootstrap estimates of mean selectivity at the size distribution estimated to occur in the environment (*PL*), and the estimated selectivity at a common size of 4 cm are presented as boxplots.

4 Results

4.1 Trawl catches

The fishes captured in the trawl hauls were generally small. For example, in the 14 paired hauls, they were primarily < 12 cm in size (Fig. 3A). The mod-Marinovich captured ~ 11.2 times more fishes in the codend per unit volume sampled than the Cantrawl in the paired hauls (Fig. 3A). The species composition of fishes (Fig. 3 B-C) in the trawl catch differed ($p < 0.001$; Chi-squared test on the aggregated trawl catch from the 14 paired trawl hauls), with Pacific sand lance, other fishes, and jellyfish comprising a higher proportion of the catch in the mod-Marinovich than in the Cantrawl. In contrast, capelin and Arctic cod made up a higher proportion of the Cantrawl catch than the mod-Marinovich catch.

A substantial number of individuals were caught in the recapture nets, indicating that there was high escapement from the mod-Marinovich (Table 1). In the 30 mod-Marinovich hauls with recapture nets, 36.8 % of all fishes captured were retained in the recapture nets, which covered only ~3.1 % of the unlined meshes in the trawl body, and 63.2 % of the total was captured in the codend. Depending on the species, between 28-52 % of the total catch was captured in the recapture nets (Table 1). The individuals captured in the codend were consistently larger than those in the recapture nets (Table 1), which indicates that larger specimens were preferentially retained in the mod-Marinovich codend.

When expressed as catch per unit volume sampled, catch rates tended to be higher for the mod-Marinovich than the Cantrawl. For example, in the 7 paired trawls with mod-Marinovich recapture nets where Arctic cod were caught, an average of 83.4 juvenile Arctic cod were calculated to enter the net (i.e. mod-Marinovich codend + escapees) for every 1000 m^3 of water sampled, with 6.9 fish (~ 8.3 %) retained in the mod-Marinovich codend, and 2.3 fish (~ 2.7 %) fish retained in the Cantrawl codend (Fig. 4 A). This indicates that the majority of small Arctic cod escaped the trawls, and that the probability of capture in the Cantrawl is lower than in the mod-Marinovich. On average, smaller individuals were caught in the recapture nets, intermediate sizes in the mod-Marinovich codend, and larger specimens in the Cantrawl (Fig. 4B). This indicates that there is a low probability that juvenile Arctic cod entering the nets will be retained in the codends, and that the probability of retention is size-dependent, with smaller individuals less likely to be retained.

4.2 Escapement pattern in the mod-Marinovich

Juvenile Arctic cod and Pacific sand lance exhibited similar escapement patterns (Fig. 5 A-D). The majority of individuals entering the trawl exited the net through the aft trawl meshes (Fig. 5 A, C), with only a small fraction of individuals retained in the trawl codend. There was higher escapement of Arctic cod in the bottom of the trawl compared to the sides and the top panel (Fig. 5 B), and Pacific sand lance escapement exhibited a similar pattern but with overlapping confidence intervals (Fig. 5D).

Juvenile saffron cod, which are similar in size (Table 1) and gross morphology to juvenile Arctic cod tended to exhibit a higher proportion of escapement in the forward meshes of the mod-Marinovich than the other species (Fig. 5 E), and higher escapement in the bottom and side panels than in the top trawl panel (Fig. 5 F). Saffron cod were relatively poorly retained in the codend compared to Arctic cod, with 3.3 % (95% CI: 2.7-4.5 %) of juvenile saffron cod and 8.7% (95% CI: 7.0-9.8 %) of juvenile Arctic cod retained in the codend (Fig 5 A, E). Capelin escapement occurred primarily in the aft part of the mod-Marinovich (Fig 5 G). The probability of capelin escapement in the top, sides and bottom of the trawl exhibited broadly overlapping confidence intervals. However, there is an indication that capelin escapement may be high in the top panel, which was not the case for the other species.

When interpreting these results, one should keep in mind that these estimates are for escapement out of the entire panel, and that the panels differ in size. For example, in the case of Arctic cod, 36.3 % of the total escapement was estimated to occur in the bottom aft panel, which represents 7.2 % of the unlined trawl meshes. Thus, escapement expressed per unit surface area would be much higher in the aft panel than depicted in Fig. 5. Additionally, the sample sizes differ substantially among species (Table 1), and the size of the confidence intervals reflects both the variability in behavior and the sample size.

Mean fish size tended to be slightly larger in the codend than in the recapture nets (Fig. 6), but there was substantial inter-haul variability in the mean size of fish capture in the various recapture nets, as shown by the overlap in the bootstrap confidence intervals. Arctic and saffron cod captured in the forward and aft recapture nets were consistently smaller than those captured in the codend (Fig. 6 A, E). Capelin captured in the forward recapture nets tended to be smaller than those in the aft recapture nets and codend (Fig. 6 G). Pacific sand lance captured in the different net partitions did not differ substantially in size. The catches of all species in the top, side and bottom recapture nets were similar in mean length (Fig. 6 B, D, E, F).

4.3 Estimates of trawl size and species selectivity

The numerical abundance and size distribution of fishes in the codends of both trawls and those calculated to escape from the meshes of the mod-Marinovich trawl (e.g. Fig. 4 A-B) were used to fit logistic size selection curves for each trawl. Overall, the estimates were highly size-dependent and for small size classes, relatively low for both trawls (Fig. 7). The mod-Marinovich retained a larger fraction of small organisms in the codend (i.e. compare Fig 7A and B at < 5 cm). The Cantrawl selectivity for jellyfish and Pacific sand lance was particularly low. The size-selectivity of the Cantrawl was steeper than that of the mod-Marinovich, with very low selectivity for individuals < ~5 cm. On average, the mod-Marinovich had a higher probability of capturing the (relatively small) species and size classes present in this environment than the Cantrawl, with the exception of the larger size classes of capelin (see dotted line in Fig. 7).

The bootstrap analysis, which reflects between-haul variation in the number and size of fish captured in the trawl partitions, indicates that the L_{50} and SR parameters are often highly uncertain (Table 2). In some bootstrap realizations there was little size dependence, and the selectivity curve was relatively flat (high *SR*), or selectivity decreased with size (negative *SR*). In cases where size dependence was low (high absolute value of *SR*), L_{50} was often variable, which contributed to the broad confidence intervals for L_{50}. However, the logistic curves described by the combination of these parameters tended to be relatively constrained for the most abundant species and size classes in the catch (e.g. see < 5 cm Arctic cod in Fig. 8). The selectivity estimates tended to be less uncertain for the mod-Marinovich than the Cantrawl (e.g. compare Fig. 8 A-B), as the estimates for the mod-Marinovich are based on more hauls and do not depend solely on the paired trawl experiment, which has a limited sample size and is subject to uncertainty introduced by differences in fish abundance in each trawl path.

Despite the variability in the parameter estimates, the conclusions drawn from the analysis are relatively robust for the size ranges observed in the trawl catches. For example, when the selectivity of the gear for 4 cm individuals as well as the size distribution estimated to be in the environment is considered (Fig. 8), two main conclusions can be drawn: 1) there are strong species-specific differences in the probability of capture. For example, Arctic cod are substantially better retained than saffron cod of equivalent size (see Fig. 9 A-B, keeping in mind that axes differ among plots). 2) Overall, the mod-Marinovich tends to be less selective than the Cantrawl (i.e. Fig. 9, compare left and right box plots in a panel). There is a tendency in many bootstrap realizations for larger capelin to be better retained by the Cantrawl than by the mod-Marinovich (Fig. 9 D), but there is substantial overlap in the bootstrap estimates indicating that this is not consistent among hauls.

5. Discussion

The trawl experiment revealed that there was substantial escapement of small fishes from both the mod-Marinovich and Cantrawl midwater trawls. Escapement from the Cantrawl was higher than the mod-Marinovich for most size/species classes encountered. In general, there was less escapement from the mod-Marinovich, but even for this relatively small net, a surprisingly small fraction (< 10%) of the small fishes in this environment were retained in the codend. It is possible that many of the small fishes in this environment exhibit relatively weak herding responses to the meshes once they enter the trawl which results in a substantial fraction of individuals encountering and then exiting from the meshes. The fish encountered in this study were relatively small, and one should be careful not to extrapolate the resulting selectivity estimates to larger size classes rarely encountered in these catches. The logistic function used to describe size selectivity is constrained to be symmetric about a selectivity of 0.5 (Wileman et al., 1996). Thus the selectivity for size classes absent from the catch cannot be estimated with any confidence..

As documented in previous studies (Nakishima, 1990, Suuronen et al., 1997, Williams et al., 2011), escapement was strongly size and species specific. Although both nets were size selective, the Cantrawl exhibited very low retention of fishes < ~5 cm, which were abundant in this environment. The Cantrawl was not very effective at capturing jellyfish, likely due to negligible herding ability in response to the large meshes that comprise most of the trawl body. Although there was substantial uncertainty in the parameters of the logistic selectivity functions, there was less uncertainty in the selectivity of the mod-Marinovich for the most commonly encountered species and size classes. The observed trawl selectivity indicates that ignoring trawl selectivity and assuming that the trawl catch accurately represents species and size composition has the potential to introduce substantial biases into AT and other trawl-based survey estimates. Although the mod-Marinovich is a relatively small mesh trawl designed to capture small fishes, a surprisingly large fraction of fish entering the trawl are lost through the meshes. The biases introduced by this trawl selectivity, which will be more severe for the Cantrawl, will result in over-estimates of large and easily captured individuals, and underestimates of the less easily captured species and smaller size classes (Nakashima, 1990, Williams et al., 2011).

The catches in the recapture nets on the mod-Marinovich revealed that escapement differs among sections of the trawl. As observed in previous studies employing recapture nets on bottom (Zijlstra, 1969, Matsushita et al., 1993) and pelagic trawls (Nakashima, 1990, Suuronen et al., 1997, Williams et al., 2011, 2013), escapement was size-dependent and tended to be highest in the aft portion of the net. In the case of Arctic cod and Pacific sand lance, escapement was highest in the bottom aft part of the trawl, as has been observed with juvenile pollock (Williams et al., 2011). Escapement for saffron cod was more evenly distributed. It was high in the bottom and sides of both the forward and aft panel, but relatively low in the top panel. Escapement of capelin exhibited a different pattern, with higher escapement in the aft part of the trawl and a tendency towards more escapement in the top rather than bottom panel as observed for the other species. The behavior of capelin is consistent with the observations of Nakashima (1990), who found that capelin escapement in a pelagic trawl tended to be upwards towards the rear of the net.

The observed escapement pattern can be exploited to design more effective nets. For example, the surprisingly high escapement of small fishes observed in the aft section of the mod-Marinovich has motivated us to further modify this net by increasing the length of the aft section to produce weaker flow out of the meshes, and reducing the mesh size to reduce escapement. Smaller, fine-mesh trawls could potentially be used to more effectively sample small fishes such as those abundant in the Arctic Eis survey area. However, small trawls are likely subject to higher avoidance of species and size classes with well-developed swimming capabilities, and may exhibit strong size selectivity. These uncertainties highlight the importance of evaluating trawl selectivity to guide selection of appropriate trawl gear, and to correctly infer the size and species composition in the environment from trawl catches.

The conclusions drawn from this analysis rest on several assumptions. The calculations are based on the assumption that escapement from meshes covered by the recapture nets is representative of meshes without recapture nets, which was not tested. However, recapture nets of a similar design have not been reported to alter the behavior of fish relative to the surrounding uncovered meshes (Nakashima 1990, Matsushita et al., 1993, Williams et al., 2013). In addition, the escapement from the trawl is estimated based on the relatively small fraction of the net covered by the recapture nets. Although the number of meshes covered by the recapture nets is known, the relatively low coverage likely introduces substantial variability as the fraction of the net which is covered by recapture nets is not the same as the fraction of escapees that is recaptured in a given trawl haul, even if escapement from meshes covered by the recapture nets is representative of meshes without recapture nets. This will contribute to the uncertainty in the estimates of escapement, and larger or more recapture nets would reduce this uncertainty. We did not observe strong gradients in size composition of escapees across recapture nets, which indicates that the size distribution in the recapture net are a reasonable approximation of the size distribution of the escapees from the entire net partition.

Furthermore, the analysis of the paired trawls assumes that the average fish density encountered by the Cantrawl and the mod-Marinovich was equivalent. Although the depth range sampled in the paired trawls overlapped substantially, the average headrope depth of the Cantrawl, which was rigged as a surface trawl, was consistently shallower than the mod-Marinovich headrope, and this may introduce biases in the selectivity values estimated for species exhibiting strong near-surface vertical abundance gradients. In addition, it is likely that at a given location, one of the trawls will encounter higher densities or different size distributions due to small-scale patchiness. This will not result in a bias if the two nets encounter the same densities on average, but will increase the variance of the counts in the trawl partitions. This additional variance is captured as between-haul variation in the process of resampling the trawl hauls to generate bootstrap confidence intervals (Millar and Fryer, 1999), and likely contributed to the wide confidence intervals of the selectivity parameters.

We have estimated mesh selection (i.e. the probability that fish will be captured in the codend as opposed to escaping through the meshes), which is only one component of selectivity and does not include selection that takes place in front of the net itself (Wileman, 1996, Suuronen et al., 1997, Heino et al., 2011). The fish in this Arctic environment are small, and mesh selection is likely the primary cause of selectivity. While some species have been reported to lack a strong herding response to the vessel, doors, and bridles (e.g walleye pollock, Somerton, 2004, Williams et al., 2015), the processes occurring prior to the time the fish encounter the mouth of a pelagic trawl remain poorly understood. In most cases, the catch rate was substantially higher for the much smaller mod-Marinovich, which suggests that mesh selection is an important factor in determining selectivity. The larger size classes of capelin may be an exception as this was the only case where the Cantrawl captured more fish per unit volume than the Marinovich. This may suggest that processes occurring prior to when the capelin encountered the net, for example herding by the trawl wings, doors , or bridles, or escapement in front of the trawl (Heino et al., 2011), may have played an important role in the capture of this species. Alternately, because the Cantrawl headrope was fished near the ocean surface (~3 m depth), whereas the average mod-Marinovich headrope depths were ~12 m deeper in the paired comparisons, the increased Cantrawl catch rate may have occurred because greater densities of capelin occurred above the depth sampled by the mod-Marinovich.

The impacts of trawl selectivity on acoustic surveys can be difficult to predict, as errors in species composition that alter the relative abundance of one species or size class will affect the proportion of backscatter assigned to all other species (Simmonds and MacLennan, 2005). The impact of trawl selectivity depends on the species present, their degree of spatial overlap, their size distributions, and their acoustic scattering properties, all of which interact (Williams et al., 2011, De Robertis et al., this issue). A practical method to evaluate the impact of trawl selectivity is to compare abundance estimates with and without accounting for trawl selectivity on species and size composition. For example, in the Arctic Eis acoustic-trawl survey the impacts of trawl selectivity on abundance estimates depend on the trawl gear used and are highly species-dependent. In the case of the 2012 survey, the Cantrawl was used for midwater and surface trawl sampling (De Robertis et al., this volume). The AT survey estimates use the selectivity estimates derived in this study to allocate acoustic backscatter to species. However, if the effects of trawl selectivity are ignored (i.e. by assuming that selectivity = 1 for all species and sizes), the abundance estimate of capelin, which are well-retained and thus over-represented in the catch, increases by > 3 fold (De Robertis et al., this issue). This over-estimate of the abundance of capelin causes the abundance of other, more poorly retained species such as Arctic and saffron cod to decrease by up to ~30 % in this scenario (i.e. backscatter from these species is allocated to capelin). In 2013, the survey results are less sensitive to trawl selectivity estimates as the high-backscatter regions were sampled with the less selective mod-Marinovich and the corrected and uncorrected estimates are thus more similar (De Robertis et al., this issue).

In cases where selectivity is primarily attributable to processes occurring inside the net rather than in front of the net, recapture nets provide a viable method to estimate the selectivity of midwater trawls used in acoustic-trawl surveys, which has been proven difficult to quantify due to the large size of these nets. One practical advantage of the method employed here is that it can be conducted without disruption to survey operations by deploying recapture nets on the survey trawl during the survey. Trawl efficiency is influenced by conditions during capture such as water temperature and light levels (Zijistra 1969, Suuronen et al., 1997, Williams et al, 2011, 2015). By conducting the trawl selectivity work throughout the survey, the range of conditions, such as species and size distributions and environmental conditions (location, sea state, temperature, time of day, light level, etc.) during the trawl selectivity work will be representative of conditions during the survey as a whole, thus reducing the impact of these potential biases. Additionally, this sampling design will ensure that there will be greater sample sizes for many of the more common species, resulting in higher certainty in the selectivity estimates for the most important species. Despite the potential limitations of the methods used in this study, and the relatively large confidence intervals in the selectivity estimates for less abundant species and size classes, the recapture net technique provides a practical method for estimating the first-order effects of trawl selectivity on an acoustic-trawl survey and other studies relying on midwater trawl catches. This is preferable to making the common implicit assumption that the size and species composition of organisms retained in a pelagic trawl reflects the size and species distribution in the environment.

6. Acknowledgements

We are indebted to Pohl Petersen of Dantrawl Inc. for designing the modifications to the Marinovich trawl net, David King and staff of the AFSC net shed for constructing the mod-Marinovich, to Brian Haley and the crew of F/V *Bristol Explorer* for their skill in fishing the trawls, and to the participants in Arctic Eis surveys for processing 'one more pocket net'. Franz Mueter, Stan Kotwicki, Dan Cooper, and Jeff Napp provided helpful comments on drafts on the manuscript. This work was funded with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior and by the Alaska Fisheries Science Center, NOAA. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Table 1: Summary of the most abundant fishes captured in mod-Marinovich hauls equipped with recapture nets. The number of hauls in which a given species was captured, and the total numbers of individuals captured, as well as the number captured in the codend and all recapture nets are listed. The mean and standard error of the fork length of the specimens and the number of specimens measured are also given.

Species	# hauls	Total # captured	# in codend	# in recapture nets	Length (cm) in codend $\bar{x}$ ± SE, (n)	Length (cm) in recapture nets $\bar{x}$ ± SE, (n)
all fishes	30	63826	40310	23516	4.6 ± 0.1 (2596)	3.7 ± 0.2 (5814)
Arctic cod	28	38172	25077	13095	4.0 ± 0.1 (941)	3.5 ± 0.2 (2337)
Pacific sand lance	28	11762	8468	3294	5.8 ± 0.1 (302)	5.3 ± 0.1 (473)
saffron cod	16	4319	2057	2262	4.0 ± 0.1 (371)	3.7 ± 0.1 (863)
capelin	20	701	482	219	6.4 ± 0.1 (169)	6.1 ± 0.1 (98)

Table 2. Description of data used to fit logistic size selection for the mod-Marinovich and Cantrawl trawls by species group, and the resulting parameter estimates. The number of individuals captured in the codend of each trawl, the number of hauls of each type where the species group was captured, and the parameters of the point estimates (i.e. estimated with all available data, see Fig. 6) of the logistic selection curves with bootstrap estimates of the 90% confidence intervals for these parameters are listed. L_{50} is the length in cm at 50% retention, and *SR* is the length in cm between 25 and 75% retention. In the case of the Cantrawl selectivity for Pacific sand lance, the point estimate of L_{50} and SR fall outside of the 90% bootstrap confidence interval.

Species Group	No. captured Marin. codend	No. captured Cantrawl codend	No. hauls paired only	No. hauls recapture only	No. hauls paired with recapture	Marin. L_{50} (cm) (90% CI)	Marin. *SR* (cm) (90% CI)	Can. L_{50} (cm) (90% CI)	Can. *SR* (cm) (90% CI)
Arctic cod	26550	23305	5	20	7	6.2 (5.4,7.2)	2.2 (1.6, 3.1)	5.6 (4.2, 6.1)	0.8, (0.1, 0.9)
saffron cod	2055	3406	0	8	5	13.0 (10.1, 26.1)	6.1 (4.2, 14.2)	6.8 (-11.3, 17.2)	1.1 (-0.9, 3.2)
Pacific sand lance	8672	532	4	11	8	13.6 (7.4, 25.4)	5.9 (2.1,15.5)	129.6 (-90.1, 87.0)	34.4 (-24.9,20.8)
capelin	496	13113	4	10	6	31.5 (-56.7, 73.7)	24.7 (-58.9, 63.7)	8.0 (-6.0, 25.8)	1.9 (-10.1, 15.5)
other fishes	5199	462	5	22	8	11.7 (10.1, 31.3)	5.3 (4.3, 15.7)	13.5 (9.7, 34.7)	2.7 (1.7, 8.2)
jellyfish	7598	1939	4	21	9	4.1 (2.0, 4.7)	1.8 (0.1, 2.1)	66.0 (-145.6, 397.1)	36.0 (-94.8, 236.8)

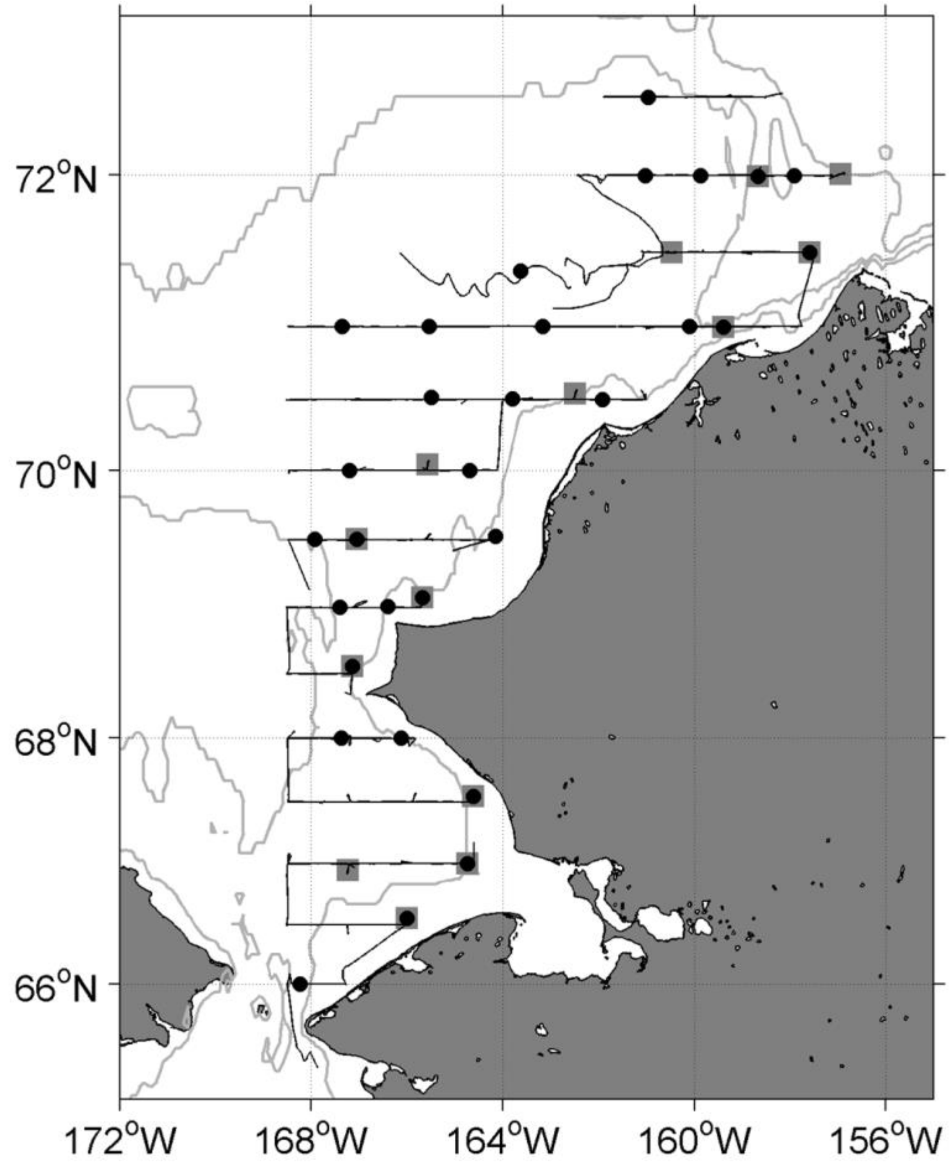
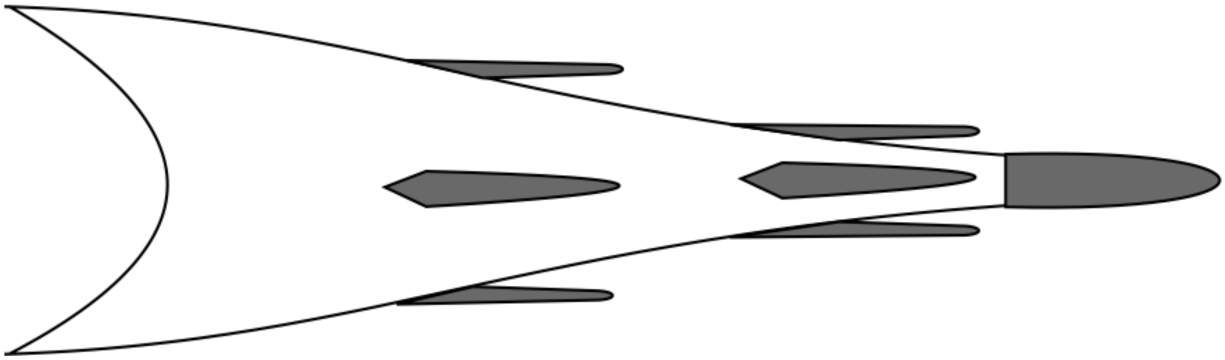


Figure 1. Estimates of trawl size and species selectivity. The locations of paired Cantrawl and mod-Marinovich trawl stations are shown as grey squares, and stations where the mod-Marinovich was fished with 8 recapture nets are given as black circles. Locations with both a circle and a square indicate the trawl stations where paired trawls and resample nets were deployed. The vessel survey track is shown as a black line and the 25, 50 and 100 m depth contours are shown as grey lines.



Section	Forward	Aft	Codend
Stretched mesh size (cm)	6.4,6.0	4.8	3.8 cm with 0.3 cm liner
Approx. length (m)	2.9,3.2	4.3	3.3
Fraction sampled	0.022	0.055	1.0

Figure 2. Illustration of recapture nets used on mod-Marinovich fishing trials. The figure depicts the net viewed from the side with recapture nets on the forward and aft sections of the symmetrical top, side, and bottom panels visible. The two forward panels of different mesh sizes are designated as the forward section, the aft section as a single unlined panel, and the codend consists of the aft section lined with a fine-mesh liner (see section 2.1 for details). The sampling fraction represents the ratio of the number of meshes covered by the recapture net or the codend and the total number of unlined meshes in each section.

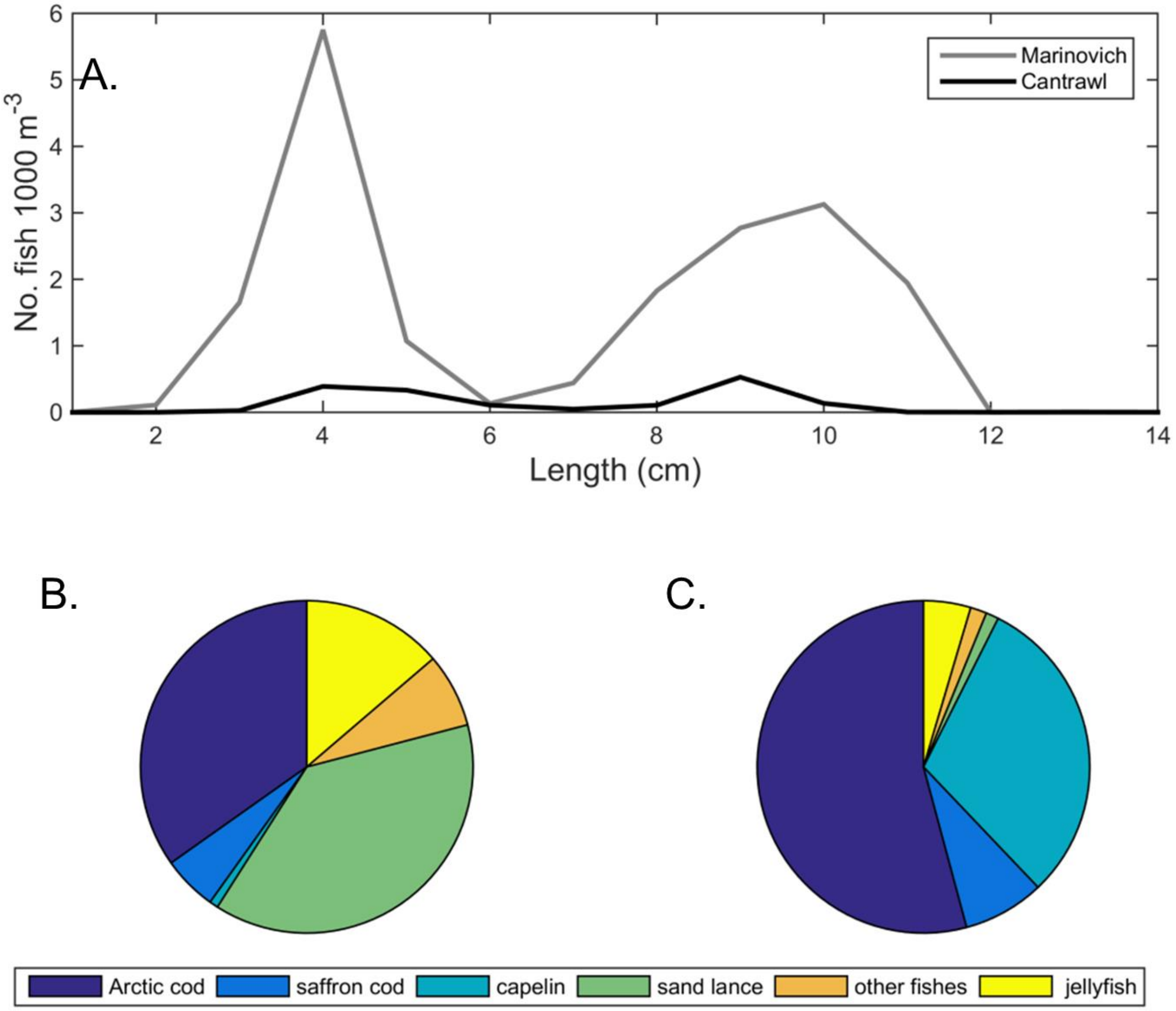


Figure 3. Summary of codend catch in the 14 locations where paired mod-Marinovich and Cantrawl hauls were conducted. A) Abundance of fishes by length captured by each trawl (all species combined). The pie graphs show the catch composition (by number) of B) the mod-Marinovich catch and C) the Cantrawl catch at these locations.

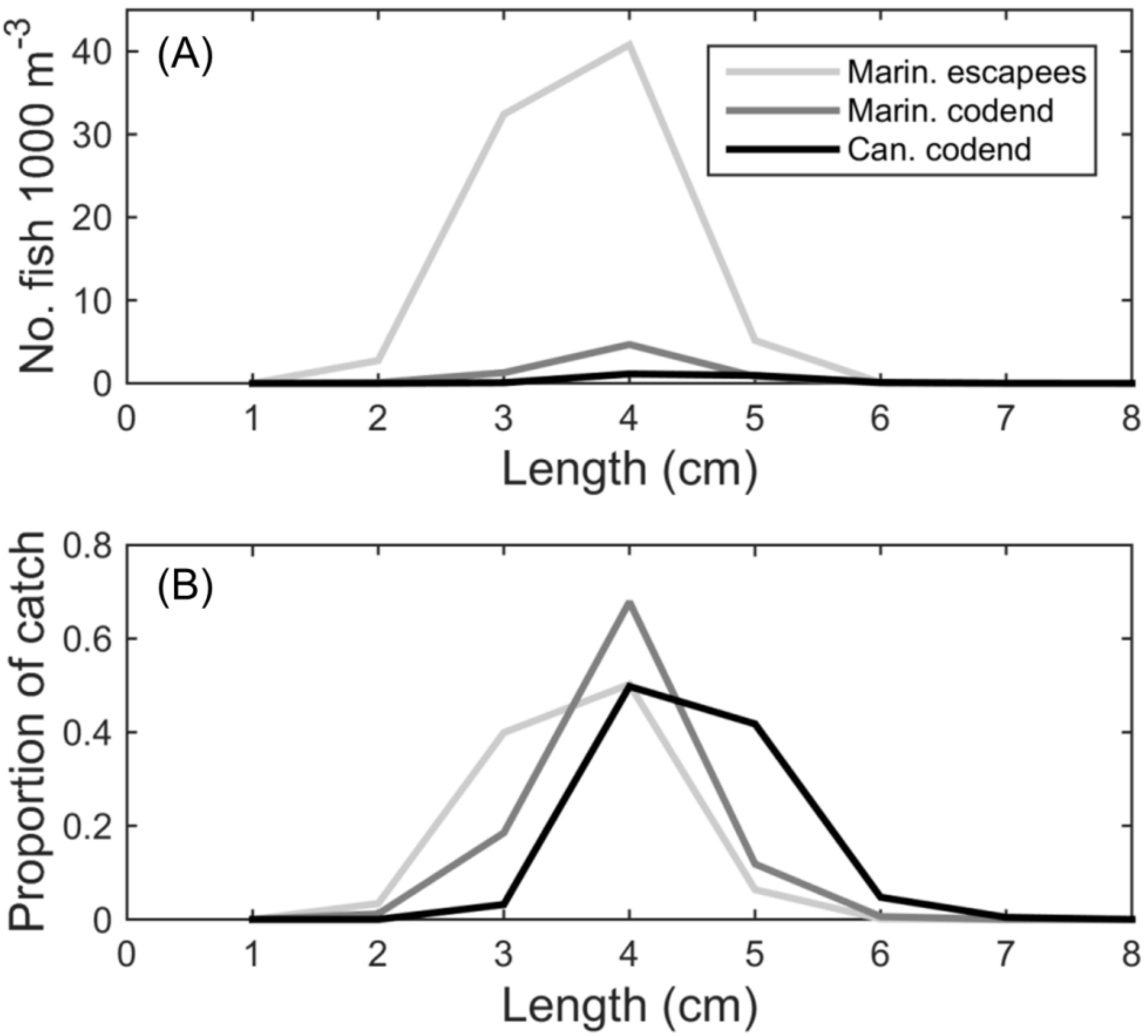


Figure 4. Abundance and size distribution of Arctic cod escaping from the mod-Marinovich trawl, and those captured in the mod-Marinovich and Cantrawl codends. The catches represent the catch in the 7 hauls where the mod-Marinovich with recapture nets and Cantrawl net were deployed and Arctic cod were caught. A) Abundance of fish as a function of length estimated to escape from the mod-Marinovich based on the recapture net catches and abundance of those captured in the codends of the mod-Marinovich and Cantrawl trawls. Abundances of escapees are computed by extrapolating the recapture net escapement over the body of the net. B) Size distribution of juvenile Arctic cod in recapture nets, and the codends of the mod-Marinovich and Cantrawl trawls.

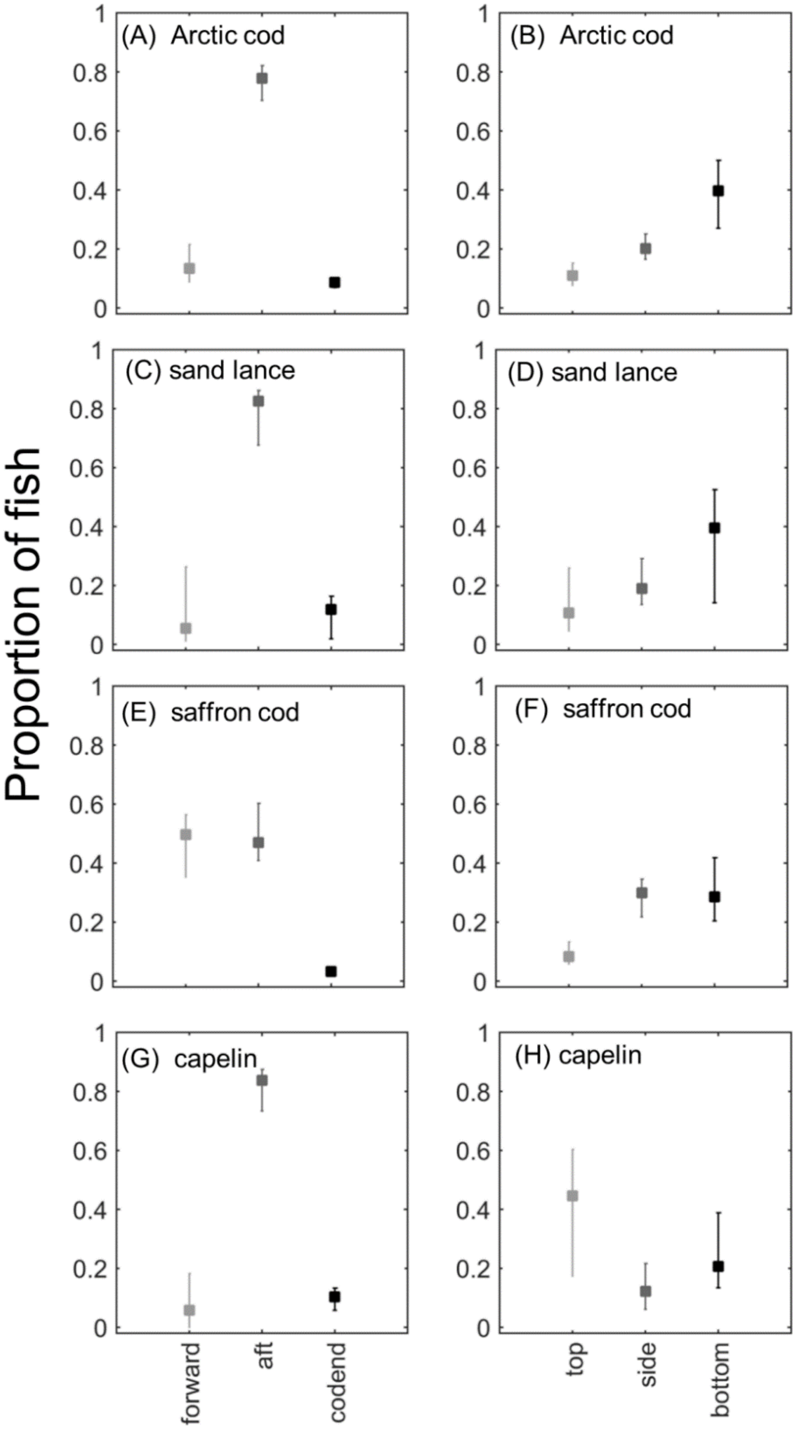


Figure 5. Escapement pattern in mod-Marinovich for abundant fish species derived from recapture net catches. A-B) Arctic cod, B-C) Pacific sand lance, E-F) saffron cod, G-H) capelin. Panels on the left indicate the proportion of fish entering the trawl mouth estimated to either escape through the forward or aft net sections or be retained in the codend. Panels to the right depict the proportion of individuals expected to exit the net through the meshes in the top, either side (i.e. total escapement from both sides divided by 2), and bottom of the trawl. The points represent the observed means, and error bars represent 95% bootstrap confidence intervals.

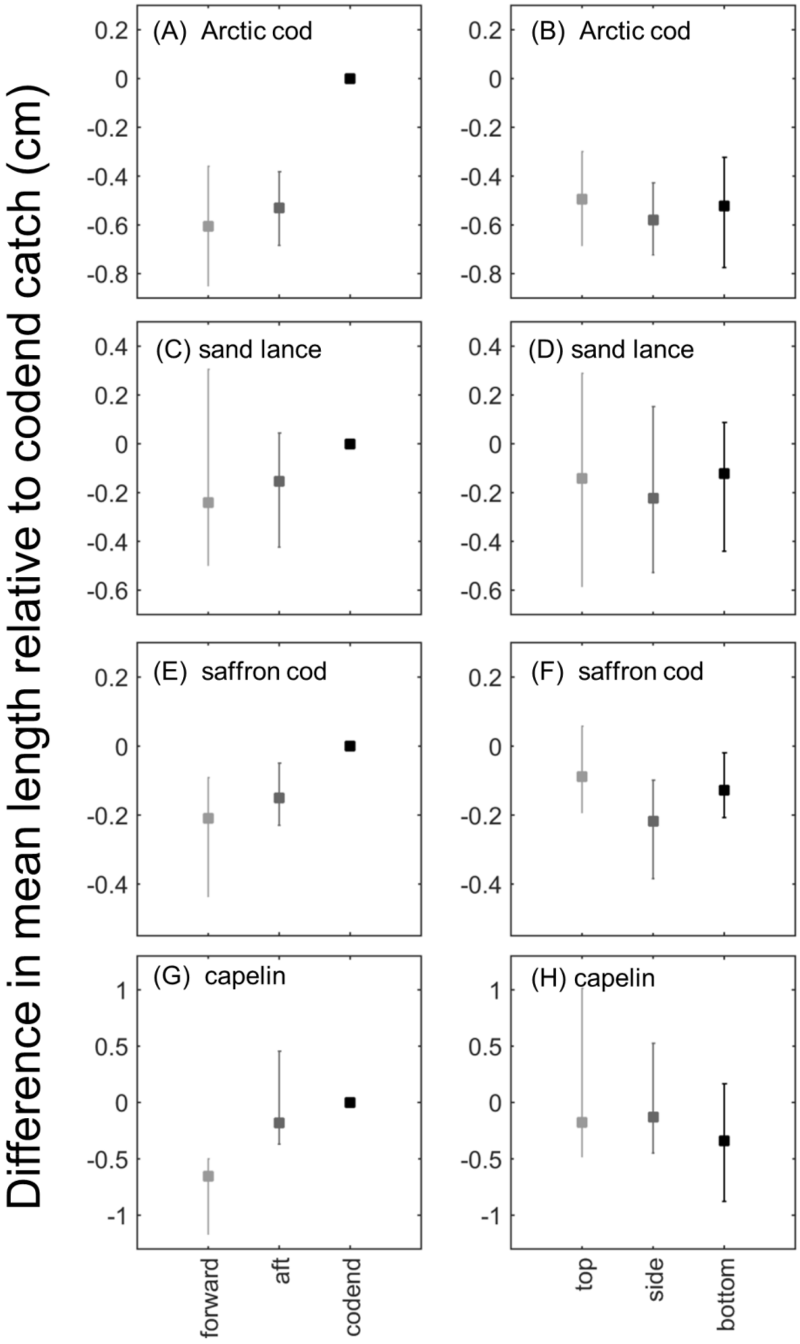


Figure 6. Size of fishes escaping from and retained in the mod-Marinovich based on catches in the codend and recapture nets. A-B) Arctic cod, B-C) Pacific sand lance, E-F) saffron cod, G-H) capelin. Panels on the left indicate the mean difference in length between fish captured in forward and aft recapture nets and those retained in the codend. Panels to the right depict the mean difference in length of fishes captured in the top, side and bottom recapture nets. The points represent the observed means, and error bars represent 95% bootstrap confidence intervals.

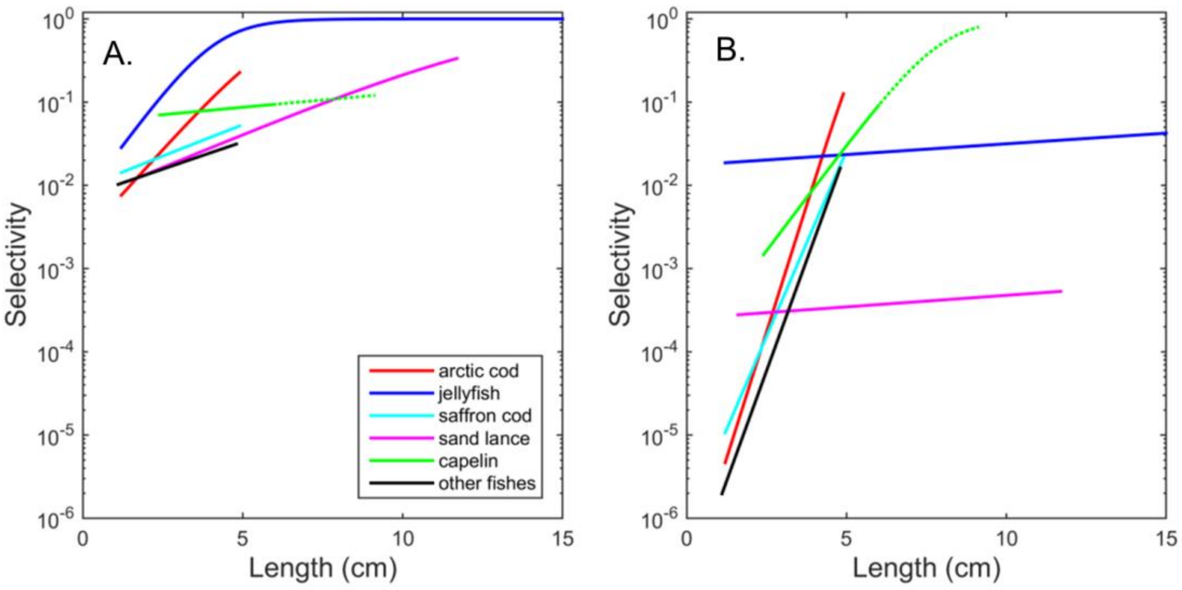


Figure 7. Estimates of size-specific selectivity by species group for A) mod-Marinovich and B) Cantrawl trawls derived from joint analysis of catches in the mod-Marinovich recapture nets and codend catches in both trawls. The logistic selectivity curves fitted in the model are depicted on semi-log plots as the probabilities of retention are low for small individuals. The predicted selectivity at a given size was higher for the mod-Marinovich than the Cantrawl except for the case of large capelin where the dotted green indicates that the calculated selectivity for capelin is higher for the Cantrawl. The curves extend over the size range encompassing 99% of the fish in the environment (as estimated by combining the mod-Marinovich codend catch with the recapture nets, equation 13). Note that the corresponding size range for jellyfish extends to 26 cm, but results are truncated to 15 cm to increase the visibility of the results for the other species.

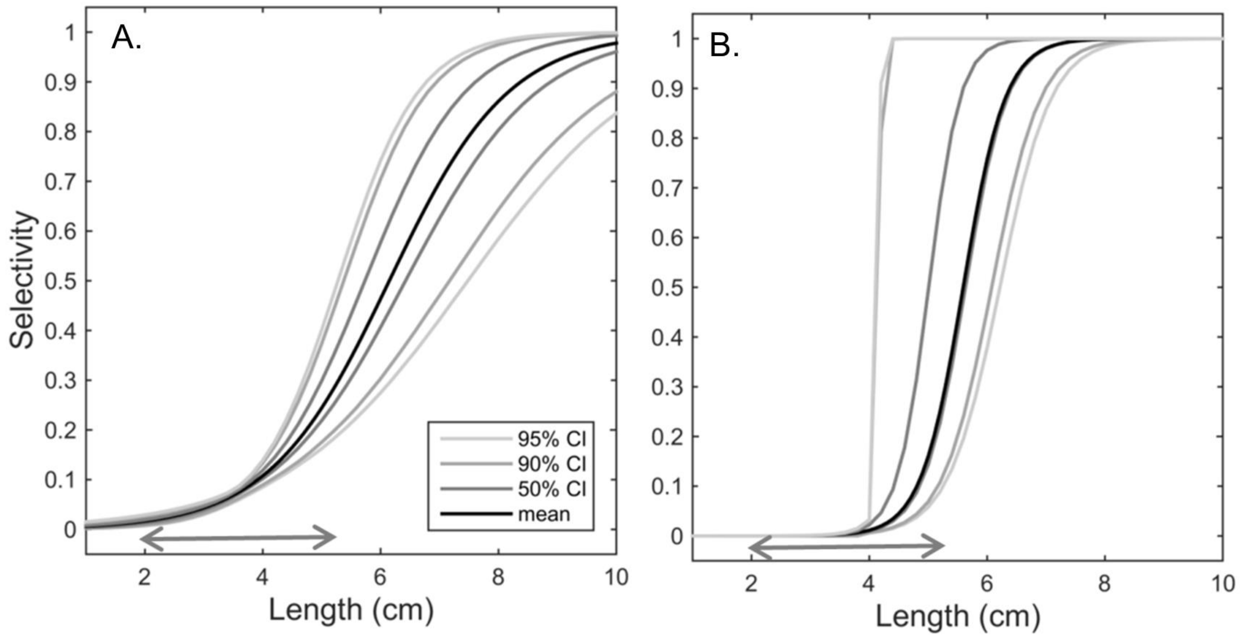


Figure 8. Confidence intervals (CI) of selectivity of A) mod-Marinovich and B) Cantrawl trawls on Arctic cod generated by taking the 95th, 90th and 50th percentiles of 10000 bootstrap estimates. The lower 50% CI in panel B is very close to the black line representing the mean value and is difficult to visualize. The arrows indicate the size range of 99 % of Arctic cod individuals as estimated from the mod-Marinovich catches.

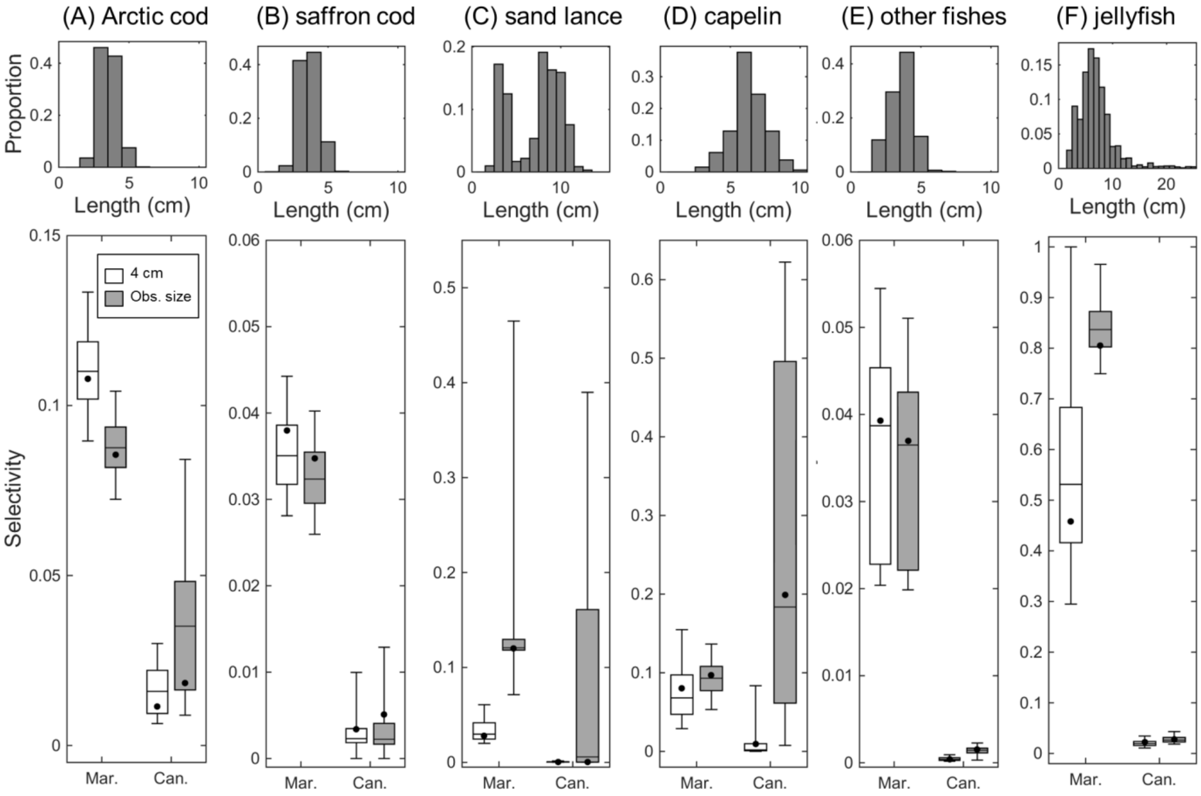


Figure 9. Bootstrap analysis of the variability in estimates of mod-Marinovich and Cantrawl selectivity for different species groups: A) Arctic cod, B) saffron cod, C) Pacific sand lance, D) capelin, E) other fishes, F) jellyfish. The top panel shows the size distribution estimated to be present in the environment based on 30 hauls with the mod-Marinovich equipped with recapture nets (eq. 13). The histograms extend over the size range encompassing at least 99% of the fish in the environment. The bottom panel shows box plots of bootstrapped probabilities of retention of a 4 cm individual (white boxes), and the probability of capturing animals with the size distribution in the upper plot. The boxplots represent the 5th, 25th, 50th, 75th and 95th percentiles of the selectivity estimate for an organism of a given size. Estimates of selectivity using parameters derived from all available data (Table 2) are shown as a black dot.

Appendix E.

Abundance and Distribution of Arctic cod (*Boreogadus saida*) and other Pelagic Fishes over the U.S. Continental Shelf of the Northern Bering and Chukchi Seas

Alex De Robertis, Christopher D. Wilson, Kevin Taylor, Edward V. Farley

March 7, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
AT	Acoustic Trawl
TS	Target Strength

List of Oral and Poster Presentations

Acoustic Trawl Surveys Up North: Baseline Surveys of the Northern Bering and Chukchi Seas. (Oral presentation) Alex De Robertis. Alaska Fisheries Science Center Seminar Series. Seattle Washington. 2 February 2016

Abundance and distribution of Arctic cod and other pelagic fishes in the Chukchi Sea based on acoustic surveys: what we know and potential next steps. (Oral presentation) Chris Wilson. 2016 AMSS Arctic Eis Workshop, Anchorage, Alaska. 29 January 2016

Abundance and Distribution of Arctic cod (*Boreogadus saida*) and other Pelagic Fishes over the U.S. Continental Shelf of the Northern Bering and Chukchi Seas. (Oral presentation) Alex De Robertis, Kevin Taylor, Chris Wilson, Edward Farley. 2016 Ocean Sciences Meeting, New Orleans, Louisiana 21-26 February 2016

Proposed Objectives and Study Chronology

The abundance and distribution of midwater fishes in the Pacific Arctic remains poorly understood. As there are no large-scale commercial fisheries in the U.S. Arctic north of the Bering Strait, broad-scale abundance surveys are not regularly conducted to inform fisheries management. Here we report on two, broad-scale, baseline acoustic-trawl surveys of pelagic fishes conducted in late summer 2012 and 2013 over the continental shelf of the ice-free U.S. northern Bering and Chukchi Seas. The goal of this work was to characterize the abundance and distribution of abundant pelagic fishes in the area. We conducted large-scale acoustic-trawl (AT) surveys of the northern Bering and Chukchi Seas during ice-free periods in 2012 and 2013. The mixed species assemblages in the study area required refinement of standard AT survey methods, and adjustment of trawl catches for the effects of trawl selectivity. These surveys indicate that midwater fishes are dominated by age-0 Arctic cod (*Boreogadus saida*) age-0 saffron cod (*Eleginus gracilis*), capelin (*Mallotus villosus*), and Pacific herring (*Clupea pallasii*). In both years, age-0 Arctic cod were distributed principally ≥ 69.5° N, age-0 saffron cod were abundant in coastal areas between 66.5-69.5 °N, and Pacific herring were distributed south of 67 °N. Arctic cod, saffron cod, herring and capelin were all > 2 times more abundant in 2013 than 2012. Sizeable populations of age-0 Arctic cod were observed in the northern Chukchi Sea, which suggests that this area is an important nursery ground. However, relatively few older Arctic cod were observed in this and other surveys of the area, which suggests that either overwinter mortality of age-0 Arctic cod is high, and/or these fish are not retained on the Chukchi shelf.

This work is under consideration for publication in Deep-Sea Research II

De Robertis, A., Taylor, K., Wilson, C., Farley, E., in review. Abundance and Distribution of Arctic cod (*Boreogadus saida*) and other Pelagic Fishes over the U.S. Continental Shelf of the Northern Bering and Chukchi Seas Deep-Sea Research II.

1. Abstract

We conducted acoustic-trawl (AT) surveys of the northern Bering and Chukchi Seas during ice-free periods in 2012 and 2013. The mixed species assemblages in the study area required refinement of standard AT survey methods, and adjustment of trawl catches for the effects of trawl selectivity. Sensitivity analyses indicate that the AT abundance estimates are relatively robust to the assumptions of the analysis. These surveys indicate that midwater fishes are dominated by age-0 Arctic cod (*Boreogadus saida*) age-0, saffron cod (*Eleginus gracilis*), capelin (*Mallotus villosus*), and Pacific herring (*Clupea pallasii*). In both years, age-0 Arctic cod were distributed principally ≥ 69.5° N, age-0 saffron cod were abundant in coastal areas between 66.5-69.5 °N, and Pacific herring were distributed south of 67 °N. These three fishes exhibited consistent associations with temperature, salinity and bottom depth: e.g., age-0 Arctic cod were abundant at lower mean water column temperatures than saffron cod. In contrast, capelin were distributed throughout the study area, and were not consistently associated with environmental measures. There was a geographic trend in body length, with smaller Arctic cod, saffron cod and capelin in northern areas, but smaller herring in the south. Arctic cod, saffron cod, herring and capelin were all > 2 times more abundant in 2013 than 2012. Sizeable populations of age-0 Arctic cod were observed in the northern Chukchi Sea, which suggests that this area is an important nursery ground. However, relatively few older Arctic cod were observed in this and other surveys of the area, which suggests that either overwinter mortality of age-0 Arctic cod is high, and/or these fish are not retained on the Chukchi shelf.

2. Introduction

There is substantial interest in the fishes of the Pacific Arctic region (northern Bering, Chukchi and Beaufort Seas) due to their important role in the food web (Bluhm and Gradinger, 2008; Whitehouse et al., 2014), and the potential for human activities to influence these species. The Arctic environment is changing rapidly. Sea ice extent and thickness has decreased and temperatures have increased dramatically in recent years (Duarte et al., 2012; Frey et al., 2015). These changes have been more rapid than those predicted by climate models, and there is substantial concern about the impacts of these changes on the ecosystem (Duarte et al. 2012). Ecological research in the region has historically been sporadic (Hopcroft and Day, 2013). However, recent concern about the potential impacts of climate change and other human activities such as oil and gas development on the ecosystem has stimulated a substantial amount of sampling of fishes in the Pacific Arctic (reviewed in Sigler, et al. 2011; Hopcroft and Day, 2013; Norcross et al., 2013, Normandeau Associates, 2012; Logerwell et al., 2015). The abundance and distribution of midwater fishes over the Chukchi shelf remains poorly understood (NPFMC, 2009; Whitehouse et al., 2014; Logerwell et al., 2015). As there are no large-scale commercial fisheries in the U.S. Arctic north of the Bering Strait (NPFMC, 2009; Hunt et al., 2013), broad-scale abundance surveys are not regularly conducted to inform fisheries management. Here we report on two, broad-scale, baseline acoustic-trawl surveys of pelagic fishes conducted in late summer 2012 and 2013 over the continental shelf of the ice-free U.S. northern Bering and Chukchi Seas.

The Chukchi and northern Bering Seas consist of extensive, shallow, continental shelves. The Chukchi Sea is the only connection between the North Pacific Ocean and the Arctic, with organisms, nutrients and heat transported primarily northward as water flows from the northern Bering Sea through the narrow Bering Strait and into the Chukchi Sea (Woodgate et al., 2006; Sigler et al., 2011; Hunt et al., 2013). The northern Bering and Chukchi Seas are highly seasonal environments which remain ice covered with a cold well-mixed water column for much of the year, and undergo extensive and rapid seasonal warming and sea ice retreat (Niebauer et al., 1998; Hunt et al., 2013). Sea ice generally begins to form in October in the Chukchi and Beaufort Seas and rapidly extends southward in November through January (Frey et al., 2015). Maximum ice extent occurs in March, when ice extends into the Bering Sea. The ice begins to retreat by May, and is north of the Bering Strait by June. Minimum sea ice levels occur in September with ice remaining only in the northern Chukchi and Beaufort Seas.

As in other areas of the Arctic, the Pacific Arctic region is changing dramatically. In the northern Chukchi and Beaufort Seas, temperatures have increased and the ice-free season is longer (Frey et al., 2015; Wood et al., 2015). There has been little multi-year ice in the Chukchi in recent years (Wood et al., 2015). In contrast, winter sea ice has increased in the Bering Sea to the south, which appears to be associated with multi-decadal variability in atmospheric circulation (Frey et al. 2015; Wood et al., 2015).

The Pacific Arctic is considered a benthic-dominated system (Grebmeier, et al., 2006), which does not support large populations of pelagic fishes (Alverson and Wilimovsky, 1966; Sigler et al., 2011; Hunt et al., 2013; Moore and Stabeno, 2015). However, earlier retreat of sea ice has resulted in earlier and more extensive phytoplankton blooms (Arrigo and van Dijken, 2011), which may shift the ecosystem to a more pelagic state (Grebmeier et al., 2006; Moore and Stabeno, 2015). Compared to the eastern Bering Sea, fishes in the Pacific Arctic are scarce and small (Sigler et al., 2011; Stevenson and Lauth, 2012). Offshore sampling of midwater fishes in the Chukchi Sea though limited in both time and space, has identified several common pelagic fishes. Arctic cod (*Boreogadus saida*) dominate these fish communities (Quast, 1974; Barber et al., 1997; Whitehouse et al., 2014; Logerwell et al., 2015), and saffron cod (*Eleginus gracilis*), Pacific herring (*Clupea pallasii*), capelin (*Mallotus villosus*), and Pacific sand lance (*Ammodytes hexapterus*) have been identified as abundant (Alverson and Wilimovsky, 1966; Quast, 1974; Craig and Skvorc, 1982; Datsky, 2015).

In recent years, there has been extensive offshore sampling of demersal fishes on the U.S. Chukchi shelf with bottom trawls (Goddard et al., 2014) and smaller-mesh beam trawls (Norcross et al., 2010, 201, Mecklenburg and Steinke, 2015). Near-surface fishes have been sampled with large surface trawls (Eisner et al., 2013), but the abundance and distribution of midwater fishes has not been characterized.

Arctic cod, saffron cod, and capelin dominate bottom and surface trawl catches (Logerwell et al., 2015), with sculpins (family Cottidae) and pricklebacks (family Stichaeidae) also abundant in the beam trawl catches (Logerwell et al., 2015; Mecklenburg and Steinke, 2015). There is evidence for interannual variability in the near-surface species composition on the Chukchi shelf: in 2007 saffron cod dominated the surface trawl catch, but in a repeat survey in 2012 capelin dominated the catch (Logerwell et al., 2015).

Midwater sampling of fishes has been very limited in the northern Bering and Chukchi Seas. Sampling with a small midwater trawl over a limited area of the Chukchi Sea shelf indicated that age-0 Arctic cod were abundant in the northern Chukchi (Quast, 1974). Arctic cod dominate midwater fishes in surveys of the Russian northern Bering and Chukchi seas (Nikolayev et al., 2008; Datsky, 2015). Midwater sampling in the Beaufort Sea has revealed substantial aggregations of Arctic cod, with age-0 fish in epipelagic layers near the surface and larger Arctic cod both in deeper water at the shelf break as well as near the coast (Parker-Stetter et al., 2011; Benoit et al., 2014). Very dense overwintering aggregations of larger Arctic cod have been reported in embayments in the Beaufort Sea (Benoit et al., 2008).

Here, we report on acoustic-trawl (AT) surveys of midwater fishes over the continental shelf of the U.S. northern Bering and Chukchi Seas as part of the 2012 and 2013 Arctic Ecosystem integrated survey (Arctic Eis). The primary goal of this work was to establish the abundance and distribution of Arctic cod and other dominant pelagic organisms in the northern Bering and Chukchi Seas. The AT methodology relies on measurements of acoustic backscatter and estimates of species and size composition along with knowledge of the acoustic scattering properties of the organisms to estimate abundance. The AT method is well-suited for quantifying abundant species, and has been applied extensively for the assessment of Antarctic krill and commercially important fishes (Simmonds and MacLennan, 2005). AT surveys have been successfully applied in low-diversity Pacific Arctic ecosystems dominated by Arctic cod (e.g. Parker-Stetter et al., 2011; Benoit et al., 2014).

During the Arctic Eis AT surveys, a mixed-species assemblage was encountered, and AT abundance estimates could not be made under the simplifying assumption that all backscatter was attributable to Arctic cod as in other areas of the Arctic (Parker-Stetter et al., 2011, Benoit et al., 2014; Geoffroy et al., 2015). Thus, methods were developed to allocate the acoustic contributions of individual species in mixed-species aggregations. This included estimating the acoustic contribution of abundant large medusae, which was poorly understood (De Robertis and Taylor, 2014). Although we relied on trawl sampling to estimate size and species composition, we accounted for trawl selectivity as the probability of capture in the survey trawls is strongly species and size-dependent (De Robertis et al., 2015). We applied these methods (i.e. apportioning species mixtures, trawl selectivity corrections) to interpret acoustic-trawl observations during the Arctic Eis AT surveys to provide baseline information on the abundance and distribution of the pelagic fishes that comprise an important and poorly characterized component of the Alaska Arctic ecosystem.

3. Methods

3.1 Survey design

Acoustic-trawl (AT) surveys were conducted during the 2012 (7 Aug. - 24 Sept.) and 2013 (7 Aug. - 25 Sept.) multidisciplinary Arctic Ecosystem integrated survey (Arctic Eis) covering the U.S. continental shelf of the northern Bering and Chukchi Seas. The AT survey was conducted aboard the 55 m chartered fishing vessel *Bristol Explorer* as the vessel transited at a speed of ~4.5 m s^{-1} among sampling stations on a 1° of longitude and 0.5° of latitude grid (Fig. 1). The vessel stopped to conduct conductivity temperature depth (CTD) probe casts, surface trawls, and zooplankton sampling at each station. The survey results are summarized for three latitudinal survey sub-regions indicated in Fig. 1: the northern Bering Sea south of the Bering Strait (59.75-65.75° N), southern Chukchi Sea south of Cape Lisburne (65.75-68.75 °N), and the northern Chukchi Sea north of Cape Lisburne (68.75-73° N).

The survey covered relatively shallow water. Bottom depths averaged 38 m and ranged between 18-55 m in 95 % of the survey area. Surface trawl samples were taken during daytime in the upper ~20 m (see below) at predetermined sites (Fig. 1). The acoustic survey was conducted during daylight hours as the vessel transited between stations, and midwater trawl hauls were periodically conducted at the depths and locations where fish aggregations were acoustically detected. The Chukchi Sea was the primary area of interest for the AT survey so more effort was allocated in this area (Fig. 1). Time needed for other survey objectives in the northern Bering Sea meant that fewer midwater trawls were conducted and the vessel transited between stations at night. The northward extent of the survey was at times limited in the Chukchi Sea by the presence of sea ice. In these instances, the intended survey trackline was altered so that the vessel could safely transit in areas of low ice concentration (Fig. 1). After the 2013 survey of the continental shelf, a qualitative ~260 nautical miles (nmi, 1 nmi = 1852 m) 'zig-zag' exploratory survey along with three midwater hauls was conducted in the vicinity of Barrow canyon to depths of ~1500 m to search for fish aggregations in deeper waters (Fig. 1, thick grey line).

3.2 Acoustic equipment, calibration, and data collection

Acoustic backscatter at 38 and 120 kHz was measured using a split-beam Simrad[3] ES60 echosounder equipped with hull-mounted ES38-10 and ES120-7C transducers at a depth of 3.7 m. Acoustic data were collected at a ping rate of 2.5 s^{-1} and a pulse length of 0.512 ms. During the deep (> 500 m) portions of the 2013 deep-water survey, a 0.4 s^{-1} ping rate was used to allow data collection at longer ranges, and longer pulse lengths (1 ms at 120 kHz and 4 ms at 38 kHz) were used to improve the signal-to-noise ratio.

The ES60 echosounder is subject to a systematic error that introduces a maximum amplitude error of ± 0.5 dB (± 12 % in linear units) which was corrected by fitting the error to the otherwise constant transmit pulse and correcting the raw acoustic data (Ryan and Kloser, 2004). The hull-mounted transducers on the F/V *Bristol Explorer* are susceptible to interference from bubbles swept under the

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

transducers in rough seas, particularly when heading into the swell. Occasionally, aerated water was swept under the hull and blocked the acoustic signal, which was evident as a weak bottom echo. To minimize the impact of this interference, which was particularly evident at 38 kHz, only pings with a peak S_v of > -25 dB re 1 m^{-1} in the 38 kHz bottom echo were used in the analysis (see MacLennan et al., 2002 for a description of the acoustic units used in this paper).

The echosounder was calibrated twice in 2012, and once in 2013 using the standard sphere technique (Demer et al., 2015). Calibration results indicated that the echosounder was stable during the surveys. Repeat calibrations in 2012 yielded similar results: gain differed by 0.01 dB at 38 kHz and 0.13 dB at 120 kHz. These results were averaged (in linear units) and applied in post-processing. The calibrations were also consistent among years: the gains derived in 2012 and 2013 differed by 0.12 dB (5.7 % in linear units) at 38 kHz and by 0.29 dB at 120 kHz (12.5 %). In 2013, the echosounder was also calibrated at the additional pulse lengths used in the Barrow Canyon deep-water survey.

3.3 Trawl sampling

Acoustic scatterers were identified using a combination of surface trawls hauls at pre-determined stations and midwater trawl hauls fished in areas of high backscatter (Fig. 1). A large Cantrawl rope trawl and a smaller modified-Marinovich midwater trawl (hereafter mod-Marinovich) were used. The trawl gear and sampling methods are described in detail by De Robertis et al., (2015) who quantify the size and species selectivity of these trawls. The surface hauls with the Cantrawl (122 m headrope, 162 to 1.2 cm mesh) were used to continue a time series (Eisner et al., 2013). During surface hauls, the Cantrawl was equipped with floats to keep the headrope near the surface and towed for 30 min. The trawl had a vertical opening of 18.7 ± 3.3 m (mean ± SD) when fishing.

In 2012, Midwater and near-bottom concentrations of fishes observed acoustically were targeted with the Cantrawl. The vertical opening of the Cantrawl during midwater hauls averaged 13.5 ± 2.9 m (mean ± SD). During the 2012 survey, the Chukchi Sea fish assemblage was dominated by small and/or juvenile fishes, which were poorly retained by the Cantrawl (De Robertis et al., 2015). Therefore, a smaller mod-Marinovich trawl (12 m headrope, 6.4 to 0.3 cm mesh) was used in 2013 for the targeted midwater hauls, as this smaller net was less selective and better retained small fishes in the study area (De Robertis et al., 2015). The vertical opening of the mod-Marinovich averaged 5.7 ± 0.7 m (mean ± SD).

Trawl catches were weighed, and organisms were identified to species and enumerated. Fork lengths of a subsample of up to 50 fishes and bell diameters of up to 50 undamaged jellyfishes were measured to the nearest 1.0 mm with an electronic measuring board (Towler and Williams, 2010).

3.4 Overview of data analysis

The abundance of species that contributed most of the acoustic backscatter in the surveyed area was determined by combining acoustic backscatter with species and size compositions estimated from trawl catches and published measurements of the acoustic properties of these species. Trawl sampling suggested that the backscatter was from multiple co-located species and sizes which likely had different probabilities of capture. Therefore, the size and species composition of animals was estimated by correcting the trawl catches for the effects of mesh selection (i.e., escapement of organisms that enter the net) using selectivity relationships determined during the 2013 survey (De Robertis et al., 2015). These corrected estimates of species and size composition (see eq. 1) were used to allocate backscatter among various taxa and derive abundance estimates for selected species.

3.5 Processing of acoustic data

Acoustic data were post-processed using Myriax Echoview software (v. 6.1). A trawl haul was assigned to each acoustic observation based on the observed depth distribution and aggregation pattern of the organisms, the geographic proximity to the haul, and the depths sampled by the haul. This assumes that the selectivity-adjusted trawl catch represents the species and size composition of the organisms observed acoustically.

A two-frequency variant of the method described in De Robertis et al. (2010) was used to exclude the contribution from organisms unlikely to be fish, such as zooplankton. Water column backscatter at each frequency was isolated by excluding data shallower than 6.5 m and deeper than 0.5 m above the bottom. The data were smoothed using a five-ping by 5 m moving average around each sample (i.e., equal weight for all samples within range) and the frequency response (i.e., $\Delta S_{v120\text{-}38kHz}$) in each cell was computed. Samples with a $\Delta S_{v120\text{-}38kHz}$ in the range of –16 to 8 dB were used in further processing.

Acoustic observations were echo-integrated at a 0.5 nmi horizontal resolution and integrated with a minimum S_v threshold of -70 dB re 1 m^{-1}. Only the observations between sunrise and sunset were analyzed to minimize diel effects on target strength and species compositions due to vertical migration of demersal species. Acoustic observations while trawling were excluded from analysis to avoid potential changes in backscatter associated with behavioral responses to trawling vessels (e.g., De Robertis and Wilson, 2006).

The acoustic data from the exploratory deep-water survey in 2013 were influenced by radiated noise from the vessel. Much of this survey was too deep for the 120 kHz data to be useful. Therefore the two-frequency classification was not applied and the observations were not pooled with observations on the Chukchi shelf. The 38 kHz data were analyzed quantitatively to a depth of ~350-400 m and visually inspected for the presence of scattering layers above an S_v threshold of -70 dB re 1 m^{-1} to a depth of ~1000 m.

3.6 Partitioning acoustic backscatter to species

The general approach taken in interpreting the acoustic backscatter measurements was that of the ‘forward problem’ (Holliday and Pieper 1995), where estimates of the size and species distribution of organisms in the water column and their acoustic scattering properties are used to convert the measured acoustic backscatter into animal abundances. Estimates of size and species composition are combined with the size and species-specific scattering properties to estimate the proportion of observed acoustic scattering attributable to each species. These estimates are then used to convert the observed backscatter to fish numbers by species and size class.

Trawl catches were corrected for the effects of size and species selectivity by dividing the observed catch by the mean selectivity derived from a trawl experiment conducted during the 2013 survey (De Robertis et al., 2015; see their Fig. 6 and Table 2). The number of individuals of a given species and length class ($N_{s,l}$) that would be expected from an unselective sampler was estimated from the observed catch and the estimated selectivity,

$$N_{s,l} = \frac{C_{s,l}}{S_{s,l}}, \qquad (1)$$

where $C_{s,l}$ is the catch of species s in the 1 cm length class l, and $S_{s,l}$ is the selectivity of the trawl for species s and size class l.

A series of target strength (TS) relationships from the literature (Table 1) were used to estimate the acoustic scattering from each species or species group in the trawls catch. Backscatter from salmonids (which accounted for ~1 % of specimens captured in surface and midwater trawls combined) was assumed to be negligible as > 99.9 % of salmonids were captured in surface trawls, which is consistent with previous work indicating that the salmon are likely distributed primarily in the surface zone (Emmett et al., 2004; Parker-Stetter et al., 2013) and thus largely outside the volume sampled by the echosounder. We did not account for the potential contribution from zooplankton, as they are generally weak scatterers compared to fish, and much of their backscatter was excluded by the dual-frequency technique.

The mean backscattering cross section (a measure of acoustic scattering in m^2 – MacLennan et al., 2002) of species s of size class l is

$$\sigma_{bs_{s,l}} = 10^{(0.1 \cdot TS_{s,l})}, \qquad (2)$$

where TS is the target strength (dB re m^2) computed using the relationships in Table 1.

The proportion of backscatter (*PB*) from species *s* of size class *l* in trawl *t* is computed from the number ($N_{s,l,t}$) of individuals of species *s* and size class *l* estimated from trawl *t* and their backscattering cross section,

$$PB_{s,l,t} = \frac{N_{s,l,t} \cdot \sigma_{bs_{s,l}}}{\sum_{s,l} N_{s,l,t} \cdot \sigma_{bs_{s,l}}} . \tag{3}$$

The measured nautical area backscattering coefficient (s_A) at location *i* (where trawl *t* is assigned to represent the species composition) was allocated to species and size as follows:

$$s_{A_{s,l,i}} = s_{A_i} \cdot PB_{s,l,t} . \tag{4}$$

The areal density ρ [individuals nmi^{-2}] of species *s* of size *l* at location *i* was computed from the measured nautical area backscattering coefficient following MacLennan et al. (2002),

$$\rho_{s,l,i} = \frac{s_{A_{s,l,i}}}{\left(4\pi\sigma_{bs_{s,l}}\right)} . \tag{5}$$

The survey area was divided into a 1° latitude and longitude grid, and the area of each grid cell in nmi^2 was computed. Portions of cells on land were excluded from the area. Geographic cells with less than 10 nmi of trackline or where sampling extended for < 0.3 degrees of longitude were excluded from further analysis to avoid biases from sparsely sampled cells. This resulted in 66 valid grid cells in 2012 and 65 grid cells in 2013, for a similar surveyed area ($8.52 \cdot 10^4$ nmi^2 in 2012 and $8.53 \cdot 10^4$ nmi^2 in 2013). The same geographic cells were sampled in the southern Chukchi in 2012 and 2013, but 11.3 % more area was sampled in the northern Chukchi in 2012 and 12.3 % more area was sampled in the northern Bering Sea in 2013 (Fig. 1). A ‘common survey area’ of 58 valid grid cells ($7.59 \cdot 10^4$ nmi^2) sampled in both years was used to compare abundance between surveys.

The survey-wide abundance for species *s* in numbers of individuals was computed by averaging the density of individuals from locations *i* within grid cell *c*,

$$\langle \rho_{s,l,c} \rangle = \frac{\sum_{i_c} \rho_{s,l,i_c}}{n_c} \,, \qquad (6)$$

where $\langle \rho_{s,l,c} \rangle$ is the mean areal density of species *s* of a length class *l* and n_c is the number of samples within grid cell *c*. This is then multiplied by the area of the grid cell, and added over the grid cells

$$N_{s,l} = \sum_c \langle \rho_{s,l,c} \rangle A_c \,, \qquad (7)$$

where $N_{s,l}$ is the total number of individuals of species *s* at length *l* in the survey area and A_c is the area of grid cell *c*.

The calculations described above require several parameters to be known (e.g., size and species composition, TS). In practice, the highest confidence will be for species that dominate acoustic backscatter (i.e., abundant and high TS taxa), and therefore the analyses were restricted to Arctic cod, saffron cod, Pacific herring (*Clupea pallasi*) and capelin. Together, these target species accounted for 92 % of organisms captured in 2012 and 79 % in 2013. The other species captured in the trawls were considered in terms of estimating their contribution to the observed acoustic backscatter (eq. 3), but their abundance was not estimated.

3.7 Environmental associations of fishes

We summarized the cumulative distributions of fishes and environmental variables in the study area to establish whether the midwater fishes occurred disproportionately under a particular range of conditions. We considered the mean latitude and bottom depth of the grid cell and the mean water column temperature and salinity derived from the closest CTD cast to the cell center (see Danielson et al., this issue for description of the CTD sampling). The mean water column temperature was used as fishes were distributed throughout the water column, and the water column mean was highly correlated with both surface temperature (r = 0.95 for all cells combined) and bottom temperature (r = 0.95). The surface (r = 0.83) and bottom (r = 0.71) salinity were also highly correlated with the water column mean.

The analysis compares the cumulative distribution of environmental metrics weighted by fish abundance with the distribution of the environmental metric in the area surveyed. We sorted the fish abundance (*N*) and the environmental (*E*) measurements in each 1° grid cell in ascending order of *E*, and computed the minimum values of the *E* at which a given percent *P* (i.e., 10, 25, 50, 75, 90 %) of total abundance for each species was observed. This can be expressed as the lowest value of the environmental characteristic E_j, fulfilling the following expression:

$$\sum_{i=1}^{j} N_i \geq \frac{P}{100}\left(\sum_{i=1}^{n} N_i\right) , \qquad (8)$$

where *i* and *j* are indices into the sorted vector of *E*, and *n* is the total number of grid cells. In addition, the distribution of environmental characteristics in the area sampled was described using this method, but weighting each grid cell equally (i.e., N=1 for all cells).

This metric summarizes the environmental conditions in the survey area and the environmental conditions under which the populations were found. For example, in the case of temperature, E_{10} can be interpreted as the minimum temperature at which at least 10 % of the population was observed. By comparing values of *E* observed for fish populations to those encountered in the survey area, one can infer whether the populations are disproportionately distributed under a certain range of environmental conditions. We used a two sample Kolmogorov-Smirnov test to identify differences in the cumulative distributions of *E* for the environmental and fish distributions.

3.8 Sensitivity Analysis

We calculated abundance under varying parameter values to explore the sensitivity of the abundance estimates to the assumptions used to allocate the backscatter to species. Five alternative scenarios were explored in a simple one-factor-at-a-time sensitivity analysis in which only a single parameter was changed and all other parameters were kept at the baseline levels described above. 1) Fish abundances were recomputed assuming that trawl selectivity is negligible (i.e., all species and size classes have an equal probability of capture). 2) The subjective trawl assignments were replaced with the geographically nearest trawl applied to the entire water column. 3) The trawl assignments were replaced with the geographically nearest trawl in a two depth-layer scheme: the nearest surface trawl was applied if the analyst had assigned a surface trawl and the nearest midwater trawl was assigned if the analyst assigned a midwater trawl to the observation. The sensitivity of the estimate to the TS relations used to partition backscatter from the mixed aggregations was evaluated by 4) increasing the TS of all species other than the target species being estimated by 3 dB (i.e., doubling the acoustic backscatter of non-target species) or 5) reducing the TS of all other species by 3 dB (i.e., halving the acoustic contribution of other species). The TS of the target species was not changed as changing the TS of the target species affects the density per unit backscatter as well as the proportion of backscatter from the target species.

4. Results

4.1 Trawl catches

Twenty-one midwater trawls and 100 surface trawls were conducted during the 2012 survey, and 44 midwater trawls and 89 surface trawls were conducted during the 2013 survey (Fig. 1). Only 4 midwater trawl hauls were conducted in the northern Bering Sea in 2012, and 1 haul was conducted in 2013. In both years, the trawl catch was dominated numerically by small fishes (80 % < 12.1/9.3 cm in 2012/2013) such as juvenile Arctic cod, juvenile saffron cod, capelin, and Pacific herring (Fig. 2). These four species dominated the catch numerically, but not in terms of wet weight. In 2012 these taxa accounted for 98.2% of individuals and 77.1 % of total weight captured in the Cantrawl midwater hauls, and 89.1 % of individuals and 20.5% of weight in the Cantrawl surface hauls. In 2013, these 4 species accounted for 51.9 % of individuals and 4.5 % of total weight captured in the mod-Marinovich midwater trawl hauls, and 85.5 % of individuals and 18.5 % of weight captured in the Cantrawl surface hauls. In terms of biomass, trawl catches were dominated by jellyfish in both years (Fig. 3), primarily the large scyphomedusa *Chrysaora melanaster* which accounted for 96.5% of jellyfish by weight. Jellyfish accounted for a small fraction of the catch by number (< 10 %) but a large fraction of the total catch by weight: 22.7 % in the 2012 midwater trawls, 75.3. % in the 2012 surface trawls, 91.8 % in the 2013 midwater trawls, and 74.5 % in the 2013 surface trawls.

Catch composition varied geographically (Fig. 2). Capelin, herring, and jellyfish often numerically dominated trawl catches in the southern portions of the survey area, with juvenile Arctic cod, jellyfish, or capelin dominating catches in the northern Chukchi (Fig. 2). Juvenile saffron cod were abundant close to shore in the center of the survey area, outside of Kotzebue Sound (Fig. 2). When expressed as contribution to catch by weight, jellyfish dominated the catch composition over much of the survey area (Fig. 3).

4.2 Composition of acoustic backscatter

The proportion of backscatter attributable to a given species (Fig. 4) resembled the proportion of catch by number (Fig. 2) more than the proportion of catch by weight (Fig. 3). This can be largely explained by the relatively low mass-specific TS of jellyfish: although jellyfish are large in size, they are weak scatterers, and are unlikely to contribute strongly to overall acoustic backscatter in the presence of strong scatterers such as fishes with swimbladders, even if they dominate the biomass (De Robertis and Taylor, 2014). Thus, small fishes (such as Arctic cod, saffron cod, capelin and herring) are the dominant contributors to 38 kHz backscatter in the survey area. This is evident in the case of mixed assemblages of jellyfish and saffron cod in the coastal stations outside of Kotzebue Sound (66-69 °N in Figs. 2-3) where backscatter (but not the catch) was dominated by small saffron cod (i.e. orange circles in Fig. 4) due to a combination of their higher relative abundance after correction for net selectivity and high acoustic scattering.

4.3 Acoustic backscatter

The 38 kHz backscatter was dominated by backscatter with a 38/120 kHz frequency response consistent with fish (96.9 % of 38 kHz backscatter in 2012 and 96.3 % in 2013 was classified as 'fish'). Backscatter was highest in the northern Chukchi sub-region (Fig. 5) in areas where juvenile Arctic cod dominated trawl catches and backscatter in both years (Figs. 2, 4). Backscatter consistent with fish was ~2.6 times higher in 2013 than 2012 when averaged over the survey area, and was higher in all sub-regions with the largest increase occurring in the northern Chukchi (Table 2, Fig. 5). High backscatter attributed to ~13 cm Arctic cod was observed in 2012 in an isolated area at ~65 °N (Figs. 4, 5). Elevated backscatter was also observed in the southern Chukchi in 2012 and in the northern Bering in 2013 (Fig. 5) in areas dominated by herring (Fig. 4).

4.4 Fish abundance and distribution

Arctic cod, saffron cod, capelin and Pacific herring were the primary pelagic sound scattering organisms encountered during the 2012 and 2013 surveys (Fig. 4). These species were estimated to account for 69.6 % of 38 kHz 'fish' backscatter in 2012 and 76.5 % in 2013. Small Arctic cod were abundant in the Northern Chukchi (Figs. 6 A-B, 7, Table 3). Arctic cod length in the Chukchi Sea averaged 3.5 cm in both years, with < 0.3 % of Arctic cod > 6.5 cm in 2012 and none > 6.5 cm in 2013 (but see Exploratory Survey section below). Larger Arctic cod were observed in the northern Bering Sea. A localized dense aggregation of ~13 cm Arctic cod was detected in the northern Bering Sea in 2012 (Figs. 6 A, 7A, Table 3), and the few Arctic cod observed in the northern Bering Sea in 2013 were > 9 cm in size (Fig. 6 B). Arctic cod were ~2.7 times more abundant in the common area sampled in 2013 than in 2012 (Table 3, Fig. 7). Note that Arctic cod were substantially more abundant than the other species described below and are shown on a different scale.

Saffron cod were abundant in coastal areas between 66.5 °N and 69.5 °N in the southern Chukchi Sea, and just north of Cape Lisburne in the northern Chukchi (Fig. 8). Saffron cod were 4 times more abundant in 2013 than 2012 (Table 2, Fig. 8). Similar to Arctic cod, saffron cod observed in the Chukchi were small (mean length was 3.7/3.8 cm in 2012/2013) with larger specimens observed in the northern Bering Sea (Fig. 6 C-D), where abundances were 1-2 orders of magnitude lower (Table 3, Fig. 8).

Capelin were patchily distributed and more broadly distributed throughout the survey area than the other species (Fig. 9, Table 3). Capelin abundance was ~1.9 times higher in 2013 than 2012 (Table 3, Fig. 9). As in the case of Arctic and saffron cod, the largest capelin were observed in the northern Bering Sea (Fig. 6 E-F).

Pacific herring were most abundant in the northern Bering Sea (> 86 % of survey total) and were ~4.6 times more abundant in the common area sampled in 2013 than in 2012 (Fig. 10, Table 3). Unlike the other species, herring were smaller in the southern part of the survey area. Those in the northern Bering Sea were primarily < 10 cm (Fig. 6 G-H). Larger herring (> 20 cm) were more abundant in the southern Chukchi Sea (Fig. 6 G-H, Table 3) where they were patchily distributed north of the Bering Strait, particularly in 2012 (Fig. 6 G-H, Fig. 10, Table 3). Low densities of herring were observed in the northern Chukchi Sea in both years (Fig. 10, Table 3).

4.5 Fish abundance in relation to the environment

Fishes other than capelin were spatially separated with Arctic cod distributed in the northern part of the study area, saffron cod farther south and nearer to shore in the Chukchi Sea, and herring close to shore in the southern part of the study area (Figs. 7-10, Fig. 11 A). For example, 91 % of Arctic cod in 2012 and 95 % of Arctic cod in 2013 were distributed at ≥ 69.25 °N, which accounted for 48 % of the sampled geographic cells in 2012 and 43 % of the samples in 2013. Arctic cod tended to be located in deeper parts of the survey area (75 % > 36/41 m bottom depths in 2012/2013), while saffron cod and herring were observed over shallower depths (Fig. 11 B). Arctic cod were most abundant at intermediate water column temperatures, with 50 % of fish observed in temperatures ranging from 3.4-6.6 °C in 2012 and 2.6-6.7 °C in 2013 (Fig. 11 C). Saffron cod and herring were distributed at the upper end of the temperature range sampled with >75 % of fish observed at temperatures > 7.5 °C (Fig. 11 C). Arctic cod were abundant at the upper end of salinities sampled (75 % > 30.4/30.8 in 2012/2013), while saffron cod and herring were more abundant at the lowest salinities sampled (Fig. 11 D).

Arctic cod, saffron cod, and herring were disproportionately abundant under a restricted range of environmental conditions (compare white and shaded box plots in Fig. 11). The conditions under which each species was abundant were consistent between years. Capelin, however, were distributed throughout the survey area and did not exhibit strong and consistent associations with latitude, temperature, salinity and bottom depth. Water column temperatures in the study area were more extreme in 2013, with a larger area of the shelf covered by < 4 °C water (i.e., compare white box plots in Fig. 11 B). In addition, maximum water column temperatures were higher in 2013, and salinity tended to be lower (Fig 11 B-C).

4.6 Sensitivity analyses

Assuming that all species are equally retained in the trawls resulted in relatively modest changes in abundance for Arctic cod relative to the baseline scenario, moderate changes for saffron cod and herring, and large changes for capelin, particularly in 2012 (Table 4, scenario 1). As trawl selectivity adjustments influence the estimates of species and size composition, abundance changes vary with the selectivity correction used. For example, in 2012 capelin abundance increases > 3 fold (Table 3) if one assumes equal selectivity for all species and size classes. This occurs because capelin are well-retained and thus over-represented in the catch of the Cantrawl relative to other species (De Robertis et al., 2015). This over-estimate of capelin abundance causes the abundance of other, more poorly retained species, such as Arctic and saffron cod to decrease by up to ~30 % in this scenario (Table 2, i.e. backscatter from these species is attributed to capelin). That is, if differences in trawl selectivity are not accounted for, species compositions shift strongly to capelin when the Cantrawl is used for midwater hauls as this trawl retained capelin better than the other species. The 2013 survey results are less sensitive to trawl selectivity corrections as the high-backscatter regions were sampled with the smaller, less selective mod-Marinovich. Similarly, ignoring size selectivity shifted the size distributions of all species towards larger, better-retained fishes (De Robertis et al., 2015). For example, 9.3 % of Arctic cod were estimated to be > 4.5 cm in 2012, but if selectivity is assumed to be equal for all species and size classes, 41.4 % of Arctic cod would be estimated as to be > 4.5 cm.

Assigning catch data from the nearest haul to the backscatter in the analysis (Table 4, scenario 2) resulted in estimates within ~ 33 % of the baseline values. The discrepancies were generally smaller when midwater and surface zones were treated separately (i.e., Table 4, scenario 3). The estimates under scenario 3 were within 10 % of those under the baseline scenario for Arctic cod and capelin, and 23 % for saffron cod and herring.

Altering the TS of all taxa other than Arctic cod by ± 3 dB (i.e., a factor of 2) changed abundance by <12 % (Table 4, scenarios 4-5) indicating that the abundance estimates were not highly sensitive to the TS values used for species other than Arctic cod, as most of the Arctic cod were found were in areas where the species accounted for most of the backscatter (Figs. 4, 7). The abundance of saffron cod, capelin and herring was more variable when the relative acoustic contribution of other species was halved or doubled (Table 4, scenarios 4-5), as they were more likely to occur in mixed-species assemblages (Fig. 2).

4.7 Exploratory survey near Barrow Canyon

The exploratory survey in the vicinity of Barrow Canyon (Fig. 1B, grey line) revealed that the near-surface layer of age-0 Arctic cod persisted over the shelf break and continental slope. A relatively small aggregation of larger, older Arctic cod was observed in deeper water in a restricted area over

Barrow Canyon (see next paragraph). The shallow scattering layer observed throughout the northern Chukchi shelf persisted in this area in the upper ~ 60 m and accounted for the majority of the backscatter observed during the exploratory survey (Fig. 5 B). Catches from two midwater trawls hauls in this layer were dominated by age-0 Arctic cod (75 and 92 % by number, respectively, Fig. 2B).

A relatively weak, deep-water sound-scattering layer was observed along ~8.7 nmi of survey trackline in the vicinity of the head of Barrow Canyon (Fig. 12 A) in water depths of ~280-330 m (71.8° N 155.0° W). The region of highest backscatter extended for ~2.5 nmi at 230-270 m depth with an average 38 kHz s_A of 164 m^2 nmi^{-2}. A midwater trawl was towed in this layer, but the net was recovered with an obstructed codend, which likely affected the catch composition. The catch was dominated by Arctic cod (97 % by number) and included larger specimens: 24 % of Arctic cod were > 7 cm. These larger fish averaged 11.2 cm (range 7.1-17.4 cm).

The deep Arctic cod aggregation was associated with a relatively warm (0.6 °C) and saline (34.8) subsurface water mass (Fig. 12 B) of Atlantic origin (Danielson et al., 2015). The scattering layer was not present in the colder water present at intermediate depths (minimum temperature was -1.6 °C at 145 m). One of the near-surface hauls was fished at ~20 m depth at the same location as the deep haul: it captured 92 % Arctic cod, with a mean length of 3.8 cm, and no individuals > 5.5 cm. Although the performance of the deep tow was compromised, the catch was sufficient to confirm the presence of low densities of larger Arctic cod in warmer, more saline deep water. If the deep layer were composed entirely of larger Arctic cod (i.e., smaller fish were captured from the < 60 m shallower layer on deployment and retrieval to ~265 m), densities in the region of highest backscatter would correspond to ~0.7 fish m^{-2}.

5. Discussion

5.1 Abundance and distribution of midwater fishes

The primary species observed in acoustic-trawl surveys of the U.S. northern Bering and Chukchi Seas were Arctic cod, saffron cod, Pacific herring, and capelin. These species are known to be abundant in the Pacific Arctic (e.g., Alverson and Wilimovsky, 1966; Eisner et al., 2013; Goddard et al., 2014; Logerwell et al., 2015) and accounted for > 70 % of backscatter in the survey area. The distributions of Arctic cod, saffron cod and herring were separated along a latitudinal gradient, with high densities of Arctic cod distributed ≥ 69.5° N in the northern Chukchi Sea, saffron cod abundant in coastal areas of Kotzebue Sound between 66.5-69.5 °N, and herring abundant south of 67°N.

Acoustic backscattering and the abundance of midwater fishes increased to the north due to the high densities of age-0 Arctic cod observed in the northern Chukchi Sea. This is consistent with observations from a 2007 surface trawl survey where Arctic cod were found to be abundant in the northern Chukchi Sea (Eisner et al., 2013). However in that survey, saffron cod were more abundant relative to the other species and they were distributed farther north than in the AT surveys reported here (Eisner et al., 2007). Unlike the other species, capelin were more patchy and more broadly distributed throughout the survey area. The general distribution patterns of all species were consistent between the 2012 and 2013 Arctic Eis surveys.

Overall, midwater fishes in the study area were small, with most individuals < 10 cm and very few fishes > 25 cm. This is consistent with previous observations that fishes in the Pacific Arctic are small (Sigler et al., 2011; Norcross et al., 2013). Arctic and saffron cod were primarily < 5 cm, which is consistent with the size of age-0 fish (Lowry and Frost, 1981; Johnson et al., 2009; Bouchard and Fortier, 2011; Helser et al., 2016). Densities of age-0 Arctic cod and saffron cod in the northern Bering Sea were low, as previously reported from surface trawl sampling in 2007 (Eisner et al., 2013). The aggregation of ~13 cm Arctic cod (likely age-1, Helser et al., 2016) observed south of the Bering Strait in 2012 is consistent with previous reports of occasional dense aggregations of larger fish in the northern Bering Sea (e.g. Lowry and Frost, 1981; Nikolayev et al., 2008). Arctic cod, saffron cod, and capelin encountered in the Chukchi Sea were smaller than in the northern Bering Sea, while Pacific herring exhibited the opposite trend, with high densities of small fish in the northern Bering Sea, particularly in 2013. Larger (> 20 cm) herring were primarily encountered in dense aggregations in the southern Chukchi.

5.2 Arctic fishes exhibit strong environmental associations

Arctic cod, saffron cod, and herring were consistently associated with a specific subset of environmental conditions in the study area, whereas capelin were not. Age-0 Arctic cod were abundant at high latitudes, intermediate temperatures and high salinities in areas of the northern Chukchi shelf influenced by the Bering-Chukchi Summer Water (Danielson et al, this issue). In contrast, both saffron cod and herring were found in the warmest and freshest waters observed in the Arctic Eis surveys, in Alaska Coastal Water influenced by solar warming and coastal runoff (Danielson et al., this issue). Saffron cod were abundant at intermediate latitudes in coastal waters of higher temperature and lower salinity which is consistent with previous observations (Alverson and Wilimovsky, 1966; Eisner et al., 2013; Sigler et al., this issue). Herring exhibited similar environmental associations as saffron cod, being abundant warm and low-salinity coastal waters, but they were distributed farther south in the northern Bering Sea. Pacific herring have demersal eggs and spawn in the nearshore (Rooper et al., 1999), which may explain the high densities of juveniles observed in the more coastal areas of the northern Bering Sea.

Arctic and saffron cod populations did not overlap spatially or in their temperature rage. Each species was observed at temperatures favorable for growth. Laurel et al. (2015) demonstrated that age-0 Arctic cod are able to maintain high growth rates at low temperature while age-0 saffron cod cannot. Growth of age-0 Arctic cod is highest at ~7°C and their growth rates exceed those of age-0 saffron cod at temperatures < 9 °C. They predicted that age-0 Arctic cod would exhibit rapid growth at 2-7 °C if not food-limited. Age-0 Arctic cod in the Arctic Eis AT surveys were primarily observed in this temperature range. Saffron cod growth increases with temperature up to 16 °C (Laurel et al., 2015), and age-0 saffron cod were disproportionately abundant in the warmest parts of the study area.

Temperature is a key characteristic structuring the habitats of Arctic fishes (Bouchard and Fortier, 2011; Hunt et al., 2013; Benoit et al., 2014; Laurel et al., in 2015; Sigler et al., this issue). Pelagic species in the Pacific Arctic exhibit strong environmental associations (Eisner et al. 2013; Pinchuk and Eisner, this issue; Sigler et al., this issue) which likely reflect strong spatial and temporal gradients in habitat suitability. The age-0 Arctic cod in the northern Chukchi may be close to their maximum growth potential compared to colder areas farther north, and increased warming of their habitat beyond this point may reduce their potential growth rate and favor saffron cod. For example, Arctic cod captured in the 2012 Arctic Eis survey exhibited higher growth rates in the Northern Chukchi, and saffron cod experienced higher growth in the Northern Bering Sea (Helser et al., 2016). Saffron cod were much more abundant than Arctic cod during a 2007 surface trawl survey (Eisner et al., 2013) when temperatures were anomalously warm. The opposite pattern was observed when the survey was repeated in 2012 when temperatures were cooler (Logerwell et al., 2015). Together, these observations suggest that the abundance and distribution of pelagic fishes in the Pacific Arctic is related to temperature.

5.3 Pelagic fishes were more abundant in 2013

Arctic cod, saffron cod, herring and capelin were more abundant and acoustic backscatter was higher in 2013 than 2012. Oceanographic conditions and plankton community composition differed substantially in the two study years, and this may be related to increased pelagic fish abundance in 2013. For example, within the northern region of the Chukchi Sea, age-0 Arctic cod were 2.7 times more abundant and their distribution extended farther south in 2013 than in 2012 (Fig. 7). This observation may be linked to interannual differences in ocean currents and plankton communities. The Alaska Coastal Current was weaker and water that overwintered on the Chukchi shelf was present on the northern shelf in summer 2013 (Danielson et al., this issue; Pinchuk and Eisner, this issue). There were cooler bottom waters on the northern shelf (i.e. in areas where age-0 arctic cod were abundant) in 2013 than in 2012 (Danielson et al., this issue; Pinchuk and Eisner, this issue). The shallow nearshore coastal habitats influenced by

Alaska Coastal water (where age-0 saffron cod and Pacific herring were abundant) were warmer in 2013 (Danielson et al., this issue). Additionally, zooplankton species of Pacific origin were less abundant, Chl *a* concentrations were lower, and phytoplankton cells were larger in 2013 compared to 2012 (Danielson et al., this issue; Pinchuk and Eisner, this issue). Surface drifters placed in areas of high age-0 Arctic cod abundance were advected off the shelf in 2012 but not in 2013 (Danielson et al., this issue), indicating potential fish transport to different areas.

It is clear that 2012 and 2013 contrasted strongly in terms of water properties, planktonic communities and pelagic fish abundance. Striking interannual differences in fish abundance, size distribution, and species composition in the Chukchi Sea have been observed and attributed to water temperature (e.g. Logerwell et al., 2015; Nikolayev et al., 2008). That is, it has been hypothesized that low temperatures favor Arctic cod and higher temperatures favor saffron cod and Pacific herring (Nikolayev et al., 2008; Logerwell et al., 2015). Similar arguments can be made for the Arctic Eis AT surveys: i.e. in 2013 the Northern Chukchi was cooler and age-0 Arctic cod were more abundant. Although these inferences are based on short time series, these observations suggest that population dynamics and dispersal mechanisms of pelagic fishes in the Pacific Arctic are tightly coupled with the highly variable environmental conditions. This is a key area for future study as mechanistic understanding of these associations will allow more accurate predictions of how pelagic fishes will respond to increased warming and environmental variability in the Pacific Arctic.

5.4 Potential Biases in the acoustic-trawl estimates

Acoustic surveys in mixed-species assemblages are analogous to a ‘zero-sum game’ (von Neuman and Morganstern, 1944) in the sense that if less backscatter is erroneously attributed to one species or size class, more backscatter is attributed to others (eq. 3). Backscattering from animals is strongly size and species-specific at the acoustic frequencies we used, and this makes it difficult to quantify weakly scattering species in mixed assemblages (McClatchie and Coombs, 2005). The methods used here to partition backscatter to species cannot be expected to produce robust abundance estimates for weak acoustic scatterers, and thus we restricted abundance estimates to common and strongly scattering species. For example, it would be difficult to quantify the abundance of jellyfish, which dominate the trawl catches by weight, but account for a small fraction of acoustic backscatter due to low mass-specific TS (De Robertis and Taylor, 2014). This is because misidentification of a small proportion of fish backscatter as jellyfish would result in large increases in jellyfish abundance, but not vice-versa. Likewise, Pacific sand lance (*Ammodytes hexapterus*) have been reported to be relatively abundant in the area (Quast, 1974), but we did not attempt to estimate their abundance as they are poorly retained in the survey trawls (De Robertis et al., 2015), and are weak acoustic scatterers as they lack a swimbladder.

The fish in the study area were small and poorly retained by the trawls, particularly the large mesh Cantrawl. The impact of net selectivity on AT survey abundance estimates depends on the trawl gear used, the species and size classes present, and the degree to which species and size classes are spatially separated (Williams et al., 2011). We estimated trawl selectivity to account for the size and species differences in the probability of capture (De Robertis et al., 2015), and applied these estimates to correct trawl-derived estimates of species and size composition. Computing abundance under the assumption that both nets are equally selective for all species and size classes had a relatively small impact on abundance estimates for Arctic cod, as most of the individuals were found in areas where fishes were dominated by age-0 Arctic cod. Capelin, however, are relatively well retained by the Cantrawl (De Robertis et al., 2015), and ignoring net selectivity resulted in a 3-fold increase in capelin abundance in 2012. This occurred because sampling with the Cantrawl (the only trawl used in 2012) overestimated the proportion of capelin present in the environment. Trawl selectivity also strongly biased size distributions towards larger, better-retained size classes (Williams et al., 2011; De Robertis et al., 2015).

The Cantrawl was not ideal for sampling midwater organisms in the study area as it is strongly size and species selective (De Robertis et al., 2015). Furthermore, the Cantrawl surface hauls did not target the depths or geographic locations where high-backscatter aggregations were detected. The midwater hauls targeted areas of high backscatter in the Chukchi, primarily high-density aggregations of Arctic cod in the north, as well as saffron cod and adult herring farther to the south. There was little midwater trawling in the northern Bering Sea region, and we relied almost exclusively on surface hauls in the upper ~ 20 m to characterize pelagic fishes. Although the surface hauls did not target high-backscatter areas, the trawl did sample most of the water column in this shallow region (bottom depth averaged (± SD) 29.9 ± 9.0 m in 2012 and 30.9 ± 9.6 m in 2013).

The size and species composition of sound scattering organisms was estimated by assigning a selectivity-adjusted trawl catch to each backscatter measurement. These assignments were made subjectively by an analyst interpreting fish aggregation patterns (e.g., schooling characteristics, depth distribution) and trawl catches. Replacing these subjective assignments with the spatially nearest trawl haul produced abundance estimates within ~ 30 % of those of the analyst. These discrepancies were reduced to differences of < 23 % overall and < 7 % for Arctic cod when the backscatter was separated into midwater and surface zones. This indicates that the results were not highly sensitive to the qualitative trawl assignments because the size and species composition of fish assemblages was spatially consistent, and midwater hauls often targeted the highest abundance areas.

There is considerable uncertainty in some of the target strengths used to estimate acoustic backscatter from organisms in the study area. When TS relationships were unavailable for a species, values from a related species were used. The TS of non-target species impacts abundance of the target species by altering the proportion of backscatter assigned to the target species (eq. 3). The impact of changing TS by ± 3 dB reflects the degree to which assemblages were mixed: in areas where only the target species exists, altering the TS of other species will have no impact on the abundance of the target species. We found that for Arctic cod, which often dominated the acoustic backscatter, the impact of doubling or halving the acoustic scattering from all other species had a minor impact (< 12 % difference). For saffron cod, this had an intermediate effect (< 24 %), and the differences were largest for capelin and herring (up to a 66 % change), depending on the year.

Biases in the target species TS will impact the proportion of backscatter attributed to that species (eq. 3) as well as the conversion of backscatter to fish abundance (eq. 5). Thus, TS is a key factor that influences the abundance estimates. Population size estimates are thus more sensitive to uncertainties in the TS relationship than relative measures such as interannual trends in abundance or spatial distribution. The TS used for Arctic cod is considered relatively reliable as it was estimated for the same species and sizes in the Beaufort Sea (Parker Stetter et al., 2011) and is consistent with previous observations of age-0 Arctic cod TS (Benoit, 2014). In addition, it is consistent with other TS relationships derived for this species, particularly for age-0 fish (reviewed in Geoffroy et al., 2015). The TS relationship used in this study produces conservative abundance estimates as it is higher for age-0 fish than existing estimates (Geoffroy et al., 2015) leading to lower abundance estimates (see eq. 5). The TS of saffron cod (and thus the total abundance of this species) is relatively uncertain as the TS for this species is unknown and a TS relationship for pollock was applied. Both herring and capelin are unable to inflate their swim bladder at depth, which will result in depth-dependent TS (Blaxter and Batty, 1990). The TS used for Pacific herring (Ona, 2003) was derived for Atlantic herring, but accounts for this depth-dependency. The TS for capelin was derived from this species in the North Pacific (Guttormsen and Wilson, 2009), but does not account for depth-dependent swimbladder inflation.

In summary, the AT survey estimates appear to be relatively robust to the assumptions made to partition backscatter to species. However, the population estimates are sensitive to the TS used to calculate abundance, and future work should focus on reducing this uncertainty. The estimates of Arctic cod should be considered the most reliable as sensitivity analyses indicate that the abundance estimates are relatively insensitive to the parameters to calculate abundance. Arctic cod were particularly amenable to AT survey methods as they were abundant, occurred over a narrow size range, have relatively well-characterized TS, and dominated species composition in widespread areas of high backscatter.

5.5 Exploratory offshore survey near Barrow Canyon

A layer of age-0 Arctic cod persisted over the exploratory survey of the shelf break near Barrow Canyon. Previous observations indicate that these aggregations of age-0 Arctic cod persist well to the east of the surveyed area (Parker-Stetter, 2011; Benoit et al., 2014; Majewski et al., 2015; Geoffroy et al., 2015).

Age-1+ Arctic cod were only observed at the easternmost point of the exploratory survey area over Barrow Canyon. These fish, which were present at low densities, were deeper (~ 230 m) and in colder water (~ 0.6 °C) than the near-surface age-0 Arctic cod, as has been observed previously in this area (Parker-Stetter et al., 2011). However, the age-1+ Arctic cod were not present in the overlying near-freezing (-1.6 °C) water, indicating that they avoid this very cold water and are associated with the comparatively warm and saline deep water of Atlantic origin (Crawford et al., 2012; Benoit et al., 2014; Majewski et al., 2015).

Detection of the deep age-1+ Arctic cod coincided with the only observation of the Atlantic water mass during the Arctic Eis cruises (Danielson et al., this issue). The location of these age-1+ fish was also close to the westernmost transect of a 2008 survey where age 1+ Arctic cod were observed in a patchy distribution over the Beaufort shelf break (Parker-Stetter et al., 2011). Peak density (~ 0.7 fish m^{-2}) of the age-1+ Arctic cod in the 2013 offshore survey was relatively low and comparable to the mean density (0.9 fish m^{-2} in water depths of 100-500 m) observed in 2008 (Parker-Stetter et al., 2011). Subsurface layers of age-1+ Arctic cod have previously been observed to be widespread over the shelf break and in schools in shallower water in the Beaufort Sea to the east of the 2013 exploratory survey (Parker-Stetter et al., 2011), and farther east in the Canadian Beaufort (Benoit et al., 2014). Additional acoustic observations suggest that densities of age 1+ Arctic cod increase east of this area along the shelf break, particularly over canyons (Crawford et al., 2012). Scattering layers were not observed over deep (750-1500 m) water, confirming that Arctic cod were not abundant well beyond the shelf break (Parker-Stetter et al., 2011; Crawford et al., 2012; Benoit et al., 2014).

5.6 Is the northern Chukchi Sea shelf a nursery ground for Arctic cod?

Arctic cod numerically dominated pelagic fishes in the survey area. Their populations in the survey area were estimated to be > 35 times larger than any of the other enumerated species. The fact that large populations of age-0 Arctic cod were observed in the Chukchi Sea in both years, with the fish almost exclusively in the northern Chukchi Sea suggests that this region may be an important nursery ground for Arctic cod. The average abundance of age-0 Arctic cod in the northern Chukchi Sea observed in this study ($1.6 \cdot 10^{11}$ individuals) is roughly comparable to the average number of age-0 walleye pollock (*Gadus chalcogrammus*) observed in AT surveys in the southeastern Bering Sea ($1.3 \cdot 10^{11}$ individuals) in 2011 and 2012 (De Robertis et al., 2014). These age-0 pollock were produced by a large spawning stock ($\sim 1.9 \cdot 10^{10}$ age-3+ pollock in 2011 and 2012, Ianelli et al., 2014), which suggests that the age-0 Arctic cod in the northern Chukchi Sea may have been produced by a large spawning stock.

Age-0 Arctic cod were abundant at ≥ 69.5 °N latitude in the northern Chukchi Sea. Densities of age-0 Arctic cod in the northern Chukchi Sea region averaged 0.6 m^{-2} in 2012 and 2.2 m^{-2} in 2013. These densities were comparable to, and generally greater than, those from previous reports from the Pacific Arctic. The abundance of a species complex of age-0 fish (the majority of which are age-0 Arctic cod) in a 2008 survey of the western Beaufort Sea averaged 1.0 fish m^{-2} in areas < 40 m deep and 0.5 fish m^{-2} in deeper water (Parker-Stetter et al., 2011). Densities of 0.5 age-0 Arctic cod m^{-2} have also been reported in the Southeastern Beaufort Sea (Benoit et al., 2014). However, Benoit et al. (2014) used a lower TS for age-0 Arctic cod, and abundances would be reduced by ~50 % if the TS used by Parker-Stetter et al. (2011) and this study had been applied. The conclusion that age-0 arctic cod are abundant over a broad area of the northern Chukchi is likely conservative as a conservative TS relationship was used in this study (see section 4.4) and this study accounts for backscatter from all species in the trawl catch, while the other surveys assume that all near-surface backscatter is from age-0 Arctic cod.

Maximum densities of age-0 Arctic cod (averaged over 0.5 nmi) in the northern Chukchi Sea were 32.7 fish m^{-2} in 2012 and 61.2 fish m^{-2} in 2013. These densities are higher than reported from the Beaufort Sea. Parker-Stetter et al. (2011) reviewed densities of age-0 Arctic cod from studies throughout the Pacific Arctic and reported a maximum density of 15 fish m^{-2}. Subsequently, Benoit et al. (2014) reported a peak density estimate of 1.6 fish m^{-2} for age-0 Arctic cod in the southeastern Beaufort Sea. Thus, age-0 Arctic cod appears to be more abundant in the northern Chukchi Sea than in the sampled areas of the Beaufort Sea.

Although large numbers of age-0 Arctic cod were observed in the AT survey of the northern Chukchi Sea in 2012 and 2013, only negligible numbers of age-1+ fish were observed in the Chukchi Sea. In contrast, high densities of pelagic age-1+ Arctic cod have been observed in some years on the Russian Chukchi shelf (Nikolayev et al., 2008), and older fish have been consistently observed near the Beaufort Sea shelf break (Parker-Stetter et al., 2011; Benoit et al., 2014; Majewski et al., 2015). The formation of very dense aggregations of overwintering Arctic cod have also been reported during periods of increasing ice cover in deep embayments in the Beaufort Sea (Benoit et al., 2008; Geoffroy et al., 2011; Geoffroy et al., 2015).

Age-1+ Arctic cod dominate the catch from demersal trawl sampling in the Chukchi Sea (Barber et al., 1997; Thedinga et al., 2013, Goddard et al., 2014; Helser et al., 2016), which suggests that Arctic cod on the Chukchi shelf become more demersal as they age (Logerwell et al., 2015). However, the densities of semi-demersal age 1+ Arctic cod on the Chukchi shelf appear low based on recent survey efforts. The 2012 Chukchi Sea bottom trawl survey estimated only 2.6 billion age-1+ Arctic cod (Goddard et al., 2014), which is substantially lower than the abundance of < 6.5 cm (age-0) Arctic cod reported here (80/247 billion fish in the Chukchi sea in 2012/2013). Bottom trawl surveys have estimated age-1+ Arctic cod abundance to be lower: 0.01 fish m^{-2} over the entire Chukchi shelf in 2012 (Goddard et al., 2014), and 0.02 and 0.006 fish m^{-2} in the Northern Chukchi in 1990 and 1991 (Barber et al., 1997). Norcross et al. (2013) estimated 0.04 fish m^{-2} based on small beam trawl samples at three sites in the northern Chukchi. Average annual abundance estimates in the nearshore have ranged from < 0.001 to 0.08 Arctic cod m^{-2} based on nearshore demersal trawl hauls (Thedinga et al., 2013). The similar Arctic cod density among these demersal trawl surveys suggests that age 1+ fish densities on the Chukchi shelf are substantially lower than those of age-0 fish observed in the 2012 and 2013 AT surveys (described above). Furthermore, abundance of age 1+ Arctic cod in the nearshore and the continental shelf do not appear to be dramatically different. The sizeable difference in abundance between the age-0 and age-1+ age-classes suggests that survivorship in the Chukchi Sea survey area may be very low, and/or that the age-0 Arctic cod observed on the shelf do not remain in the area.

We thus hypothesize that age-0 Arctic cod either emigrate from the northern Chukchi shelf and/or experience high mortality over their first winter. The AT-surveys of the Chukchi Sea shelf indicate that there are large numbers of age-0 Arctic cod in the northern Chukchi, and this study combined with previous reports of demersal sampling suggest that there are comparatively few age-1+ Arctic cod in the Chukchi Sea. Arctic cod spawn under-ice in winter, producing buoyant eggs that develop into ice-associated larvae (reviewed in Bouchard and Fortier, 2011, Logerwell et al., 2015). It remains to be determined where the age-0 Arctic cod on the Chukchi shelf were spawned, and their movement patterns via migration and/or advection as they transition to age-1. In the Canadian Beaufort, age-0 Arctic cod have been inferred to perform an ontogenetic migration into deep water by December (Benoit et al., 2014; Geoffroy et al., 2015), and the Age-0 Arctic cod on the Chukchi shelf may undertake similar migrations. High densities of pelagic age-1+ Arctic cod were observed with acoustic-trawl survey methods on the Russian Chukchi shelf in 2003, but were absent in subsequent surveys (Nikolayev et al., 2008, Datsky, 2015). These surveys indicate that age-1+ Arctic cod may be episodically abundant on the Chukchi shelf.

Age-0 Arctic cod in the northern Chukchi Sea experience warmer temperatures than in the high Arctic (e.g. Benoit, 2014), which may increase growth rates (Laurel et al., 2015). This favorable thermal habitat on the northern Chukchi shelf may have demographic consequences over a broader region. Growth rates in the Chukchi area are high (Helser et al., 2016) and increased size at the end of the summer may reduce overwinter mortality (Bouchard and Fortier, 2011, Heintz et al., 2013). The distribution of Arctic cod outside of the ice-free summer months in the northern Chukchi and the fate of the sizeable population of age-0 Arctic cod present in the areas in late summer is unknown. It is unclear whether the northern Chukchi Sea serves as source of recruits for populations in adjacent areas (e.g., the western Chukchi, Bering, Beaufort, or East Siberian Seas) due to advection or emigration of age-0 Arctic cod, or whether the area serves an ecological sink where the abundant age-0 fish in late summer experience high overwinter mortality due to a host of factors such as predation, physiological stress, or starvation (Hurst, 2007). We hope that our observations will stimulate further studies to determine the spawning location(s) of the age-0 Arctic cod that reside on the northern Chukchi shelf in late summer, and to determine whether these fish experience high overwinter mortality on the shelf, or whether the area serves as a nursery area for age-0 fish and a source of recruitment to other areas.

6. Acknowledgements

We are indebted to the captain and crew of F/V *Bristol Explorer*, Jared Weems, Jim Murphy, Franz Mueter, and the participants in Arctic Eis cruises for their assistance at sea. Patrick Ressler, Robert Levine, Mike Sigler and two anonymous reviewers provided helpful comments on manuscript drafts. We thank Seth Danielson and Lisa Eisner for providing the CTD data. This work was funded in part with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service U.S. Department of the Interior (grants10-CIAP-010 and F12AF00188) and by the Alaska Fisheries Science Center, NOAA. The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Table 1. Target strength (TS) to size relationships from the literature used to allocate 38 kHz acoustic backscatter to species in this study. The symbols in the equations are as follows: r is the bell radius in cm, L is length in cm, Z is depth in m. The species for which the TS was derived is given. The TS for sandlance, smelts, gadiids, squid and herring are for related species to those occurring in the study area, as TS to length relationships are not available for these species. The gadiid species group includes saffron cod, Pacific cod, and walleye pollock. The TS used for smelts (which included Pacific sand lance and rainbow smelt) was measured at 120 kHz.

Species or group	**TS** (dB re 1 m^2)	**TS derived for which species**	**Reference**
Arctic cod	$TS = 8.03\log_{10}L - 60.78$	*Boreogadus saida*	Parker Stetter et al., 2011
Capelin	$TS = 20\log_{10}L - 70.3$	*Mallotus villosus*	Guttormsen and Wilson, 2009
Gadiids	$TS=20\log_{10}L-66$	*Gadus chalcogrammus*	Traynor, 1996
Jellyfish	$TS = 10\log_{10}(\pi r^2)-86.8$	*Chrysaora melanaster*	De Robertis and Taylor, 2014
Herring	$TS = 20\log_{10}L - 67.4 - 2.320\log_{10}(1+z/10)$	*Clupea harengus*	Ona, 2003
Sand lance	$TS = 56.5 \log_{10}L - 125.1$	*Ammodytes personatus*	Yasuma et al., 2009
Smelts	$TS = 20\log_{10}L - 65.9$	*Osmerus eperlanus*	Peltonen et al., 2006
Squid	$TS = 20\log_{10}L - 75.4$	*Todarodes pacificus*	Kang et al., 2005
Other fishes	$TS = 20\log_{10}L - 67.5$	Physoclist fishes	Foote, 1987

Table 2. Mean nautical area backscattering coefficient observed for 38 kHz backscatter with a frequency response consistent with 'fish' by year and survey area. The common area refers to the 1° by 1° geographic cells that were adequately sampled in both surveys.

Year	**N. Bering** s_A (m^2 nmi^{-2}**)**	**S. Chukchi** s_A (m^2 nmi^{-2})	**N. Chukchi** s_A (m^2 nmi^{-2}**)**	**Entire area** s_A (m^2 nmi^{-2}**)**	**Common area** s_A (m^2 nmi^{-2}**)**
2012	40.6	35.8	88.0	63.6	69.4
2013	92.2	57.0	267.2	164.9	163.0

Table 3. Abundance of fishes by year and area estimated with acoustic-trawl methods in the 2012 and 2013 Arctic Eis surveys of the northern Bering and Chukchi continental shelf. The common area refers to the 1° by 1° geographic cells that were adequately sampled in both years.

Species	**Year**	**N. Bering** (No. fish)	**S. Chukchi** (No. fish)	**N. Chukchi** (No. fish)	**Entire area** (No. fish)	**Common area** (No. fish)
Arctic cod	2012	$6.5 \cdot 10^{9}$	$1.9 \cdot 10^{8}$	$8.0 \cdot 10^{10}$	$8.7 \cdot 10^{10}$	$8.5 \cdot 10^{10}$
	2013	$1.4 \cdot 10^{2}$	$2.3 \cdot 10^{9}$	$2.4 \cdot 10^{11}$	$2.5 \cdot 10^{11}$	$2.3 \cdot 10^{11}$
Saffron cod	2012	$5.0 \cdot 10^{7}$	$7.8 \cdot 10^{8}$	$6.9 \cdot 10^{8}$	$1.5 \cdot 10^{9}$	$1.5 \cdot 10^{9}$
	2013	$1.5 \cdot 10^{7}$	$4.4 \cdot 10^{9}$	$1.6 \cdot 10^{9}$	$6.0 \cdot 10^{9}$	$6.0 \cdot 10^{9}$
Capelin	2012	$3.3 \cdot 10^{8}$	$3.1 \cdot 10^{8}$	$8.1 \cdot 10^{8}$	$1.4 \cdot 10^{9}$	$1.0 \cdot 10^{9}$
	2013	$7.4 \cdot 10^{8}$	$2.7 \cdot 10^{7}$	$1.2 \cdot 10^{9}$	$2.0 \cdot 10^{9}$	$1.9 \cdot 10^{9}$
Herring	2012	$1.3 \cdot 10^{9}$	$1.7 \cdot 10^{8}$	$9.4 \cdot 10^{6}$	$1.5 \cdot 10^{9}$	$1.4 \cdot 10^{9}$
	2013	$7.5 \cdot 10^{9}$	$4.0 \cdot 10^{7}$	$9.1 \cdot 10^{4}$	$7.6 \cdot 10^{9}$	$6.6 \cdot 10^{9}$

Table 4. Sensitivity analysis applying alternate post-processing scenarios to estimate species composition of observed acoustic backscatter in the acoustic-trawl surveys (see text for details). The results are expressed as the percent change in numerical abundance compared to that computed using the baseline scenario described in this paper. The shading indicates the difference in abundance relative to baseline under each scenario: white shading indicates a difference of < 15 %, light grey a difference of 15-25 %, and dark gray a difference > 25 %.

Target species	**Year**	**1) no trawl selectivity**	**2) Nearest haul**	**3) Nearest haul with midwater and surface zones**	**4) Increase TS of all taxa but target by 3 dB**	**5) Decrease TS of non-target species by 3 dB**
Arctic cod	2012	-11.2	-32.6	-6.9	-8.4	+6.7
	2013	+2.4	-15.1	+4.1	-11.9	+8.8
Saffron cod	2012	-27.3	+29.1	-10.2	-23.1	+23.0
	2013	-16.5	-3.9	+22.7	-9.0	+11.4
Capelin	2012	+328.8	+33.1	+7.8	-34.6	+52.9
	2013	+28.2	+7.0	-2.0	-37.3	+66.5
Herring	2012	-28.6	-18.6	-19.9	-49.8	+15.2
	2013	-3.4	+0.2	+13.0	-49.9	+1.9

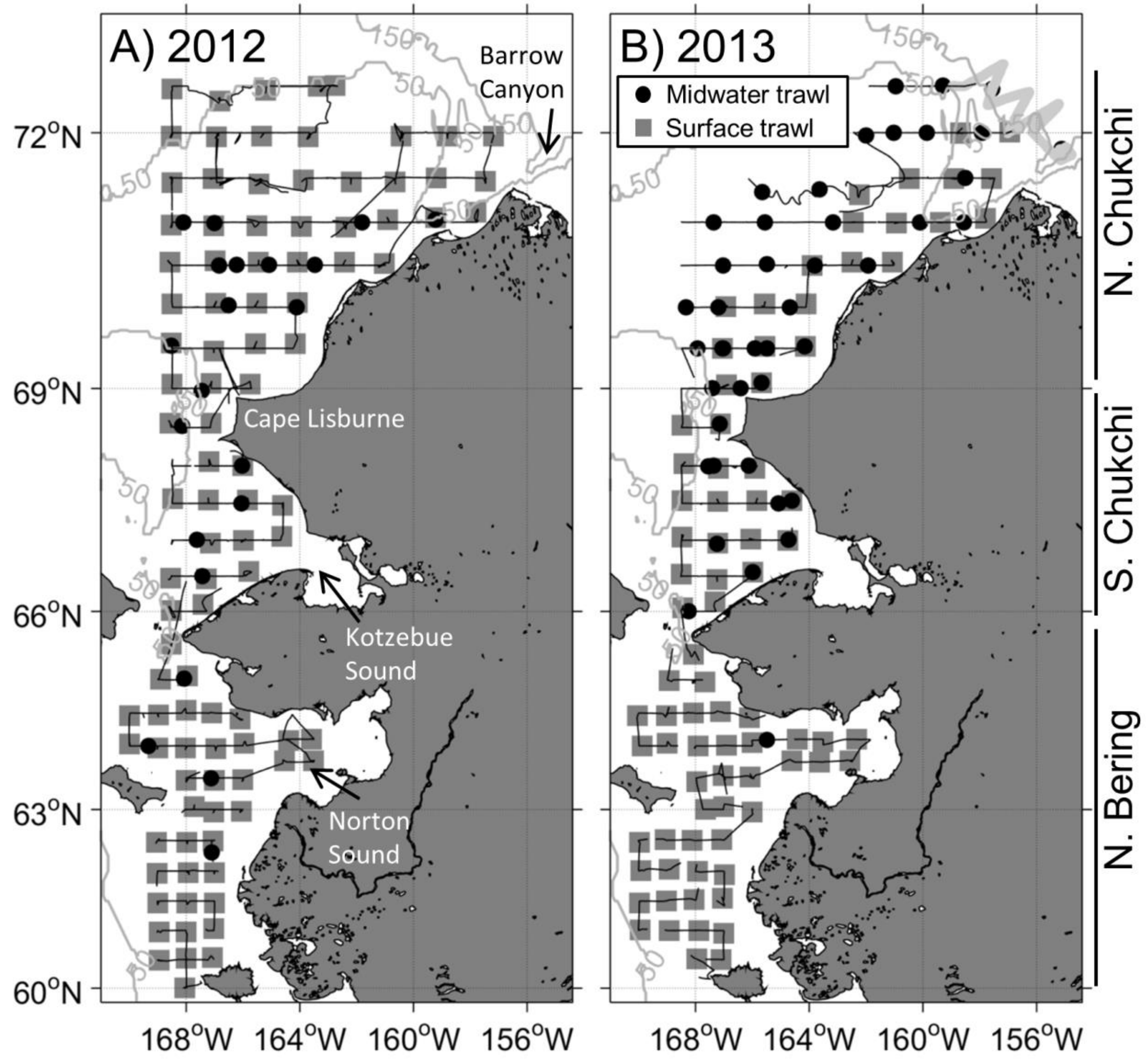

Figure 1. Study areas in A) 2012 and B) 2013. The survey track line is depicted as a black line, surface trawl stations as grey squares, and midwater trawl sites as black dots. The extent of the 2013 exploratory survey conducted in the vicinity of Barrow Canyon is represented as a thick grey line. Survey sub-regions defined in the text are indicated to the right. The 50 and 150 m depth contours are shown as light grey lines.

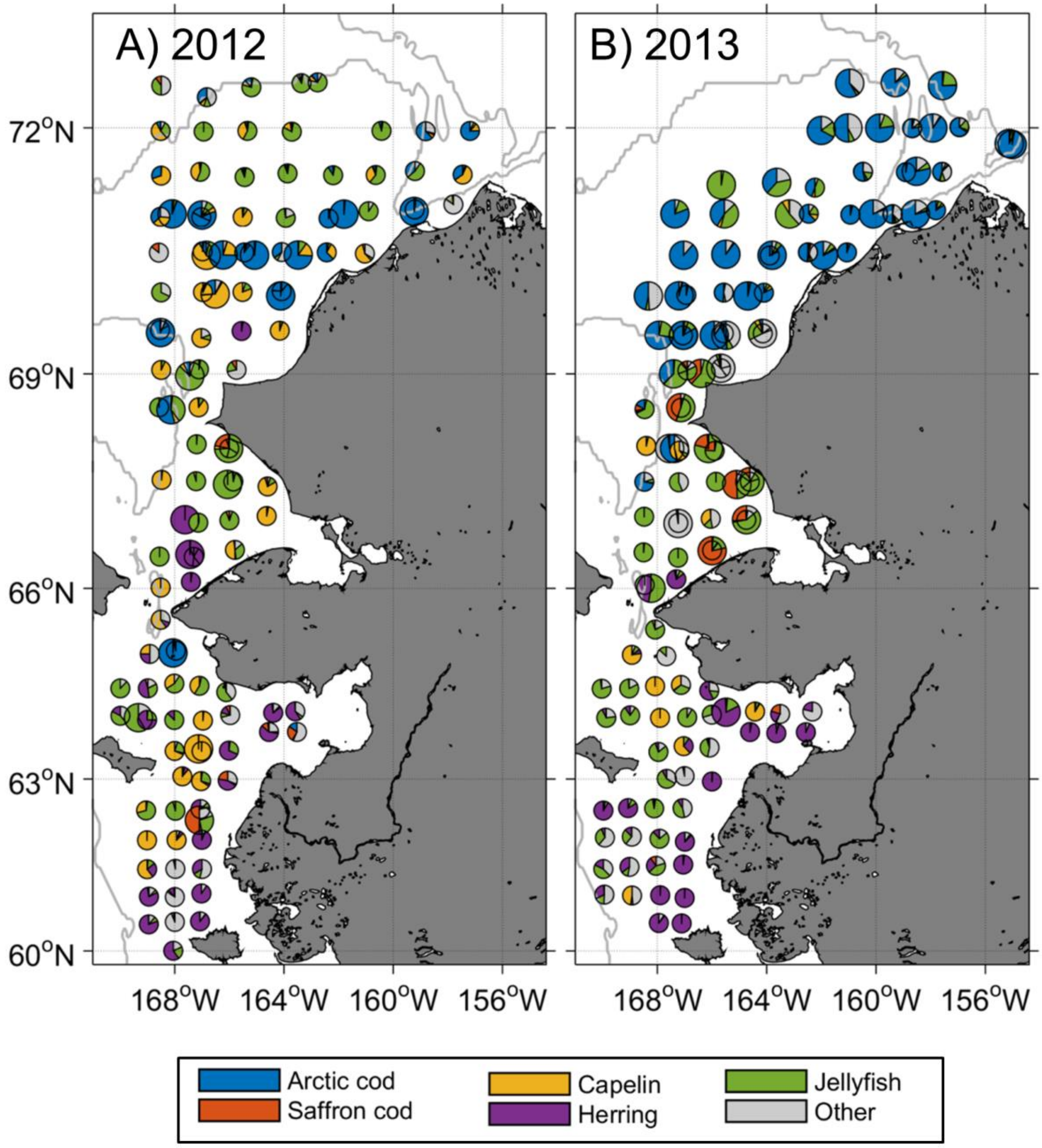

Figure 2. Catch composition expressed as proportions of individuals captured in trawl hauls in A) 2012 and B) 2013. The larger pie graphs represent midwater trawl hauls (Cantrawl in 2012, mod-Marinovich in 2013) and the smaller ones represent surface Cantrawl hauls. The 50 and 150 m depth contours are shown as light grey lines.

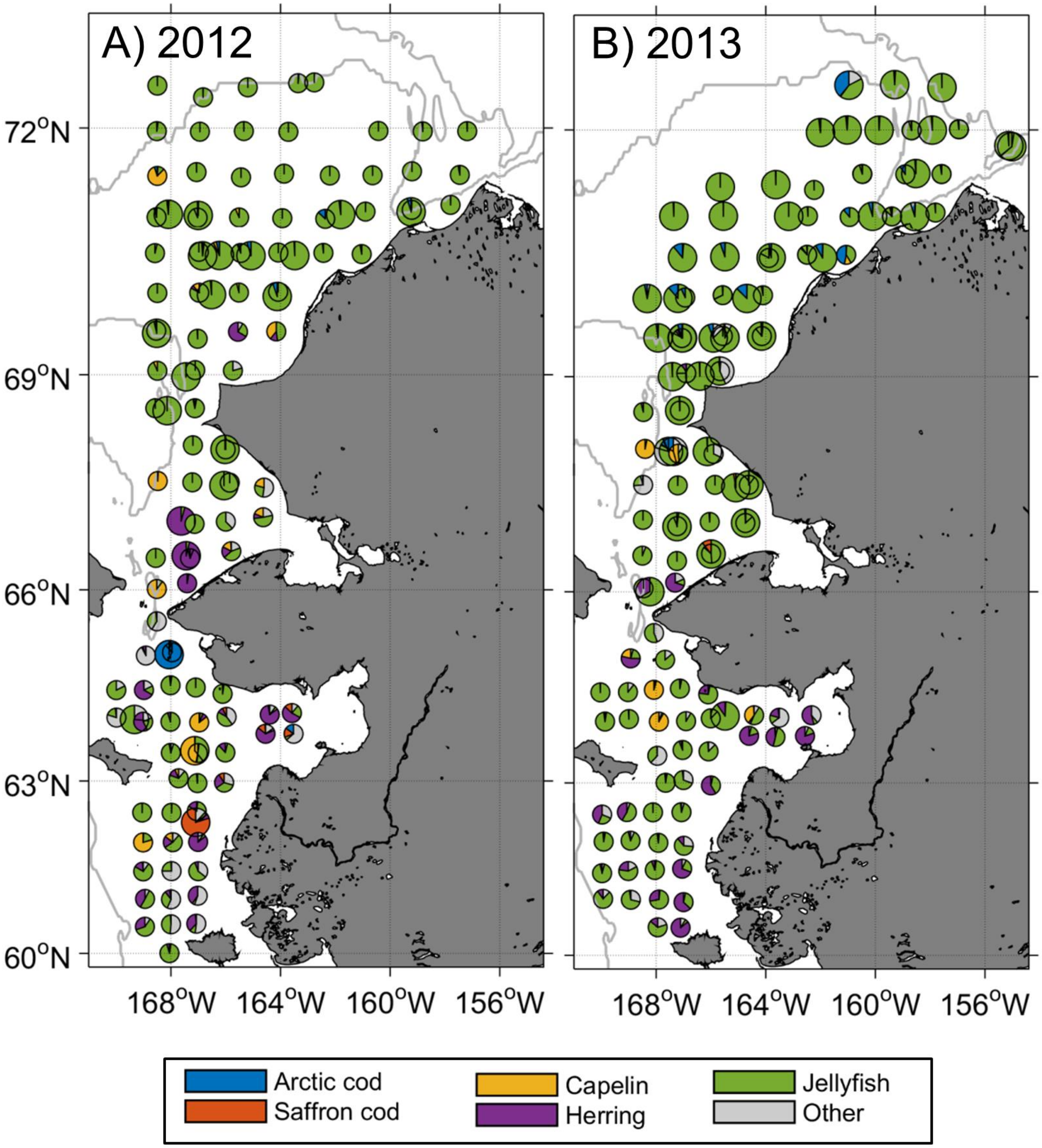

Figure 3. Catch composition expressed as proportions of trawl catch by weight in A) 2012 and B) 2013. The larger pie graphs represent midwater trawl hauls (Cantrawl in 2012, mod-Marinovich in 2013) and the smaller ones represent surface Cantrawl hauls. The 50, and 150 m depth contours are shown as light grey lines.

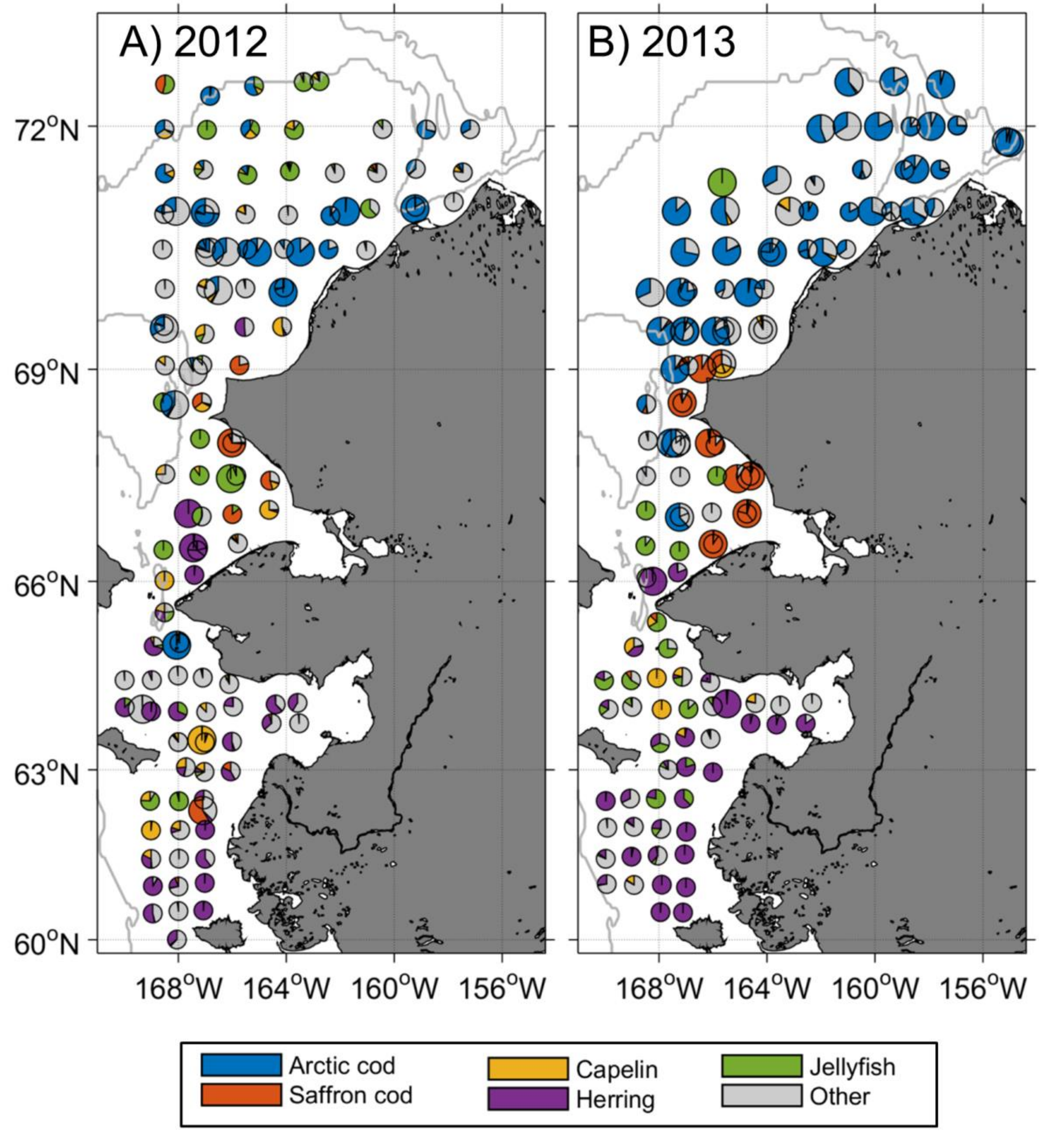

Figure 4. Estimated proportion of backscatter (*PB*, see eq. 3) attributable to key species derived by combining estimates of species composition from trawl catches and estimates of target strength listed in Table 1 for the Arctic Eis acoustic-trawl survey in A) 2012 and B) 2013. The larger pie graphs represent estimates for midwater hauls and the smaller ones represent surface hauls. The 50, and 150 m depth contours are shown as light grey lines.

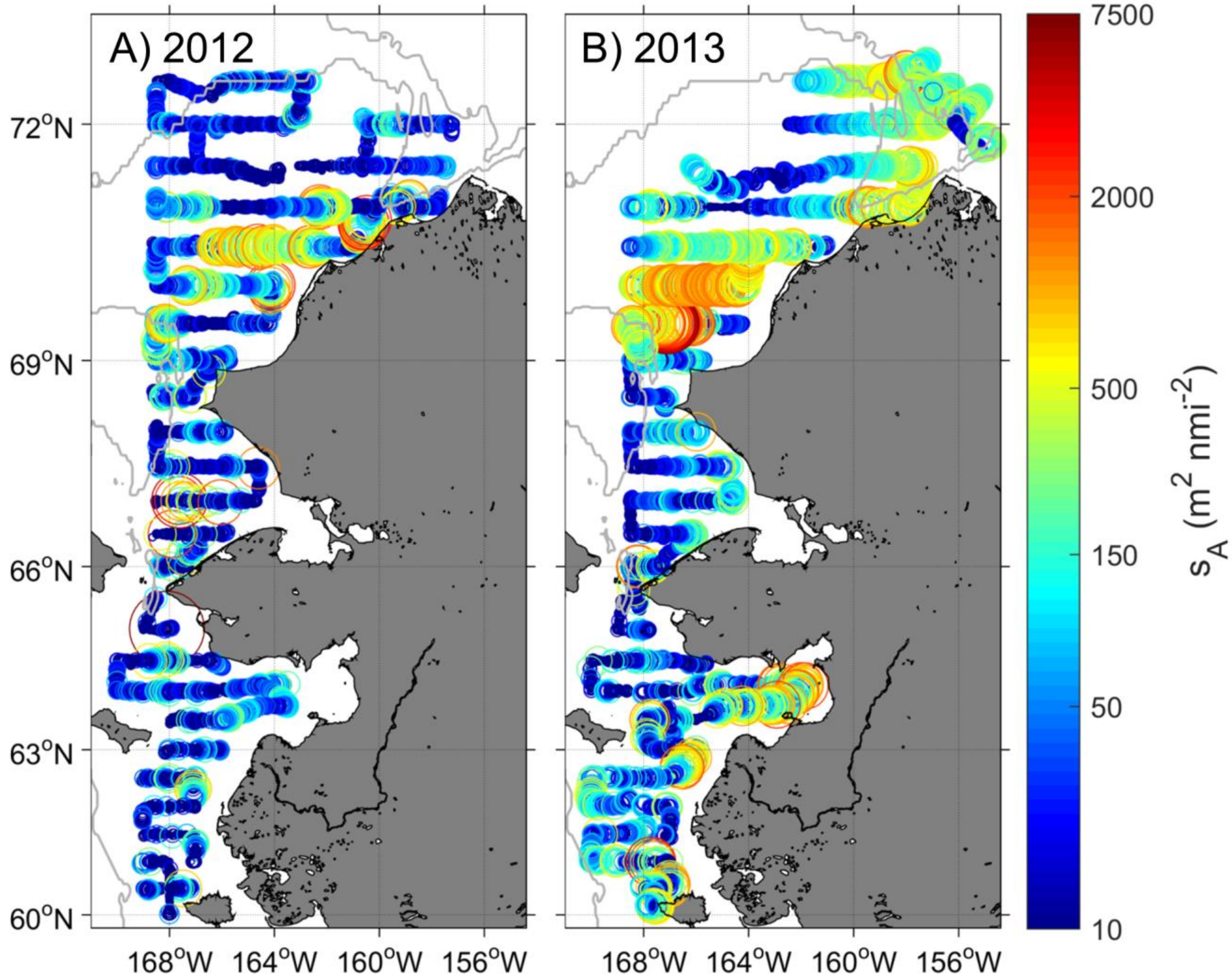

Figure 5. Integrated 38 kHz backscatter with a frequency response consistent with fish (i.e. $\Delta S_{v120\text{-}38kHz}$ = –16 to 8 dB) along the vessel track in A) 2012, and B) 2013. Symbol size and color is proportional to the observed backscatter. The 38 kHz backscatter from the 2013 exploratory survey in deeper waters in the vicinity of Barrow canyon (~72 °N, 156 °W, see Fig. 1) is also shown. The 50 and 150 m depth contours are shown as light grey lines.

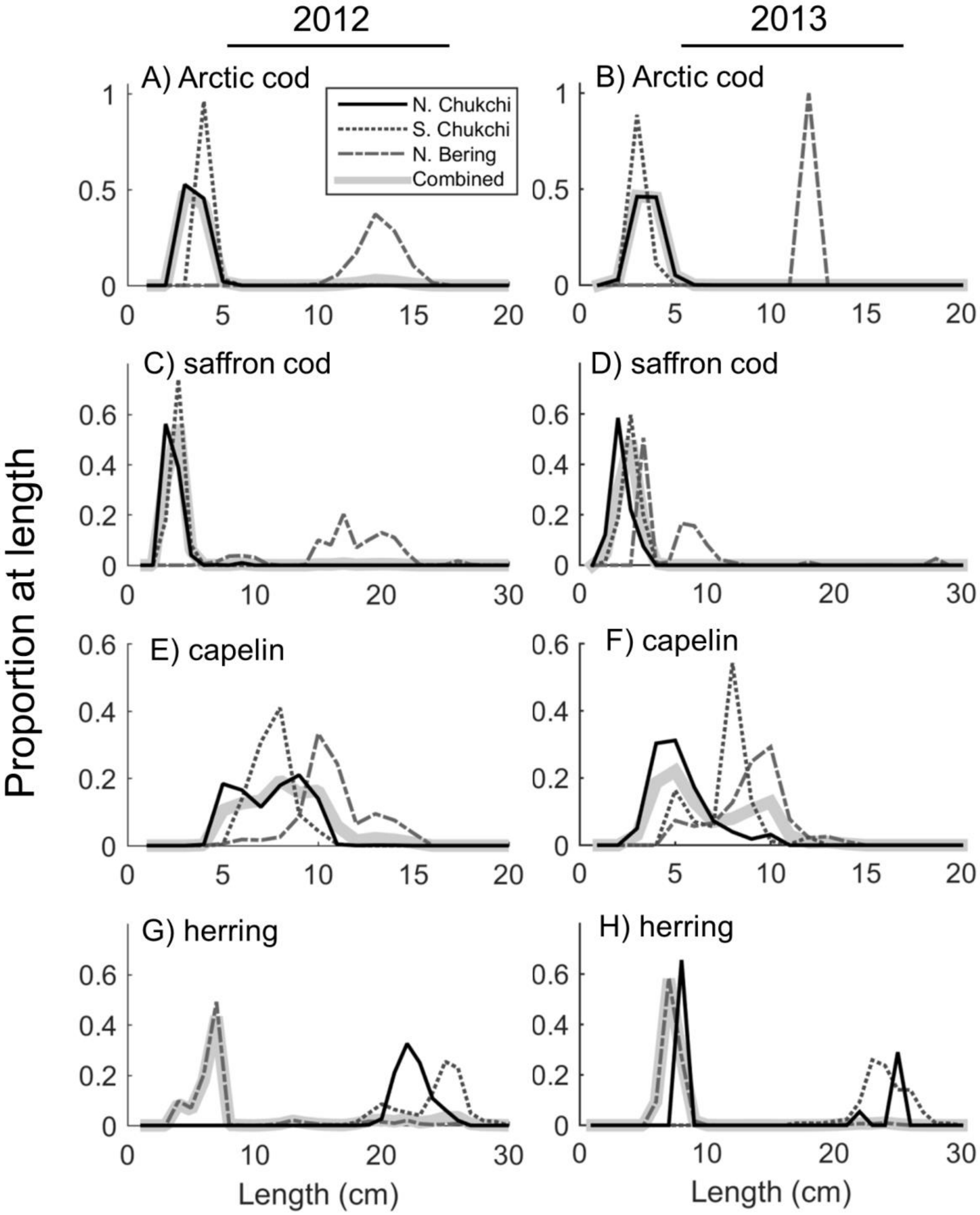

Figure 6. Size distributions of A-B) Arctic cod, C-D) saffron cod, E-F) capelin and G-H) herring by year and area. The size distribution for the entire study area is shown as a thick grey line, and can be very similar to that of a sub-areas if most fish were observed in that area (e.g., overlapping gray and black lines in Fig. 6A indicate that almost all Arctic cod were encountered in the northern Chukchi Sea).

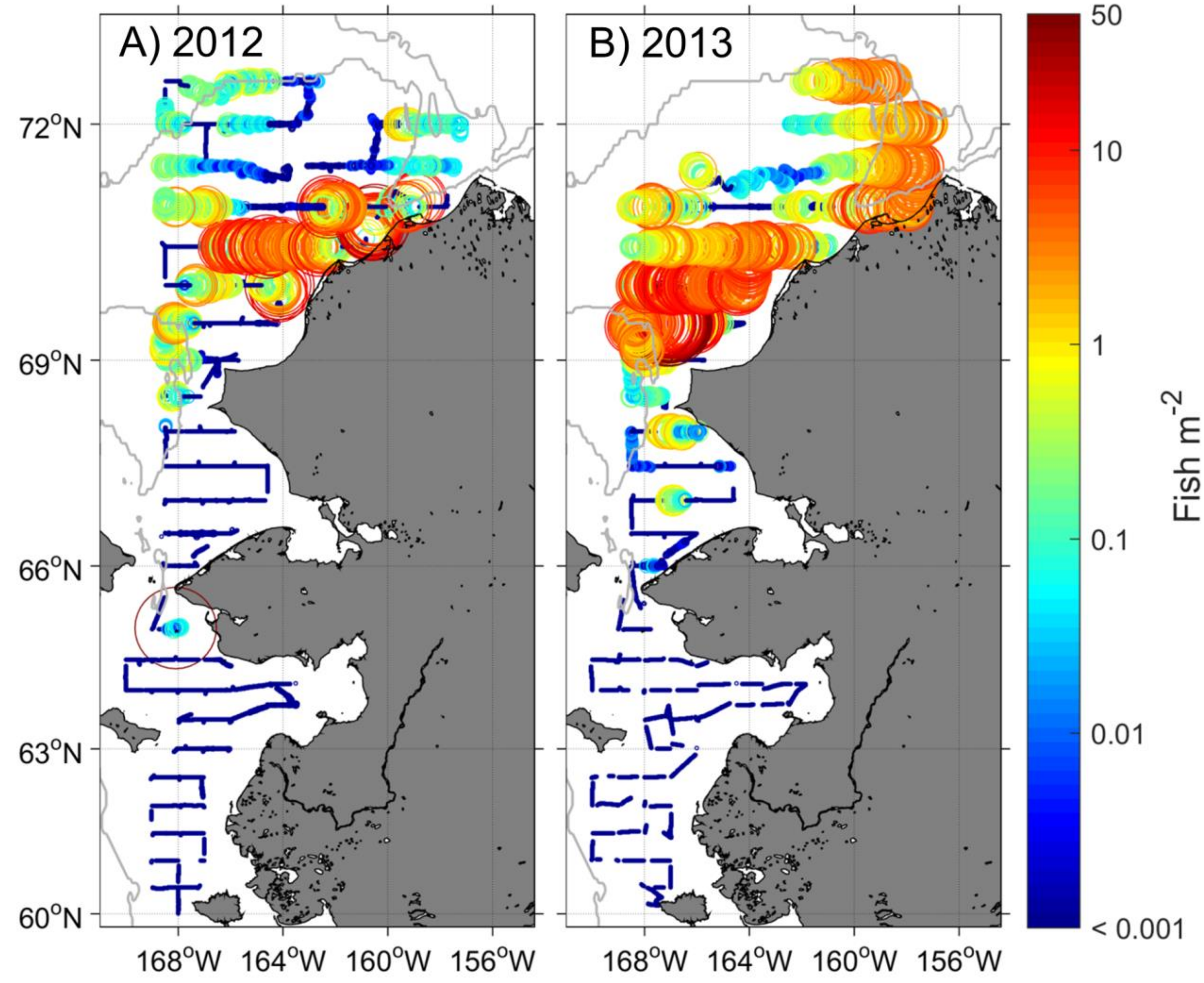

Figure 7. Density of Arctic cod estimated by acoustic-trawl methods in 0.5 nmi along-track intervals in A) 2012 and B) 2013. Most Arctic cod were small (Fig 6 A-B), with lengths consistent with those of age-0 fish. The 50 and 150 m depth contours are shown as light grey lines.

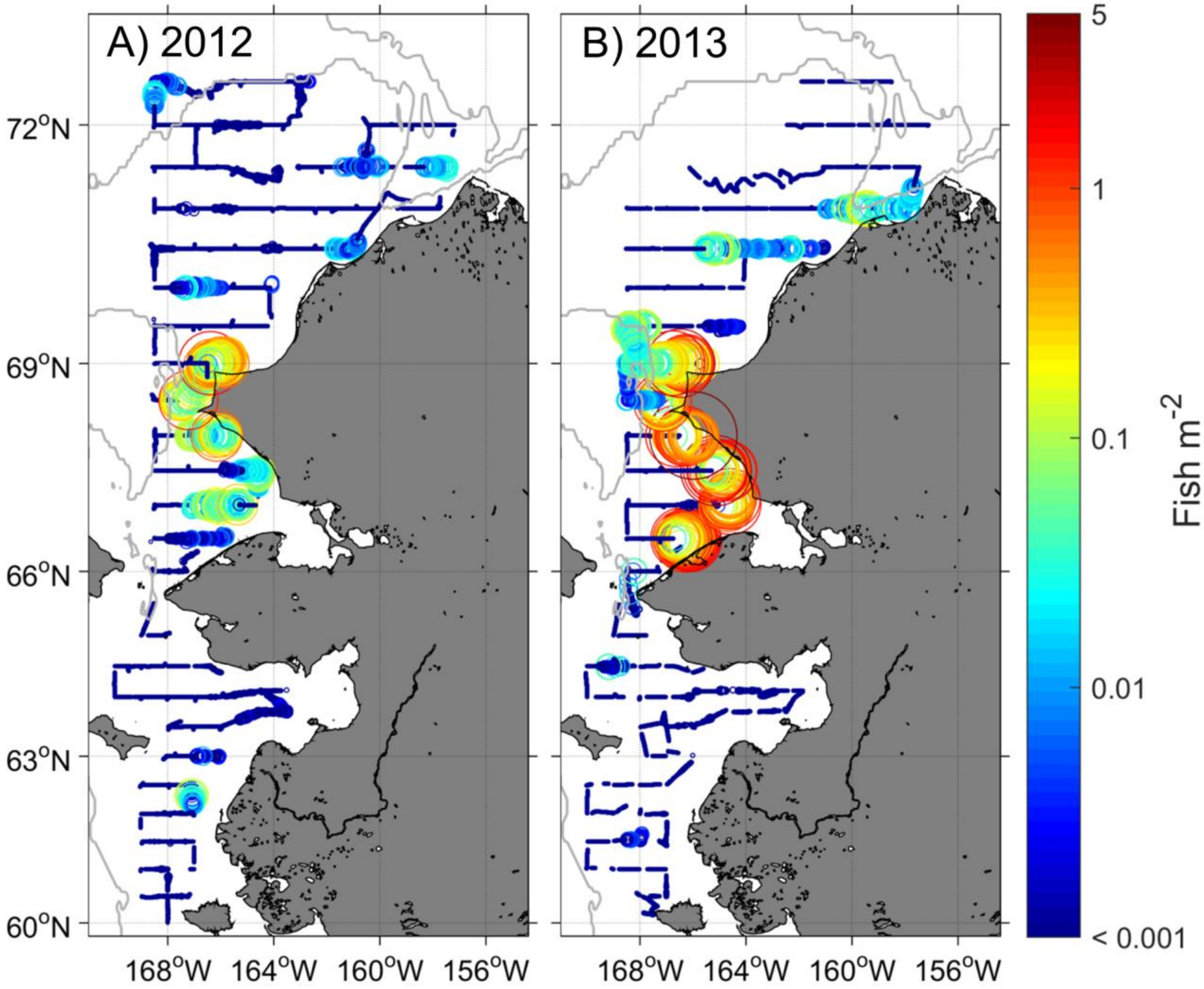

Figure 8. Density of saffron cod estimated by acoustic-trawl methods in 0.5 nmi along-track intervals in A) 2012 and B) 2013. Most of saffron cod were small (Fig 6 C-D), with lengths consistent with those of age-0 fish. The 50 and 150 m depth contours are shown as light grey lines.

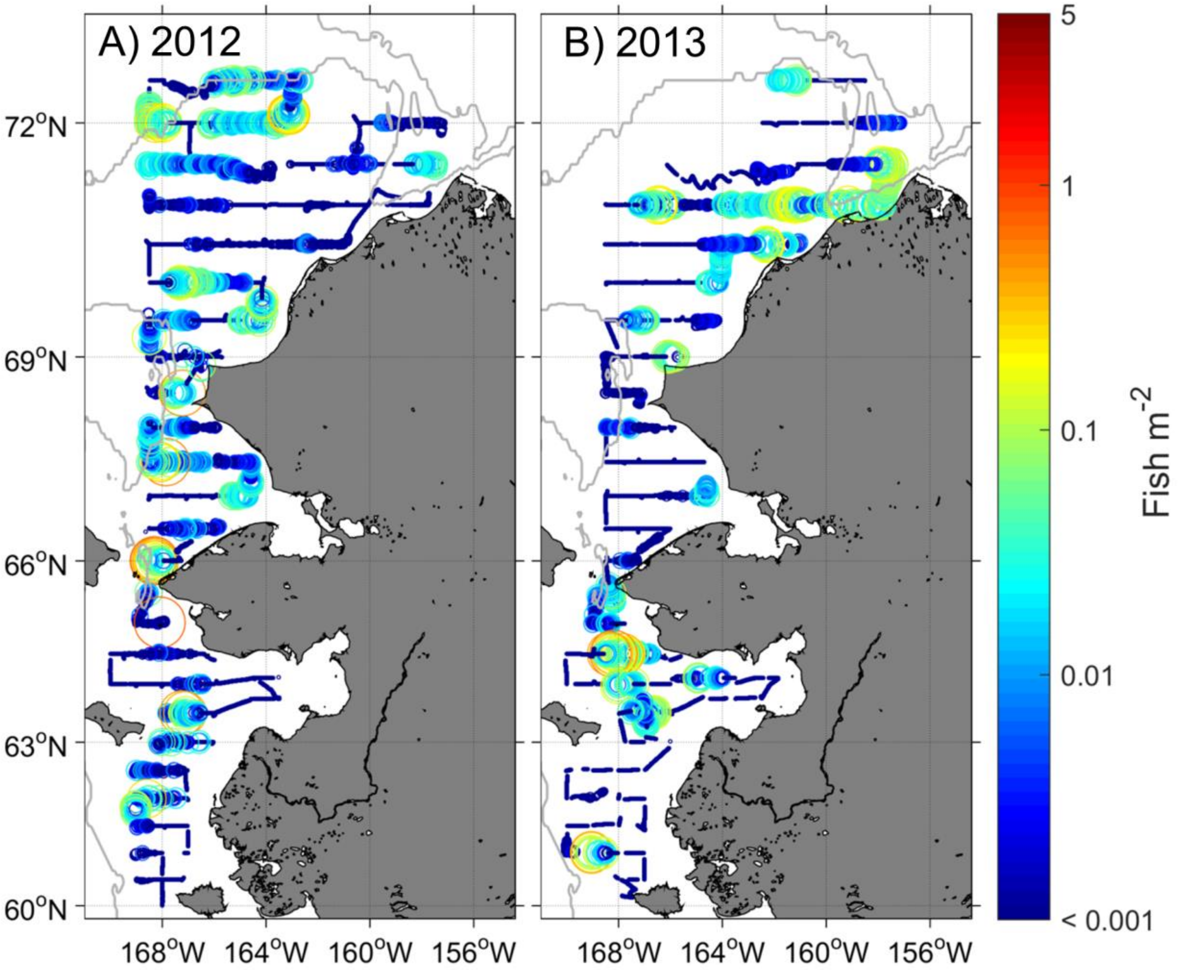

Figure 9. Density of capelin estimated by acoustic-trawl methods in 0.5 nmi along-track intervals in A) 2012 and B) 2013. The 50 and 150 m depth contours are shown as light grey lines.

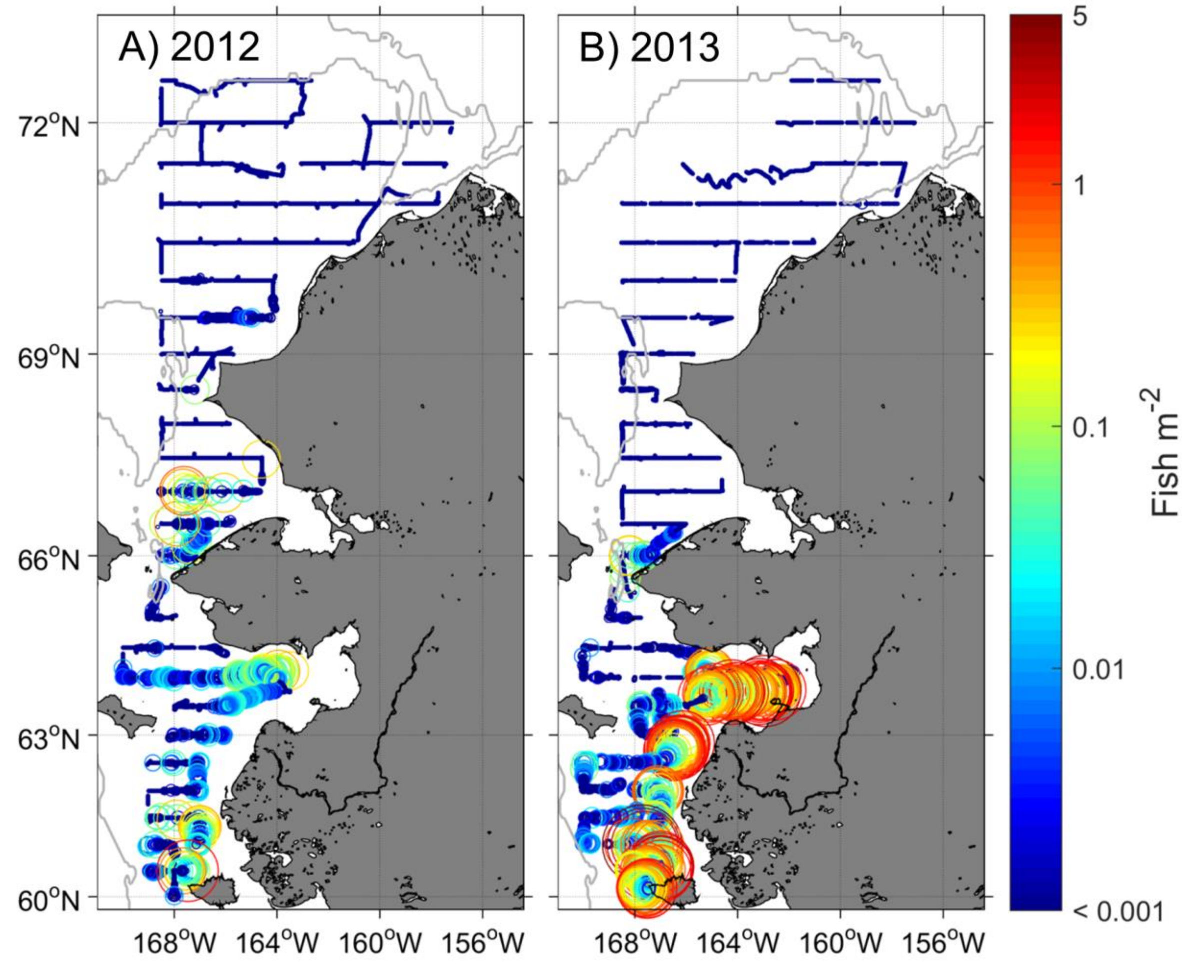

Figure 10. Density of Pacific herring estimated by acoustic-trawl methods in 0.5 nmi along-track intervals in A) 2012 and B) 2013. The 50 and 150 m depth contours are shown as light grey lines.

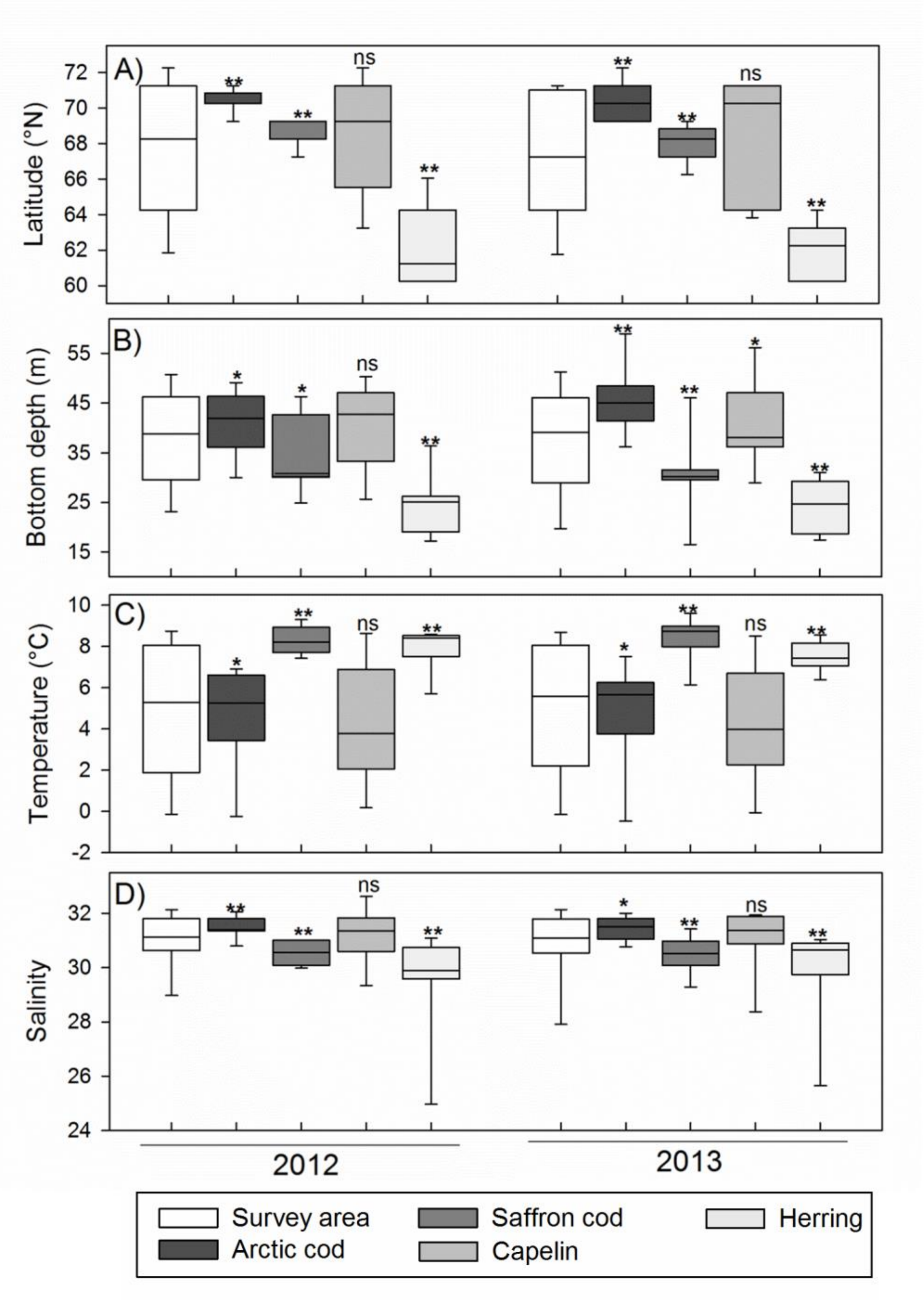

Figure 11. Comparison of the environmental conditions in the survey area and those under which fish populations were distributed. Distributions in 2012 and 2013 are depicted in relation to A) latitude, B) bottom depth, C) mean water column temperature, and D) mean water column salinity. The white box plots show 10th, 25th, 50th, 75th and 90th percentiles of each variable in the survey area. The filled box plots show the environmental conditions at which a given percent of the total fish abundance was observed. In some instances, the 10th (or 90th) percentiles overlap with the 25th (or 75th) percentiles and are indistinguishable from one another. The results of a two sample Kolmogorov–Smirnov test comparing the distribution of each species to conditions in the surveyed area is indicated above each box plot (ns = not significant, * $p < 0.05$, ** $p < 0.001$).

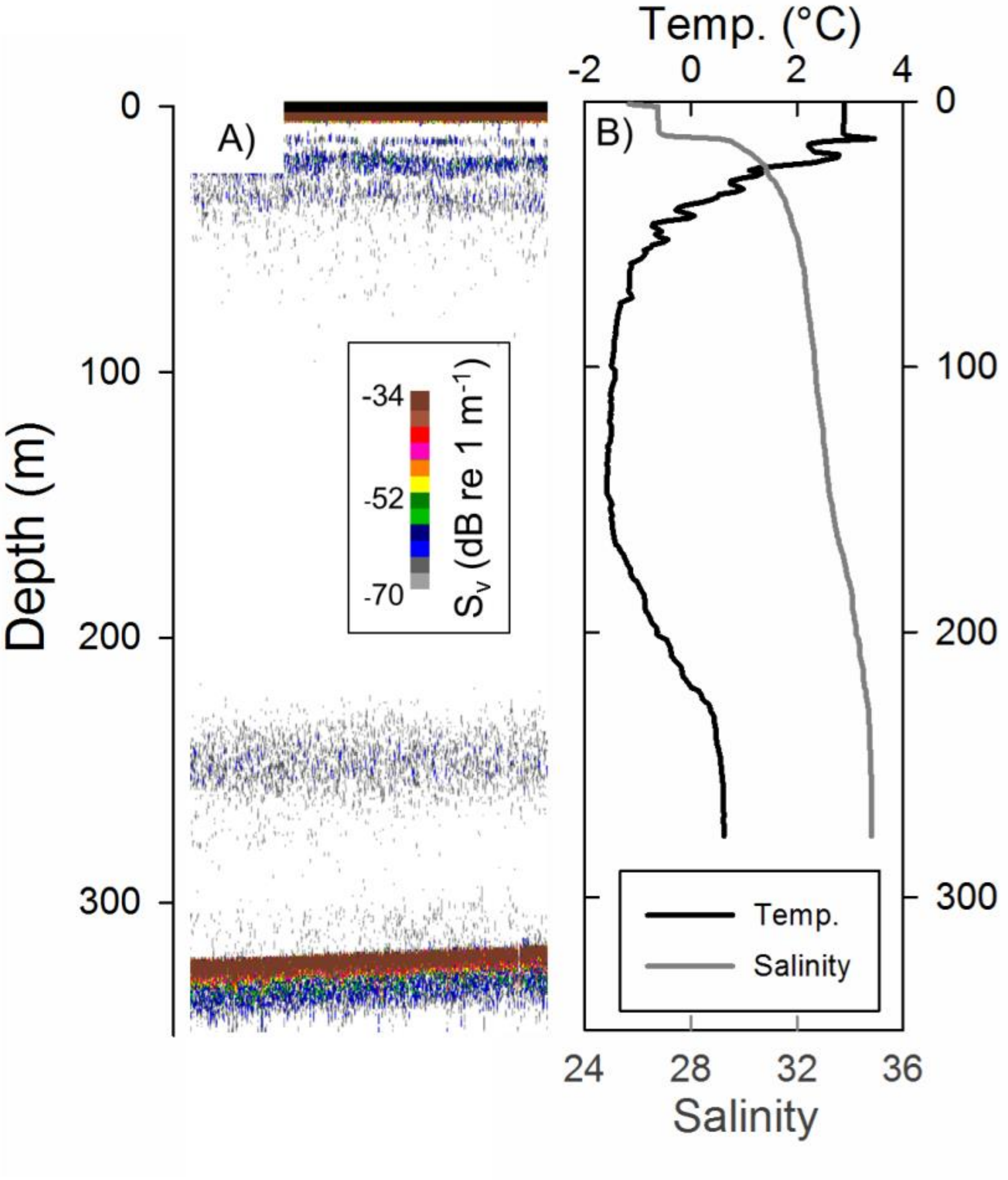

Figure 12. A) Echogram showing the Arctic cod near-surface layer (age-0) and the deep layer (age-1+) observed during the offshore exploratory survey near Barrow Canyon. The color scale is shown as an inset. B) Temperature and salinity profiles from this location show that the age-1+ fish layer coincides with warmer and more saline water.

Appendix F.

Snow crab life history, population dynamics and diet studies in the Chukchi and Beaufort Seas

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July 26, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

List of Oral and Poster Presentations

Divine LM 2016. Trophic dynamics and stock characteristics of snow crab (*Chionoecetes opilio*) in the Alaskan Arctic. UAF-SFOS Dissertation Defense. Faibanks, Alaska. March 2016.

Lauren M. Divine, Franz J. Mueter, Gordon H. Kruse, Bodil A. Bluhm, Katrin Iken. 2016. New estimates of growth, size-at-maturity, mortality and biomass of snow crab, *Chionoecetes opilio*, in the Arctic Ocean off Alaska. Alaska Marine Science Symposium 2016. Poster.

Lauren Divine, Katrin Iken, Bodil Bluhm, Robert Foy, Bob Lauth, Brenda Norcross, Kerim Aydin, Andrew Whitehouse. 2015. Snow crab (*Chionoecetes opilio*) ecology in the Alaska Arctic. Alaska Marine Science Symposium 2015. Oral presentation.

Lauren M. Divine, Bodil A. Bluhm, Katrin Iken. 2014. Can you stomach it?: Regional diet and stable isotope analysis of snow crab (*Chionoecetes opilio*) in the Alaskan Arctic. Interagency Crab Meeting 2015. Poster.

Lauren M. Divine, Bodil A. Bluhm, Katrin Iken. 2013. Can you stomach it?: Regional diet and stable isotope analysis of snow crab (*Chionoecetes opilio*) in the Alaskan Arctic. Wakefield Symposium 2013. Poster.

Proposed Objectives and Study Chronology

Snow crab life history, population dynamics and diet studies

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Snow crab, *Chionoectes opilio* is a widely distributed and abundant crab species on the Bering, Chukchi and western Beaufort shelves. Several coincident trends warranted detailed study of Pacific Arctic snow crab: (1) The recent northward contraction of the distribution range of *C. opilio* in the Bering Sea (Orensanz et al. 2004), (2) the assumed biomass increase of snow crabs in the Chukchi Sea (Bluhm et al. 2009), (3) the increase in human activities in the Chukchi and Beaufort seas including oil and gas exploration over the past decades that can interact and impact snow crabs on the Arctic shelves, and (4) the recently established Arctic Fisheries Management Plan (NPFMC 2009) in which snow crabs are one target species. Our goals were, therefore, to improve estimates of snow crab population size, stock characteristics, role in the food web, energetics, and reproductive potential. While the focus of the Arctic EIS project is on the Chukchi Sea, we were able to expand the study for several aspects to the Beaufort Sea based on additional funding through a CMI project (Bluhm et al. 2015).

Our specific **objectives** were to

(1) Determine fecundity and sperm reserves in female snow crab (p 1)

(2) determine energy allocation in mature female and male crabs (p 1)

(3) identify diet and trophic position of snow crab in different geographic areas and size classes (p 8)

(4) assess crab population dynamics and the potential for harvestable biomass (p34)

Objective 1 was co-investigated within a BOEM/Coastal Marine Institute-funded project and was recently reported on in that project's final report (Bluhm et al. 2015). The sperm reserve results are briefly summarized again here while the fecundity estimates are reported as part of a PhD thesis chapter and manuscript-in-preparation with objective 4. Results of *objective 2* are reported below. Results addressing *objective 3* are reported in form of a published manuscript in the Arctic Eis special issue in Deep-Sea Research II (Divine et al. 2016), and form PhD dissertation chapter 2 of Lauren Divine's dissertation. Results of *objective 4* reflect a draft version of dissertation chapter 3 (Divine et al. in prep.).

Objective (1)

Determine fecundity and sperm reserves in spermathecae in female snow crab

The capability of storing sperm in spermathecae for later fertilization of eggs enhances reproductive potential in snow crab, and brachyurans in general (Sainte-Marie et al. 2008). Through this mechanism, a female crab can produce viable clutches in consecutive years following a single mating and immature females can be mated successfully. Sperm limitation may still arise when insufficient male gametes are available to fertilize all eggs in a population, for example when a fishery selectively exploits males only (Sainte-Marie et al. 2002). While quantitative assessments of sperm storage have previously been conducted for parts of the Canadian Arctic and the Bering Sea (Sainte-Marie et al. 2002, Stichert et al. 2013), it was our objective to assess if female snow crab in the Chukchi Sea also store sperm. For result on female fecundity assessed through egg counts see results for objective 4.

Methods

Spermathecae were removed from female crabs by cutting crabs in half from rostrum to the mid-point of the outer carapace edge. The spermathecal content of each left spermatheca was carefully peeled out of the surrounding membrane and weighed to the nearest mg in n=195 mature females from the Chukchi Sea. The number of ejaculate layers, evident as bands of differing color shades, was recorded after cutting the spermathecae in half. Spermathecal load, measured as weight of the sperm stored in the left spermatheca in female crabs, was classified ‘low’ from ≤0.1 g, ‘moderate’ from 0.2-0.5 g, and large ≥ 0.6 g in accordance with the categories developed by Sainte-Marie et al. (2002). The relationship of sperm reserves with various variables was tested using Pearson rank correlations.

Results and discussion

Spermathecal load ranged from 0.001 to 0.240 g. Most of the loads were low (0.025±0.032 g) according to Sainte-Marie et al. (1998, 2002) and were neither related to female body weight, nor to shell condition or water depth (Figure 1-1). The number of sperm layers ranged from 1-4 with the majority (71%) of mature females having only one layer of sperm in their spermathecae (Figure 1-2). Females found in the Chukchi Sea stored sperm in low to moderate amounts comparable to the Bering Sea and Canadian waters (c.f., Sainte-Marie et al. 1998, Stichert et al. 2013), but whether that amount would be sufficient to produce a subsequent clutch needs further study.

Objective (2)
Energy allocation in mature female and male crabs

Caloric (energy) content varies between and within species. Within a species, caloric content varies between tissue types, seasons, life history stages, sexes, age groups etc. (Griffiths 1977). Energetic expense into the different tissues is a trait-off that balanced the needs for somatic growth, reproductive success, maintenance metabolism, molting, defense against competitors and predators among other factors. Somatic growth investment is higher in earlier life stages while the energetic expense of reproduction increases during maturation, and is often higher in females. Here, we studied the energetic investment of male and female snow crab into the main tissue types that make up their bodies.

Methods

Mature females and immature males were selected from plumb-staff beam trawl hauls and 83-112 trawl hauls taken in the Chukchi Sea during the 2012 Arctic Eis bottom trawl survey (Britt et al. 2013, Goddard et al. 2013). A few additional mature females were supplemented from the 2012 RUSALCA survey (see Crane et al. 2015 for information on that program), collected with the same type of plumb-staff beam trawl. Since mature males were virtually absent from the Chukchi Sea (Bluhm et al. 2015 and objective 4) they were collected from the Beaufort Sea 2013 BREA survey. Body sizes and station names of all samples used for this objective are in the data archive.

Frozen individuals were thawed, blotted dry, carapace width was measured to 0.1 mm, and individual wet weights were determined to 0.1 g wet weight. To determine the relative composition of crab tissues by weight and caloric content, snow crabs were completely dissected by tissue types (muscle, hepatopancreas, gonad tissue, shell, and eggs in mature females). All tissues were individually weighed after freeze-drying to constant weight for 24–48 h. To determine energetic content, sub-samples of each tissue type were taken from both the tissues of the dissected crabs and also from additional mature females of additional crabs. Dried samples were ground to a homogeneous powder using mortar and pestle. Sub-samples of the powder were weighed, put into gelatin capsules (Parr, 0.9 ml) and measured for their caloric content on an oxygen bomb calorimeter (Parr model 6300) in the marine mammal lab at the University of Alaska Fairbanks. Measured energy content was corrected for the energy content of the gelatin capsules by running 12 replicates of empty capsules as blanks and subtracting their average energy content from each tissue value. The mean absolute caloric content per gel capsule ± standard deviation was 0.530±0.032 kcal. Instrument error was determined by analyzing 10 runs of a benzoic acid standard (Parr Instrument Co.) and was ±0.009 kcal g dw^{-1}. Tissue caloric content was determined after combustion as kilo calories per gram dry weight (kcal g^{-1} DW). Total caloric content of a given tissue type was calculated by multiplying the caloric content of a given tissue sample (given in kcal per gram dry weight of a tissue) by the total tissue dry weight of an individual crab.

Tables 1 and 2 give the sample sizes, which for caloric content are unequal due to occasional misfires of the calorimeter. Due to a freezer failure, one set of mature female crabs was used for determining tissue proportions by dry weight, while another (from the same area with a similar crab size range) was used to determine caloric content. Tissue weight proportions from the first set combined with mean energetic content of tissue sub-samples from the second set were used to determine whole tissue caloric content. Shell caloric content could not be determined for female crabs due to intermittent instrument repairs. Whole shell caloric values for females was therefore calculated using the mean caloric content of the shell from males, based on the lack of a sex difference in caloric content per gram dry weight in muscle and hepatopancreas (data shown in results).

Differences in caloric content between tissue types and between sexes were analyzed using ANOVA with prior testing of normal distribution and Tukey's post-hoc test for pairwise comparisons for tissue differences. The degree to which caloric content was predicted by body size was analyzed using simple linear regression analysis. The distribution of caloric data by tissues and sexes was visualized in box-whisker plots where the boxes show the median and upper and lower quartile, and the whiskers show the highest and lowest values except for outliers which are indicated as asterisks (>1.5 times the interquartile range) and circles (>3 times the interquartile range). Statistical analyses were done in Systat version 13.

Results

The composition of whole crabs by dominant tissue types was first determined by *dry weight* for immature males and mature females from the Chukchi Sea and for mature males from the Beaufort Sea. Dry weight composition for immature males was determined from n=10 from the Chukchi Sea with a mean size of 58.7 ± 74.5 mm CW and a mean body weight of 74.5 ± 15.8 g ww. These small immature males consisted of only one third shell weight and half muscle weight (Figure 2-1a). A fifth of dry weight was gonad weight in immature males compared to just 1% in mature males. For mature females, n=20 crabs from the Chukchi Sea were used with a mean body size of 46.1 ± 3.8 mm CW and a mean body weight of 33.4 ± 8.9 g ww. Dry weight in these mature female was composed of about half shell weight and over one third of reproductive tissues (gonads and eggs), with only a tenth of muscle (Figure 2-1c). Mature females also had the highest proportion of hepatopancreas weight of the three sex categories. Dry weight composition was also determined for 20 mature male crabs from the Eastern Beaufort Sea with a mean body size of 117.1 ± 13.7 (SD) mm carapace width (CW) and a mean body weight of 756.0 ± 243.3 g ww (see data archive for full data). By dry weight, these mature male crabs were composed of almost three quarters of shell, with about a quarter of mass contributed by muscle and 5% by hepatopancreas and gonad combined (Table 1, Figure 2-1b).

Then, the composition of crabs by dominant tissues was determined by *caloric content*. For that purpose, it was necessary to first determine energetic content of a small tissue sample (expressed as kcal per gram dry weight of tissue) and multiply this by the absolute dry weight (or %) of a given tissue type. To determine caloric content per gram dry weight (Table 2, data archive), the same mature male crabs as for dry weight proportions were used. For mature females, n=64 crabs of a mean size of 49.6 ± 5.5 mm CW and mean weight of 43.8 ± 15.4 g ww were used, though not all tissues were successfully run for each crab. Mean caloric content per gram dry weight differed significantly between tissue types in both mature males and mature females (Figure 2-2). Mean caloric content was highest in hepatopancreas in both mature males and females, followed by gonad and muscle tissue with the latter difference being significant in females but not in males (Figure 2-3). Mean caloric value for eggs was significantly lower than for all other tissues in females, and caloric content for shell was significantly lower than for all other tissue in males (shell was not run for females). Differences in caloric content per gram dry weight between mature males and mature females were significant for gonad tissue (with higher values in females), but not for muscle and hepatopancreas (Table 2, Figure 2-3). Shell caloric content was only determined for male crabs, and egg caloric content obviously only for females (Figure 2-3d, e). On a per gram dry weight basis, caloric content remained stable over the body size range measured; none of the regression equations of tissue caloric content per gram dry weight against body size were significant (not shown).

By caloric content of total tissues, the relative proportions of shell and muscle were higher in mature males than females. Gonad tissue and eggs combined contributed a third of the caloric investment in female crabs compared with only 3% in males (Figure 2-1d-e). Hepatopancreas proportion was also higher in mature females than males. Total tissue caloric content differed significantly between some tissues in mature females and between all tissues in mature males (Figure 2-2b, d). In mature females it was higher in eggs, hepatopancreas and muscle than in gonad and shell (Figure 2-2d). In mature males, it was highest for shell, followed by muscle, hepatopancreas and then gonad (Figure 2-2b). Differences in total tissue caloric content between sexes were significant for muscle (Figure 2-4a) and gonads (Figure 2-4b) with higher values for muscle in males than females, but higher values in gonads in females than males despite the difference in body size. Total energy content for hepatopancreas did not significantly differ between sexes (Figure 2-4c, Table 2). Total caloric content per tissue type in each crab – although highly variable within both mature females and mature males - increased with body size for all tissues in mature females (Table 3), and for muscle and hepatopancreas in mature males (Table 3).

Discussion

Energy allocation to different tissue types in snow crab sampled during summer varied between tissue types and sexes. Large proportions of total caloric expenditure were allocated to muscle and shell in mature males, while comparatively more energy went into reproductive tissues in mature females. Per gram tissue, hepatopancreas was most calorie-rich, shell was least calorie-rich.

It is typical for male crustaceans to invest more into body growth (muscle tissue) than females (e.g., Augusto and Masui 2014) given that sperm production is less energetically demanding than egg production. Muscle is obviously needed for locomotion, but also for capturing and handling prey and for males to hold on to females during mating. In terms of locomotion, there is no clear evidence that males would move more (and hence need more muscles) given that – at least in the Bering Sea – both sexes conduct substantial ontogenetic migrations (Ernst et al. 2012), although migration patterns in the Chukchi and Beaufort Sea are not yet clear. In terms of muscle capacity to obtain prey, diets between males and females were not significantly different within a given region in the Chukchi and Beaufort seas (Divine et al. 2016). Large size and muscle mass is, however, a competitive advantage for reproductive success and allows the larger males to hold on to females during mating (Conan and Coneau 1986), obviously a benefit outweighing the energetic cost here documented of producing large muscle mass.

The energetic investment into the shell is also substantial for crustaceans in general and for snow crab males in our study in particular. Since crabs molt periodically, the shell gets lost and with it, part of the energy invested into its formation. Part of that energetic investment into the shell, however, can be recycled by resorption of varying fractions of the minerals and cuticle layers in different crustacean species, and occasionally also by consumption of the molt (Roer and Dillaman 1984). The relative proportion of energy contained in the shell in mature snow crab males from our study area was large, but since molting is infrequent in later instars (Sainte-Marie et al. 1995) that energy is a relatively long-term investment in the large-sized male crabs analyzed here. In immature crabs that molt more frequently, the proportion of shell (as indicated by dry weight proportions) is less than in mature males, but the shell is molted and the energy therefore mostly lost several times a year. Post terminal-molt crabs of both sexes continue to live and reproduce for several years so that energetic expenditure for shell production ceases and becomes available for egg and sperm production. Even before the terminal molt, mature females carrying a clutch cannot molt, reducing the energetic cost for shell production during the time of high energetic expenditure and instead investing it towards a new generation (reviewed by Hartknoll 2006).

Producing egg clutches is a high energetic expenditure for mature female snow crab, and one that is recurrent for each reproductive event. Clearly, the energetic cost for mature males as reflected in total caloric content was substantially smaller. Our tissue composition analysis, however, does not capture reproductive cost related to mating or guarding behavior, which can result in periods of reduced food intake in both sexes in crabs as well as enhanced physiological cost (Hartknoll 2006). Tissue composition in snow crab (and hence presumably caloric content) may, hence, change seasonally and during periods of starvation (Hardy et al. 2000), but was here only determined for the summer, when females carried their clutches.

Hepatopancreas was highest in energy content per gram dry weight of tissue. As the energy storage organ in crabs (Ceccaldi 1989), high lipid content is in part responsible for this high per unit weight energy content, and in decapods those lipids get used for ovarian development and vitellogenesis (Haefner and Spaargaren 1993). The caloric expenditure into this tissue type can, therefore, at least in part be considered an investment into reproduction, together with gonad tissue and egg clutch (Lovrich et al. 2005), which disproportionally increases the energy allocation to reproduction in mature female snow crab even more. Other functions of other hepatopancreas compounds include supporting energy during the molting (starvation) processes (Sanchez-Paz et al. 2007), which is presumably a more balanced cost between mature males and females.

Energetic expenses vary with life cycle-specific events and with seasons and, in addition, are influenced by environmental temperatures through metabolic rates. Snow crab is a cold-water species that is most common in bottom waters below 5 °C. Such low temperatures are currently wide-spread in the Chukchi and Beaufort Seas, although higher bottom water temperatures may occur along the Alaskan coast of the Chukchi Sea. Higher temperatures (above ~7 °C) lead to energetic expenditures overwhelming food intake so that crabs no longer 'break even' (Foyle et al. 1989). Future conditions in the Pacific Arctic, therefore, may change distribution and energetic requirements of Pacific Arctic snow crab.

Acknowledgments
Undergraduate student Elizabeth Kandror and technician Mette Kaufman, University of Alaska Fairbanks (UAF), assisted with tissue dissections and calorimetric measurements. We thank Lara Horstmann (UAF) for letting us use the freeze-dryer and calorimeter in her lab. Collaborators from the Canadian BREA project kindly provided mature male crabs.

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Table 1: Mean snow crab composition by dry weight (DW) for immature males (IM, Chukchi Sea), mature males (MM, Beaufort Sea) and mature females (MF, Chukchi Sea).

	Mean total DW (g)			**Standard deviation**			**Sample size**		
Tissue type	**IM**	**MM**	**MF**	**IM**	**MM**	**MF**	**IM**	**MM**	**MF**
Muscle	3.61	48.42	0.41	1.57	16.67	0.23	10	20	20
Hepatopancreas	0.09	8.84	0.30	0.05	4.11	0.24	10	20	20
Gonad	1.34	2.31	0.41	0.56	0.63	0.25	10	20	20
Eggs			0.89						
Shell	2.32	142.47	1.76	0.46	49.50	0.64	10	20	20
Total	7.35	202.02	4.06						

Table 2: Mean snow crab composition by total caloric content per tissue type, calculated from caloric content per gram dry weight (g dw) and dry weight proportions, for mature males (MM, Beaufort Sea) and mature females (MF, Chukchi Sea). Total shell caloric content for mature females is based on dry weight proportions of the shell in females and the mean per gram dry weight caloric value from males.

	Mean Kcal g dw^{-1}		**Standard deviation**		**p-value**	**Mean total Kcal**		**Standard deviation**		**p-value**	**Sample size**	
Tissue type	**MM**	**MF**	**MM**	**MF**	**sex diff.**	**MM**	**MF**	**MM**	**MF**	**sex diff.**	**MM**	**MF**
Muscle	4.72	4.98	0.28	0.74	0.70	62.51	34.35	27.08	11.51	**<0.001**	20	50
Hepatopancreas	7.08	6.92	0.48	1.14	0.48	25.47	27.70	13.21	10.66	0.17	20	21
Gonad	4.88	5.49	0.15	0.66	**<0.001**	3.82	15.51	1.11	4.78	**<0.001**	20	45
Eggs		3.66		0.52			32.41		9.56			11
Shell	1.23		0.51			86.35	19.71	32.72	5.82		20	
Total						178.14	129.68					

Table 3: Results of linear regression analysis of total caloric content of each tissue type (kcal) against body size (carapace width in mm) for mature female (Chukchi Sea) and male snow crab (Beaufort Sea). Sample sizes are as given in Table 2. Total shell caloric content for mature females is based on dry weight proportions of the shell in females and the mean per gram dry weight caloric value from males.

Dependent Variable	**df**	**F-ratio**	**p-value**	**R^2**	**Intercept**	**Slope**
Total kcal muscle mature females	(1, 56)	138.82	**<0.001**	0.71	-69.00	2.12
Total kcal muscle mature males	(1, 18)	3.54	0.544	0.16	-29.61	0.76
Total kcal gonad mature females	(1, 50)	271.98	**<0.001**	0.85	-38.90	1.12
Total kcal gonad mature males	(1, 18)	0.09	0.765	0.01	3.28	0.01
Total kcal hepatopancreas mature females	(1, 24)	174.78	**<0.001**	0.98	-71.42	2.01
Total kcal hepatopancreas mature males	(1, 18)	12.38	**0.002**	0.41	-56.31	0.69
Total kcal shell mature females	(1, 58)	484.67	**<0.001**	0.89	-41.92	1.26
Total kcal shell mature males	(1, 18)	2.22	0.153	0.11	-12.79	0.81
Total kcal eggs mature females	(1, 58)	484.26	**<0.001**	0.89	-68.91	2.08

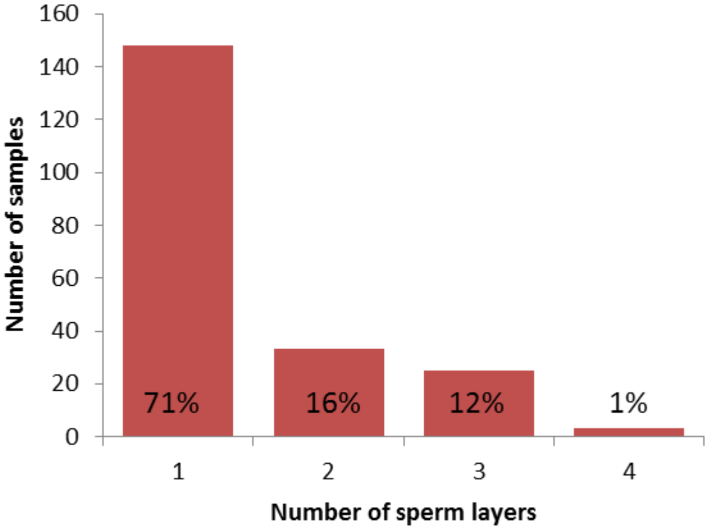

Figure 1-1. Female reproductive characteristics: Number of sperm layers in spermathecae.

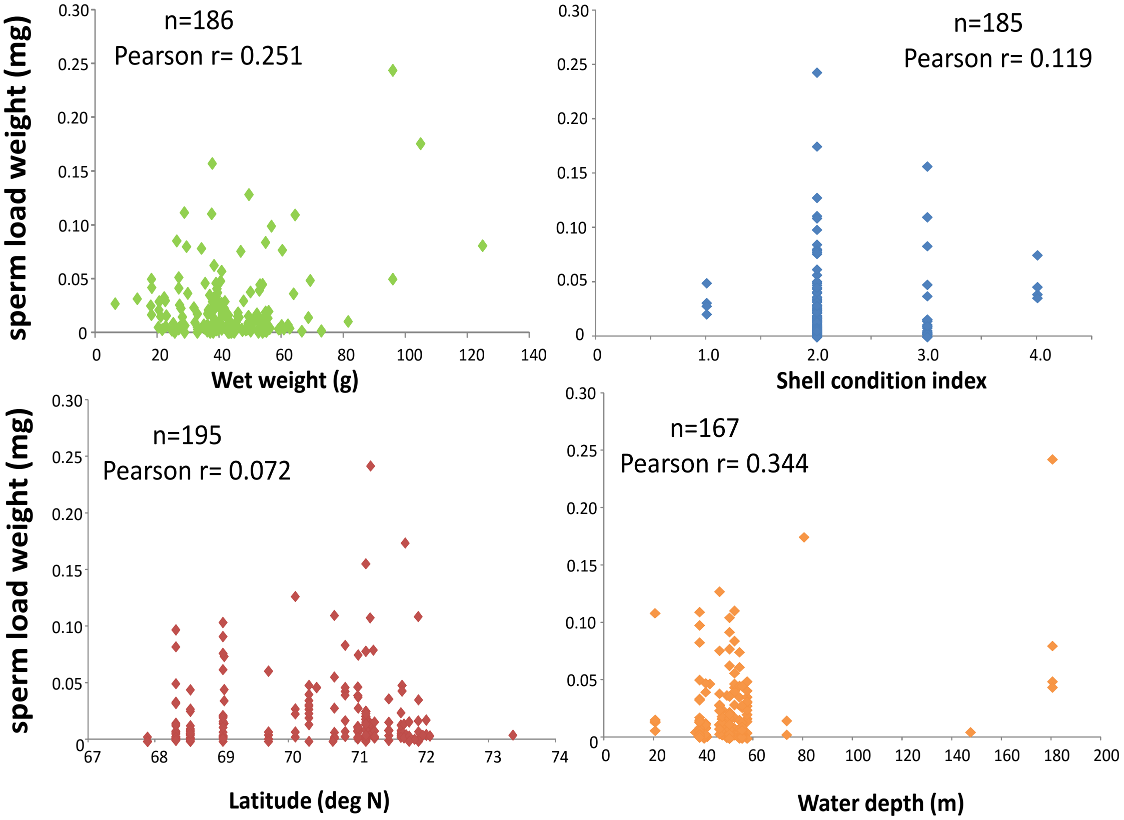

Figure 1-2. Sperm reserves (as weight of sperm load in the left spermathecal) in mature females from the Chukchi Sea, plotted against (A) body weight, (B), shell condition index, (C) latitude and (D) water depth. None of the relationships was particularly strong.

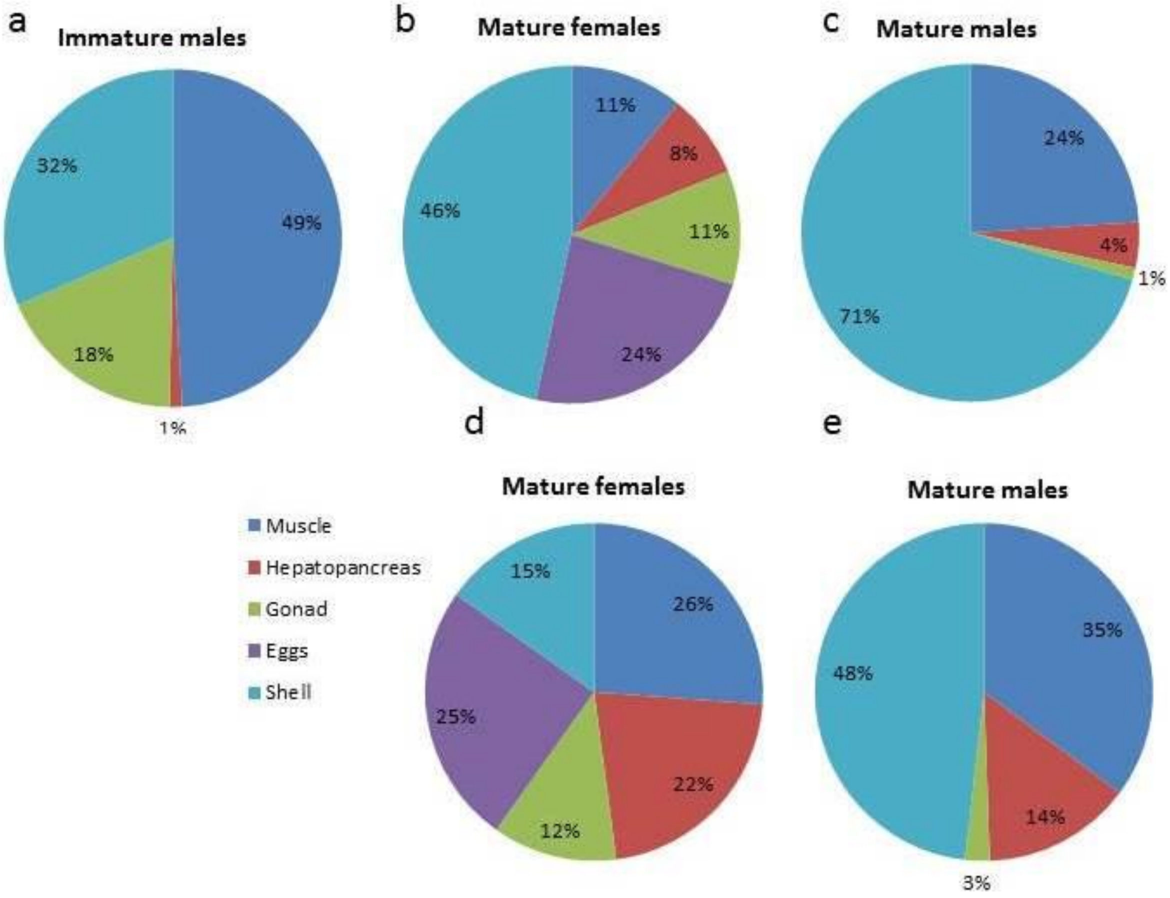

Figure 2-1. Relative composition of crab tissues by dry weight (a-c) and caloric content (d-e). Immature males and mature females are from the Chukchi Sea while mature males are from the Beaufort Sea. So far, virtually no mature males have been caught in the Chukchi Sea and no mature females have been caught in the Beaufort Sea, hence the unequal regional distribution of samples.

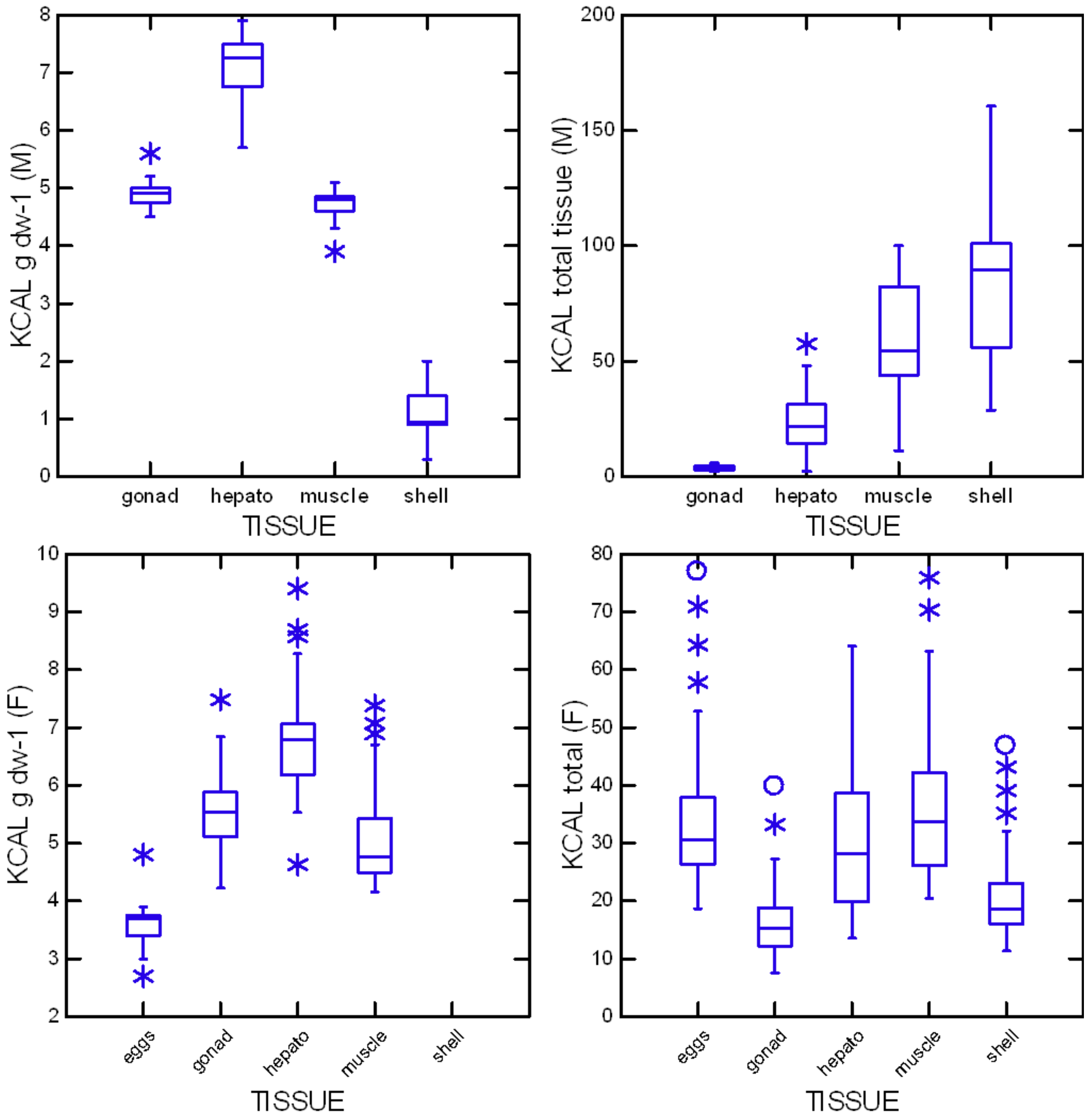

Figure 2-2. Caloric content of different tissue types in mature male (M) snow crab (a, b) from the Beaufort Sea and mature female (F) crab (c, d) from the Chukchi Sea. (a) and (c) shows caloric content per gram dry weight (dw), (b) and (d) per total tissue type. Letters indicate significant differences (ANOVA, α=0.05, and Tukey's post-hoc pairwise comparisons). The boxes show the median and upper and lower quartile, the whiskers show the highest and lowest values except for outliers. Outliers identified with an asterisk are greater than 1.5 times the interquartile range, outliers identified with a circle are greater than 3 times the interquartile range.

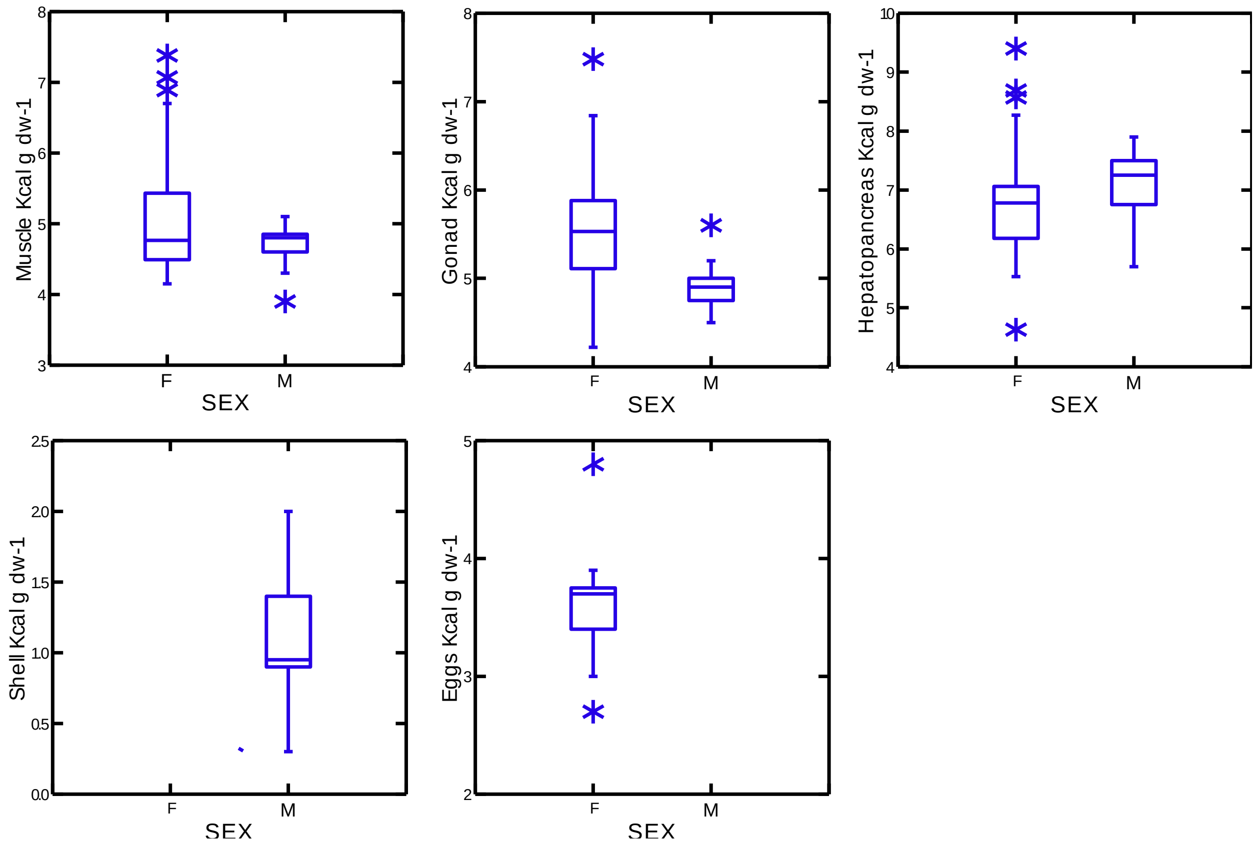

Figure 2-3. Caloric content per gram dry weight of different tissue types in mature female (F; Chukchi Sea) and mature male (M, Beaufort Sea) snow crab. Significant differences are indicated (ANOVA). See figure 2 and text for box whisker plot explanation.

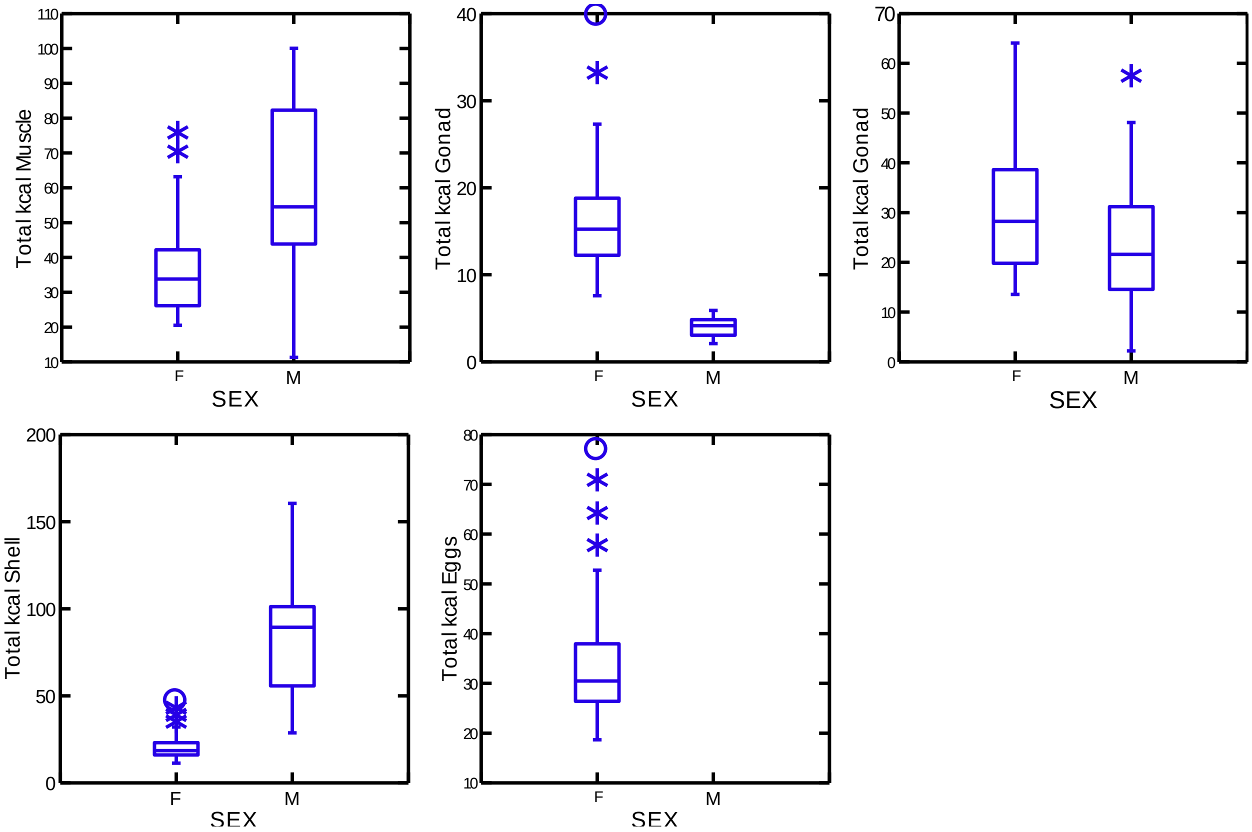

Figure 2-4. Total caloric content per tissue type in mature female (F; Chukchi Sea) and mature male (M, Beaufort Sea) snow crab. Significant differences are indicated (ANOVA). See figure 2 and text for box whisker plot explanation.

Objective (3)

Identify diet and trophic position of snow crab in different geographic areas and size classes

Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes

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*Published online 2016 in Deep-Sea Research II, Arctic Eis special issue.

Abstract

We used stomach content and stable $\delta^{13}C$ and $\delta^{15}N$ isotope analyses to investigate male and female snow crab diets over a range of body sizes (30-130 mm carapace width) in five regions of the Pacific Arctic (southern and northern Chukchi Sea, western, central, and Canadian Beaufort Sea). Snow crab stomach contents from the southern Chukchi Sea were also compared to available prey biomass and abundance. Snow crabs consumed four main prey taxa: polychaetes, decapod crustaceans (crabs, amphipods), echinoderms (mainly ophiuroids), and mollusks (bivalves, gastropods). Both approaches revealed regional differences. Crab diets in the two Chukchi regions were similar to those in the western Beaufort (highest bivalve, amphipod, and crustacean consumption). The Canadian Beaufort region was most unique in prey composition and in stable isotope values. We also observed a trend of decreasing carbon stable isotopes in crabs from the Chukchi to those in the Canadian Beaufort, likely reflecting the increasing use of terrestrial carbon sources towards the eastern regions of the Beaufort Sea from Mackenzie River influx. Cannibalism on snow crabs was higher in the Chukchi regions relative to the Beaufort regions. We suggest that cannibalism may have an impact on recruitment in the Chukchi Sea via reduction of cohort strength after settlement to the benthos, as known from the Canadian Atlantic. Prey composition varied with crab size only in some size classes in the southern Chukchi and central Beaufort, while stable isotope results showed no size-dependent differences. Slightly although significantly higher mean carbon isotope values for males in the southern Chukchi may not be reflective of a gender-specific pattern but rather be driven by low sample size. Finally, the lack of prey selection relative to availability in crabs in the southern Chukchi suggests that crabs consume individual prey taxa in relative proportions to prey field abundances. The present study is the first to provide a baseline of the omnivorous role of snow crabs across the entire Pacific Arctic, as well as evidence for cannibalism in the Chukchi Sea. In light of climate change predictions for the Alaska Arctic, and the potential for future fisheries harvest of snow crabs in this region, continued monitoring of snow crabs, including population and trophic dynamics, is increasingly important to assess snow crab impacts on benthic communities and vice versa.

Key words: Beaufort Sea, cannibalism, Chukchi Sea, diet, snow crab, stable isotopes

1. Introduction

Snow crabs (*Chionoecetes opilio*, O. Fabricius, 1788) are widely distributed across subarctic and arctic regions of the northern parts of the North Pacific and North Atlantic Oceans (Armstrong et al. 2010), where they play important roles in benthic ecosystems. Since 2004, snow crabs have also established a non-native, but self-sustaining, population in the Barents Sea (Alvsvåg et al. 2009, Agnalt et al. 2011). Pacific Arctic snow crabs are considered a panmictic population across their geographic range (Albrecht et al. 2014). They are a major contributor to epibenthic biomass across the Chukchi Sea shelf (Bluhm et al. 2009, Hardy et al. 2011, Blanchard et al. 2013a,b, Ravelo et al. 2014) despite their generally small body sizes on the Chukchi shelf (Konar et al. 2014). Large individuals were recently found on the western Beaufort Sea shelf where they are also major contributors to biomass (Rand and Logerwell 2011, Ravelo et al. 2015). While commercially fished snow crab populations have been extensively studied over decades (e.g., Tarverdieva 1981, Lefebvre and Brêthes 1991, Lovrich and Sainte-Marie 1997, Squires and Dawe 2003), comparatively little is known about their biology, ecology and role in the non-harvested Pacific Arctic distribution range, including their diet and trophic role.

Snow crabs generally occupy a predatory and scavenging role. Where diet studies have occurred, snow crabs consume a large variety of benthic prey including bivalves, gastropods, polychaetes, ophiuroids, and crustaceans (Bering Sea: Tarverdieva 1981, Kolts et al. 2013a; Chukchi Sea: Feder and Jewett 1978; Sea of Japan: Yasuda 1967, Chuchukalo et al. 2011; western North Atlantic: Lefebvre and Brêthes 1991, Wieczorek and Hooper 1995, Lovrich and Sainte-Marie 1997, Squires and Dawe 2003). In some regions, cannibalism on juveniles, combined with predation on other crab species, also is an important contribution to their diet (Lovrich and Sainte-Marie 1997, Chuchukalo et al. 2011). However, the importance of cannibalism may vary by location and be related to the relative abundance of juveniles compared with abundance and size spectra of other available prey taxa. Ontogenetic diet shifts occur as crabs become larger and acquire larger chelae, allowing them to prey on larger prey items and harder-shelled mollusks and clams (Squires and Dawe 2003, Kolts et al. 2013a).

Snow crabs support lucrative commercial fisheries in the northwest Atlantic (eastern Canada and western Greenland), the Sea of Japan, and the eastern Bering Sea. However, warming trends observed in the Bering Sea over the past three decades have resulted in a northward contraction of the commercially exploited stock out of historical fishing grounds in the southeastern portion (Zheng et al. 2001, Orensanz et al. 2004). The current center of distribution of snow crabs in the Bering Sea has shifted northward of 60°N (Orensanz et al. 2004, Mueter and Litzow 2008). This northward contraction of snow crabs raises critical questions of dispersal and migration dynamics affecting commercial fishing in the eastern Bering Sea, as well as connectivity among populations in the northern Bering, Chukchi, and Beaufort seas. In addition to the decline of the exploitable snow crab stock in the southeastern Bering Sea, increased open waters of the Arctic due to reductions in sea ice associated with climate warming makes these Arctic regions potentially attractive to fishing (Hollowed et al. 2013). Although fisheries biomass removal is not currently permitted in the Alaska Arctic, the Arctic Fishery Management Plan lists snow crabs as a potential future fisheries target (NPFMC 2009). In-depth knowledge of snow crab habitat requirements, including dietary preferences and prey availability, is therefore needed for effective fisheries management in this Arctic region.

Snow crabs occupy environmentally complex and disparate regions of the Chukchi and Beaufort seas. The Chukchi shelf is wide and shallow shelf with an average depth of 50 m, with well-documented “hot spots” of high primary production and tight benthic-pelagic coupling that support high benthic standing stocks (Grebmeier et al. 1988, 2006a,b, 2015). Variability in primary production across the shelf is related to the hydrography of several distinct overlying water masses (Walsh et al. 1989). Anadyr Water (AW) delivers high salinity, nutrient-rich waters to the western Chukchi, Alaska Coastal Water (ACW) is comparatively less saline with lower nutrient content in the eastern Chukchi, and the Bering

Shelf Water (BSW) of intermediate water properties runs between the AW and ACW (Coachman 1987). Distribution of epibenthic organisms in the Chukchi Sea is structured by sediment characteristics, water depth, and these water masses and their properties, which supply nutrients and carbon to the seafloor through pelagic-benthic coupling (Feder et al. 1994, 2005). Snow crabs on the Chukchi Sea shelf are members of the epibenthic communities that are typically dominated by crustaceans, echinoderms (mostly ophiuroids), and gastropods (Bluhm et al. 2009, Blanchard et al. 2013a, Ravelo et al. 2014). Snow crab abundance and biomass seem to vary regionally and interannually on the Chukchi shelf (Bluhm et al. 2009, 2015, Ravelo et al. 2014), and crabs occur even in areas where bottom temperatures are below their experimentally defined lower thermal limit (≤ -1°C, Foyle et al. 1989).

In contrast to the Chukchi shelf, the Beaufort shelf is a narrow, interior shelf receiving nutrient-rich water inflow from the Chukchi Sea in the west and more oligotrophic waters to the east (Dunton et al. 2006). Overall benthic biomass and abundance are lower in the Beaufort than the Chukchi Sea, reflecting generally lower primary production in the Beaufort Sea with some exceptions, such as the Cape Bathurst area or upwelling-induced algal blooms (Macdonald et al. 1989, Tremblay et al. 2011). Freshwater runoff and land fast ice limit the abundance and diversity of epifauna and infauna of the nearshore Beaufort Sea to ~25 m depth (Dunton et al. 2005, Ravelo et al. 2015). Epibenthic biomass is highest at the shelf break of the western Beaufort Sea (100-200 m; no deeper locations were sampled, Ravelo et al. 2015); snow crabs are most common at depths of 100-500 m along the western to central Beaufort slope (Rand and Logerwell 2011), where they reach larger sizes than those in the Chukchi Sea including commercial-sized snow crabs (>78 mm carapace width [CW] defined for the Bering Sea stock) collected at depths of > 200 m on the Alaska Beaufort slope (Logerwell et al. 2011, Bluhm et al. 2015).

From other large-bodied crabs, such as red king crabs (*Paralithodes camtschaticus*), it is known that they can have substantial top-down influence on benthic community abundance and composition through their feeding activities (e.g., Jørgensen 2005, Britayev et al. 2010). Vice versa, snow crabs are themselves can be prey, for example for some fish species (e.g., Livingston et al. 1993). Given the high abundance of snow crab in the Pacific Arctic (Paul et al. 1997, Bluhm et al. 2009, Ravelo et al. 2014, Kolts et al. 2015), their northward range shift (Orensanz et al. 2004), and the mandate to fill knowledge gaps in species of potential commercial interest (NPFMC 2009), our goal was to study snow crab diet and trophic position in the Chukchi and Beaufort seas. Stomach content (SCA) and stable isotope (SIA) analyses are common and complementary methods to address diet composition. SCA can provide high taxonomic resolution and at times, depending on preservation state, size information of prey items that were recently consumed (Hyslop 1980). SCA is a suitable tool to compare diets of crab species occupying similar or different habitats, investigate seasonal diet changes (e.g., Sundet et al. 2000), or ontogenetic shifts in diet composition (Stevens et al. 1982). However, soft bodied, easily digested, or crushed prey organisms are likely to be underestimated in importance (Hyslop 1980) and SCA are snapshots of diet at a given time and location. These limitations of SCA can be at least partially overcome with the complementary use of SIA. Trophic studies based on SIA commonly use $\delta^{13}C$ and $\delta^{15}N$ ratios to identify primary carbon sources and trophic positions of species or higher taxa within a local or regional food web (Post 2002). SIA indicates diet over a longer period, from weeks to months in polar invertebrates depending on turnover time of consumer tissues (Mintenbeck et al. 2007, Kaufman et al. 2008, Weems et al. 2012), and is not limited to recent feeding of the organism (Lovvorn et al. 2013). However, distinguishing relative proportions of specific prey in consumers that eat a variety of taxa that themselves have similar diets (and thus similar isotope values) is difficult using SIA. The combined use of SCA and SIA is a more powerful approach for diet studies than each individual method (e.g., Kolts et al. 2013b).

In the present study, we used the complimentary methods of SCA and SIA to provide insight into the diet composition of male and female snow crabs over a range of body sizes and different benthic environments in the Alaska Arctic. Specifically, we sought to address the following questions for the Chukchi and Beaufort seas: (1) Do regional differences occur in snow crab diets across the Chukchi and Beaufort seas?, (2) Does body size affect snow crab diets within and across study regions?, (3) Do trophic differences occur among some sex-age classes (male, immature female, mature female) within and across study regions?, and (4) Do snow crabs preferentially select for specific prey types or do they feed on prey in similar relative abundances to the prey's availability in the field?

2. Methods

Snow crabs of sizes 30-130 mm CW were collected across five geographic regions during several cruises in the Chukchi and Beaufort seas from 2011 to 2013 (Table 1, Fig. 1). These regions were defined based on a combination of previous sampling schemes, hydrography and circulation, and sample size distribution: southern Chukchi Sea (bounding box: 66.05 to 70.00 °N, 164.14 to 168.50 °W), northern Chukchi Sea (70.50 to 73.00 °N, 157.18 to 168.51 °W), western Beaufort Sea (70.10 to 70.90 °N, 144.95 to 147.07 °W), central Beaufort Sea (70.50 to 71.30 °N, 147.28 to 151.34 °W), and Canadian Beaufort Sea (69.93 to 71.33 °N, 123.49 to 140.40 °W). The Alaska Chukchi Sea was divided into north and south regions at 70°N latitude to correspond with geographic terminology used in previous diet studies (e.g., Iken et al. 2010, Norcross et al. 2015). In addition, hydrographic conditions differ between the two regions: Water masses entering the southern Chukchi Sea through Bering Strait slow and allow advected particles to settle, leading to benthic hotspot regions (Grebmeier et al. 2015). Benthic communities in the northern Chukchi Sea are driven by the complex hydrography of water around Hanna Shoal, creating a mosaic of depositional and advective microhabitats (Blanchard et al. 2013b). The western and central Alaska Beaufort regions correspond with previous groundfish and benthic invertebrate sampling regions (Frost and Lowry 1983, Rand and Logerwell 2011, Divine et al. 2015). The western Beaufort also is under stronger influence and nutrient-rich particle advection from the Chukchi Sea than the central Beaufort Sea (Ashjian et al. 2005), serving as food source for benthic communities (Divine et al. 2015). The Canadian Beaufort region encompassed stations east of the U.S.-Canadian border. Chukchi Sea snow crabs were collected in July-August 2012 aboard the F/V *Alaska Knight* as part of the Arctic Ecosystem Integrated Survey (Arctic EIS) using either an 83-112 eastern otter trawl (mesh size: 10.2 cm wings and body, 8.9 cm intermediate and codend, 3.2 cm codend liner, Goddard et al. 2014 for trawl operations) or a modified plumb staff beam trawl (PSBT-A, mesh size: 7 mm, 4 mm codend liner; Abookire and Rose 2005). We assume that any potential bias due to differences in sampling gears used in the Chukchi Sea was small and not relevant for the objectives of this study as we obtained a range of crab sizes representative of those observed previously in these regions. Crabs from the U.S. Beaufort Sea were collected in August-September aboard the R/V *Norseman II* during the 2011 BeauFish cruise and in August-September during the 2012 and 2013 U.S.-Canadian Transboundary cruises using the PSBT-A (for additional sampling details see Norcross et al. 2015, Ravelo et al. 2015). Snow crabs from the Canadian Beaufort Sea were collected in 2012 and 2013 aboard the R/V *Frosti* using a modified Atlantic Western IIA otter trawl (mesh size: 1.27 cm cod-end and intermediate liner, A. Majewski [DFO] pers. comm.) as part of the Beaufort Regional Environmental Assessment (Department of Fisheries and Oceans Canada). In all cases, stomachs were removed from crabs through incisions in the dorsal carapace and preserved in ethanol or 10% buffered formalin until analysis. A muscle sample for SIA was removed from a pereiopod of each crab and dried at 60°C for 24 h. In all cases, crabs were sexed and CW measured using digital calipers to the nearest 0.01 mm.

2.1 Stomach content analysis

Stomach contents were removed and placed in a Petri dish for visual inspection under a dissecting microscope (Leica M165) outfitted with a Leica DFC420 camera. Each prey item was photo cataloged for taxonomic verification. Contents were identified to lowest taxonomic level possible and presence or absence of diet items was determined for each crab stomach. The frequency of occurrence (FO) for each prey item was determined as the percentage of all crab stomachs in which a diet item occurred within each region, body size, or sex-age class, depending on category of analysis. Hence, each prey item FO value ranged from 0-100% and was independent of the FO values for all other prey items (Brown et al. 2012). FO for each diet item was first averaged for all crabs within each region (regardless of size or sex-age class), and we compared averages to determine regional differences in means. Then we partitioned crabs by size and sex-age classes and calculated FO for these groups, first by pooling across regions and then by comparing sizes and sex-ages within individual regions. The highly degraded state of many prey items as a result of grinding by the gastric mill in snow crab stomachs precluded enumerating prey items per stomach or measuring the dominant taxa by volume or mass.

2.2 Stable isotope analysis

Samples for SIA from pereiopod muscle tissue were dried, and lipids were removed with 2:1 chloroform: methanol because lipids may be depleted in ^{13}C and thus may bias carbon values (Mintenbeck et al. 2007, Logan et al. 2008). Tissue samples were then re-dried at 60° C for 24 h. Samples were analyzed at the Alaska Stable Isotope Facility at the University of Alaska Fairbanks on a Thermo Finnigan Delta Isotope Ratio Mass-Spectrometer with V-PDB and atmospheric N_2 as standards for carbon and nitrogen, respectively. Sample isotope ratios were expressed in the conventional δ notation as parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N of the crab tissue sample and R is the corresponding ratio ^{13}C/^{12}C or ^{15}N/^{14}N. Instrument error was < 0.2 ‰ for both δ^{13}C and δ^{15}N values.

2.3 In situ prey availability

To assess the degree of selectivity in snow crabs diets, we compared a subset of snow crab stomach contents to benthic prey availability. For this purpose, macro-invertebrate abundance (individuals m^{-2}) and biomass data (g C m^{-2}) generated from 0.1 m^2 van Veen grab samples rinsed over 1 mm mesh from the 2012 Russian-American Long-Term Census of the Arctic (RUSALCA) program were provided from five stations in the southern Chukchi Sea (CS17, CL1, CL3R, CS8R, CS12R) by J. Grebmeier and L. Cooper (both U. Maryland). These stations were chosen based on their close proximity to 2012 Arctic EIS stations where snow crabs were collected for stomach content analysis (see Fig. 1). No prey information was available for the other regions so that this analysis was only done for the southern Chukchi Sea region. Prey taxa were grouped at the class level and ranked separately for abundance and biomass from 1 to 10 (1 being highest, 10 the lowest, 0 is absent) at each station (Table 2). Frequency of occurrence of prey taxa occurring in snow crab stomachs at the same stations in the southern Chukchi Sea were grouped by the same higher taxa as reported for prey biomass and abundance (see Table 2). Prey selectivity was compared only to macro-infaunal prey and not epifaunal prey as infauna comprised most snow crab diet items.

2.4 Statistical analysis

We used permutational multivariate analysis of variance (PERMANOVA) at a significance level of $\alpha=0.05$ for all statistical analyses (PRIMER v7 with PERMANOVA). We determined differences in SCA within and among regions, size groups, and sex-age classes based on presence/absence data analysis in a Jaccard Similarity Index resemblance matrix. For statistical analyses involving crab sizes, crabs were grouped into size classes of 10 mm CW (e.g., the 40 mm CW size class included all crabs with 40.0-49.9 mm CW) based on previous snow crab diet studies (Kolts et al. 2013a). Sex-age groups were male, mature female, and immature females. Males were not separated into immature and mature classes because there was high variability in the ratio of carapace width to chela height, a maturity metric used in other regions, which precluded our ability to confidently determine a CW break for immature versus mature male sizes. Maturity of females was determined based on the shape of the abdominal flap and presence or absence of an egg clutch. Immature and mature females overlapped in their size ranges. We treated region, CW, and sex-age class as fixed factors in the PERMANOVA for both SCA and SIA analyses. Post-hoc pairwise comparisons detailed the differences in diets across CW size classes among regions and within a region. Similarity of Percentages (SIMPER) analysis determined the prey taxa that contributed most to the differences in diets of the crab size classes within each region. We used non-metric multidimensional scaling (nMDS) plots to visualize the differences in diets of different size classes within those regions where significant differences occurred. Similarly, we investigated regional, size, and sex-age differences in snow crab $\delta^{13}C$ and $\delta^{15}N$ stable isotope values via PERMANOVA. Post-hoc pairwise comparisons were conducted across and within each region to explore which regions contributed to significant differences. Canadian Beaufort crabs were excluded from within-region comparisons because only males were collected in this region.

To rule out potential environmental influences on snow crab diets and stable isotope values that may confound SCA or SIA results, we correlated environmental variables (water depth, bottom-water temperature and salinity) with FO diet data and stable isotope values using the BIO-ENV routine in PRIMER. Ranked prey abundance and biomass data (Table 2) were compared with ranked snow crab stomach FO data to determine if crabs were selectively feeding on various prey taxa using non-parametric

Mann-Whitney U-tests. Selectivity was defined as a significant difference between ranked prey abundance or biomass *in situ* and rank of prey FO in crab stomachs.

3. Results

3.1 Regional diet patterns

Together, SCA and SIA methods indicated Alaska Arctic snow crabs are omnivorous and consume a wide variety of benthic invertebrate prey across all study regions. The most frequently occurring diet items across all regions were the polychaete *Cistenides hyperborea* (59.5%), bivalves (57.1%), and 'other polychaete' worms (42.9%). Less frequent prey items included a variety of crustaceans including amphipods (27.2%) and crabs and shrimps (25.7%), ophiuroids (22.2%), and teleost fishes (7.4%). Other items included unidentifiable tissue parts and sediment particles. Regional differences occurred in snow crab diets as revealed in both SCA and SIA (p= 0.001 for both approaches, Table 3 and 4). Crabs in the southern Chukchi region most frequently fed on bivalves (FO= 61%), followed by *C. hyperborea* (FO= 47%) and amphipods (FO= 31%, Fig. 2). Compared with all other regions, crabs in the southern Chukchi had the highest FO for brachyuran crabs (possibly juvenile snow crabs, FO= 23%). Crabs in the northern Chukchi region had a similar diet composition to those in the southern Chukchi, including relative high FO for brachyuran crabs (possibly juvenile snow crabs, FO= 15%). In contrast, brachyuran crabs occurred in less than 5% of stomachs in any of the Beaufort regions (Fig. 2). Otherwise, snow crabs in the western Beaufort fed in similar proportions to those in the northern and southern Chukchi regions on bivalves (FO= 60%), 'other polychaetes' (FO= 28%), and amphipods (FO=25%), but had a higher proportion of *C. hyperborea* (FO= 70%) compared with Chukchi regions. Crabs in the central Beaufort region most frequently fed on *C. hyperborea* (FO= 83%), with intermediate consumption frequency of 'other polychaetes', ophiuroids and bivalves (FO= 39%, 29%, and 28%, respectively), and low consumption of teleost fishes and amphipods (FO= 15% and 14%, respectively). Canadian Beaufort Sea crabs were quite different in their stomach contents compared with all other regions (PERMANOVA pair-wise comparison, p< 0.05 for all comparisons, Table 3), due mainly to high FO of 'other polychaetes' (FO= 50%), low FO of *C. hyperborea* (FO= 13%) and amphipods (FO= 3%), and several common taxa in other regions being absent in the stomach contents of Canadian Beaufort crabs (e.g., brachyuran crabs, 'other crustaceans').

Stable $\delta^{13}C$ and $\delta^{15}N$ isotope values were also regionally different for snow crabs (PERMANOVA, p= 0.001, Table 4, Fig. 3). Across all regions, $\delta^{13}C$ ranged from -21.50 ‰ to -15.82 ‰

and $\delta^{15}N$ ranged from 11.71 ‰ to 17.27 ‰ in individual crabs. Canadian Beaufort male crabs (the only sex group sampled in that region) had the lowest $\delta^{13}C$ values and were statistically different from crabs in all other regions (PERMANOVA, $p < 0.01$ for all post-hoc comparisons, Table 4, Fig. 3). Crabs of all sex-age groups in the central Beaufort region were similar to each other in mean values of both isotopes, and were characterized by slightly lower $\delta^{13}C$ and higher $\delta^{15}N$ values compared with crabs from other regions (significant regional differences in all comparisons [$p < 0.01$], except with the northern Chukchi [$p = 0.07$]).

3.2 Effects of size on snow crab diets

Crab size was a significant factor for SCA only in the interaction between region and size class (PERMANOVA, $p = 0.002$, Table 3). These diets differences among size classes based on SCA only occurred within the southern Chukchi and central Beaufort regions (PERMANOVA pair-wise comparison, $p = 0.001$ and 0.007, respectively, Table 3, Fig. 4 and 5). In the southern Chukchi, the largest size class of snow crabs examined (80 mm CW) was different from all other size classes within that region (SIMPER analysis; average dissimilarity= 59.3%, Fig. 4, A.1) and most frequently consumed the polychaete *Cistenides hyperborea* (FO= 67%) and had higher FO of the bivalve *Yoldia hyperborea* (FO= 33%) and 'other polychaetes' (FO= 100%) than other size classes. Small crabs (40-60 mm CW) more commonly consumed bivalve sp. 1, bivalve sp. 2, amphipods, and gastropods (Fig. 4A and B), as well as ophiuroids, which were absent from the diets of 80 mm CW crabs. Bivalve prey partitioning was seen among crab size classes in the southern Chukchi: *Ennucula tenuis* and bivalve sp. 1 were consumed equally among all size classes, while *Serripes groenlandicus* and 'other bivalves' (species others than those identified here) were consumed only by small crab size classes. *Yoldia hyperborea* was consumed most commonly by the smallest (40 mm CW) and largest (80 mm CW) size classes (17% and 33%, respectively).

In the central Beaufort, the two smallest size classes examined (50 mm and 60 mm CW) had significantly different stomach content composition compared with each other and most other size classes (PERMANOVA pair-wise comparisons $p < 0.05$, Table 3, Fig. 5). Dissimilarities of the 50 mm CW class were driven, among other factors, by the lack of 'other polychaetes' and teleost fish parts in their diets (Fig. 5A) and low FO of detritus/sand/rocks (FO= 25%). Stomach contents within the 60 mm CW size class were characterized by high FO of ophiuroids (FO= 60%) and detritus/sand/rocks (FO= 100%), relatively low FO of 'other polychaetes' (FO= 20%), and the lack of *Yoldia hyperborea*, gastropods, and other prey taxa compared with other size classes (Fig. 5A and B). Several prey taxa were found only in intermediate size classes, such as the bivalve *Y. hyperborea*, gastropods, and teleost parts (Fig. 5A). In contrast to effects on SCA, body size was not a significant factor in stable isotope values of snow crabs (PERMANOVA, $p= 0.72$, Table 4).

3.3 Effects of sex-age on snow crab diets

SCA generally indicated similar diets for male, mature female, and immature female crabs across all study regions (PERMANOVA, $p= 0.72$, Table 3, Fig. 3). Within the southern Chukchi Sea, males were enriched in ^{13}C compared with immature and mature females (Fig. 3). SIA indicated sex-age differences in several regions (Table 4). Diet of most sex-age groups of the western Beaufort, northern and southern Chukchi Sea were relatively similar, except for slightly higher $\delta^{13}C$ and $\delta^{15}N$ values in southern Chukchi males (PERMANOVA, $p< 0.01$ for all post-hoc comparisons, Table 4, Fig. 3). Western Beaufort mature females were characterized by distinctly lower $\delta^{15}N$ values than any other group (~1.0 ‰ lower, Fig. 3) but were not statistically different (PERMANOVA, $p= 0.06$ for all post-hoc comparisons, Table 4).

3.4 In situ prey availability (southern Chukchi region only)

Macro-infaunal prey taxa occurred at similar rank orders in snow crab stomach contents as they did *in situ* in the southern Chukchi Sea ($p> 0.05$), with the exception of Sipuncula ($p= 0.02$ for biomass and abundance) and Nemertea ($p= 0.02$ for biomass, Table 5). Sipuncula contributed a large fraction of *in situ* biomass and abundance at one station (ranked 1st in biomass and 6th in abundance, Table 2) but was absent in crab stomachs. Nemertea ranked 5th in biomass at one station but was also absent in crab stomachs.

4. Discussion

4.1 Regional diet trends

Together, data from SCA and SIA provided regional diet information that contributes to our understanding of snow crab ecology, trophic level, and resource partitioning on the Alaska Chukchi and Beaufort seas shelves. Overall, snow crabs mostly consumed four main invertebrate prey taxa including polychaetes, crustaceans, bivalves, and ophiuroids; in addition, fish were consumed in low frequencies.

The range of main prey groups observed in the present study was consistent with previous diet studies of *Chionoecetes* crabs of similar size range in the Bering Sea (Feder and Jewett 1980, Kolts et al. 2013a), Gulf of Alaska (Jewett and Feder 1983), Cook Inlet (Paul et al. 1979), and Canadian North Atlantic (Wieczorek and Hooper 1995, Lovrich and Sainte-Marie 1997, Squires and Dawe 2003).

Snow crab diets included members of infaunal and epifaunal communities, both of which are patchily distributed throughout the study area as a consequence of varying combinations of hydrography, sediment properties, food supply and trophic interactions (Bluhm et al. 2009, Iken et al. 2010, Ravelo et al. 2014, 2015, Blanchard and Feder 2014, Whitehouse et al. 2014, Grebmeier et al. 2015). Infaunal abundance and biomass is typically dominated by polychaetes, bivalve mollusks, and amphipod crustaceans across the Chukchi and Beaufort seas (Bilyard and Carey 1979, Grebmeier et al. 2006a, Feder et al. 2007, Blanchard et al. 2013a). Our comparative analysis of stomach contents with macro-infaunal prey in the southern Chukchi region showed that frequency of consumption of these groups as prey is closely related to their availability. This agrees with previous findings in the northern Bering Sea where *Chionoecetes* crabs tend to consume prey in relative proportions to prey abundance in the field (Kolts et al. 2013a). Some occasionally abundant taxa seemed to be consumed less frequently compared with their *in situ* abundance in our study, especially some soft-bodied taxa. We suggest, however, that the lack of Sipuncula and Nemertea in crab stomachs in the southern Chukchi Sea is likely based on the lack of identifiable hard parts in these taxa, which typically leads to underrepresentation in stomach content data (Warwick and Somerfield 2008).

On the northeastern Chukchi shelf, polychaetes, bivalve mollusks, and crustaceans account for > 80% of total macro-infaunal abundance (Schonberg et al. 2014). Each of these taxa also had very high (> 50%) FO in crab stomachs from that region, again suggesting that the main prey items reflect local overall prey abundances. Macro-infaunal data for the Beaufort Sea are sparse and in part date back several decades (e.g., Wacasey et al. 1977, Bilyard and Carey 1979, Carey et al. 1984) or cover depths where snow crabs do not occur (e.g., < 10 m depth, Dunton et al. 2012). Thus, our ability to interpret snow crab diets in the context of prey availability is limited. The polychaete *C. hyperborea* was a particularly prominent prey item in crabs from the western and central Beaufort Sea, while other polychaetes were the most abundant prey item in crabs from the Canadian Beaufort Sea. Limited available data suggest that polychaete abundance in the central and eastern Beaufort Sea is highest at depths of 200 m along the outer continental shelf, and decreases sharply with increasing depth (Bilyard and Carey 1979, S.M. Hardy, UAF, unpublished data). This coincides well with the depth distribution of crabs on the Beaufort Sea shelf, which are most common along the shelf break and upper slope region (Logerwell et al. 2011). Across the Canadian Beaufort shelf, echinoderms (ophiuroids in particular) and bivalves comprise > 70%

total macrofaunal biomass and polychaetes contribute up to ~40% biomass (g ww m^{-2}, Conlan et al. 2008, 2013, Roy et al. 2014). In summary, our results suggest that regional differences in snow crab stomach content observed in the present study likely reflect *in situ* community composition of prominent benthic macro-infaunal prey across the study region.

In addition to high consumption of infaunal prey taxa, snow crab also preyed on epibenthic fauna. Ophiuroids and crustaceans typically dominate abundance and biomass of epibenthic communities in varying proportions across both shelves (Chukchi Sea: Feder et al. 2005, Bluhm et al. 2009, Ravelo et al. 2014; Beaufort Sea: Roy et al. 2014, Ravelo et al. 2015). Ophiuroids account on average for > 40% biomass (g ww m^{-2}) and > 60% abundance in the southeastern and northeastern Chukchi Sea, although with high spatial variability (Feder et al. 2005, Bluhm et al. 2009, Ravelo et al. 2014), and for > 40-90% in biomass (g ww m^{-2}) and abundance on the Beaufort Sea shelf (Roy et al. 2014, Ravelo et al. 2015). Ophiuroids were common prey items and occurred at equal frequencies in snow crab stomachs in all regions. Despite the clear dominance of ophiuroids in epibenthic communities across the study regions, crabs in all regions consumed a variety of prey taxa, such as polychaetes, bivalves, and amphipods more frequently than ophiuroids. As these more common prey taxa are mostly infaunal, diet results from this current study may indicate that snow crab prey on epifauna taxa mostly opportunistically or that they are a less preferred food item due to their relatively low energy content (Hondolero et al. 2012).

One epifaunal prey group that showed strong regional differences in crab stomachs were brachyuran crabs, which were common prey items especially in Chukchi Sea crabs (FO= 23% and 15% in the southern and northern Chukchi Sea, respectively) but not in Beaufort Sea crabs (FO < 5% for all Beaufort regions). Brachyuran crabs, especially *C. opilio* and the lyre crab *Hyas coarctatus*, are common in the Chukchi Sea (Feder et al. 2005, Bluhm et al. 2009, Blanchard et al. 2013a, Ravelo et al. 2014). Although we could not fully confirm identity from the stomach content fractions, the appearance of fragments seemed to point to juvenile snow crabs as this prey category. This FO may indicate an appreciable amount of cannibalism in the Chukchi Sea. Cannibalistic feeding has been a common occurrence in laboratory studies of snow crabs, with 55% of crabs < 50 mm CW cannibalized by larger crabs (Dutil et al. 1997). Cannibalism has also been observed in populations in the northern Bering Sea (Kolts et al. 2013a), Newfoundland (Wieczorek and Hooper 1995, Squires and Dawe 2003), and the Sea of Japan (Chuchukalo et al. 2011). For example in the Sea of Japan, crabs were the main single prey item of snow crabs by FO (17.6%) and prey mass (18%, Chuchukalo et al. 2011). In the northern Bering Sea, cannibalism on small juveniles (< 20 mm CW) occurred in localized regions and reached an FO of ~40% in snow crab stomachs (Kolts et al. 2013a). Potentially cannibalized crabs were found in the stomachs of Chukchi Sea crabs ranging from 30-80 mm CW, while we found little evidence of cannibalism in the larger crabs (90-130 mm CW) of the Beaufort Sea. In the St. Lawrence estuary, cannibalism was also more prominent in smaller snow crab < 50 mm CW than larger adults (Lovrich and Sainte-Marie 1997); thus, the lack of conspecific prey in larger crabs may be due to a prey shift to other larger, perhaps more nutritious, prey items. More likely, however, the regional differences in cannibalism we observed were not based on a size-difference in the predatory crabs but result from there being very few small, juvenile crabs in the Beaufort Sea to serve as prey (Rand and Logerwell 2011, Ravelo et al. 2015), while small crabs are very common in the Chukchi Sea (Konar et al. 2014). In general, intraspecific predation may benefit adolescent snow crabs in the Chukchi Sea directly by increasing food supply and indirectly by reducing competition for resources. Severity of cannibalism is typically density-dependent, with smaller snow crabs at ~15-30 mm CW possibly the most susceptible to cannibalism (Lovrich and Sainte-Marie 1997). Cannibalism has been suggested to regulate recruitment and establish cohort strength during the early stages of snow crab ontogeny (Sainte-Marie et al. 1996, Lovrich and Sainte-Marie 1997) and is known as a significant source of mortality in other crab species (Hines and Ruiz 1995, Fernandez 1999). Cannibalism may be an important part of total mortality in the Chukchi Sea given the high abundances of snow crabs, including young stages (Konar et al. 2014), while it seems a negligible source of mortality in the Beaufort Sea. Cannibalism was not included in a previous assessment of snow crab mortality in the eastern Chukchi Sea (Whitehouse et al. 2014) but, based on results from the present study, should be considered in population dynamics and assessments of possible future snow crab fisheries in the Chukchi Sea.

Regional differences in trophic structure also existed in the time-integrated measure of stable isotope analysis, despite overall high variability in the isotope data within each region. The main regional separation based on SIA was observed between the Chukchi Sea and the central and Canadian Beaufort Sea, similar to the regional diet differences we observed based on SCA. Most of this separation was along the carbon stable isotope axis, which represents differences in basal food sources (DeNiro and Epstein 1978). Benthic food webs along the Alaska Beaufort Sea shelf and upper slope receive more marine carbon in the western Beaufort Sea versus stronger terrestrial carbon inputs in the central Beaufort Sea (Dunton et al. 2012, Divine et al. 2015, Bell 2015), which can be traced by the lighter δ^{13}C values of the terrestrial carbon sources (Wooller et al. 2007). Therefore, the depleted ^{13}C signal in central and Canadian Beaufort Sea crabs in the present study likely reflects the strong imprint of terrestrial source on the benthic food web in the western part of the Beaufort Sea.

4.2 Size and sex-age effects on snow crab diets

Generally, most size and sex-age classes within each region had similar diets with respect to both stomach contents and stable $\delta^{13}C$ and $\delta^{15}N$ isotopes. We found size effects only in SCA and sex-age effects only in SIA. Size-related differences in stomach contents were due to the unique diet composition of the largest size class (80 mm CW) relative to all other sizes for southern Chukchi crabs and diet compositions of the two smallest size classes (50 and 60 mm CW) in the central Beaufort Sea. Crabs > 80 mm CW in the southern Chukchi region did not consume several prey taxa that were common in smaller size classes (e.g., ophiuroids, bivalve sp. 1; both FO= 0%, A.1). Since > 80 mm CW was the largest size class of crabs encountered in the Chukchi regions, it is possible that we detected a shift in diets with increased body size, as has been observed in snow crabs in the northern Bering Sea (Kolts et al. 2013a). However, since size-based diet differences occurred only between a few size classes in two regions with no consistent patterns or trends across all regions, the size-based results may be artifacts of the low sample sizes or from binning crabs into 10 mm CW size classes. These factors may also explain the lack of detectable differences in SIA among size classes. Due to the overall narrow ranges of $\delta^{13}C$ and $\delta^{15}N$ isotope values among all crabs and high variability within any size grouping, larger sample sizes would be necessary to detect subtle differences.

In general, all sex-age groups consumed similar diets in the present study. Previous gender-specific SCA studies among similar-sized males and females have produced mixed results at different spatial scales in some regions. For example, no differences were found in the diets of male and female snow crabs of similar sizes in Bonne Bay, Newfoundland (Wieczorek and Hooper 1995), but differences between male and female feeding habits occurred at a larger scale across the northeast Newfoundland shelf (Squires and Dawe 2003). In that area, males consumed more ophiuroids, fish, polychaetes, and clams (considered harder to capture prey items), while females preyed more on easily accessible prey items such as shrimp, gastropods, crabs and sea urchins. In the northern Bering Sea, diets were identical for males and females of similar sizes and in general reflected *in situ* prey availability (Kolts et al. 2013a). Additionally, Lovrich and Sainte-Marie (1997) found males were more likely to engage in cannibalism in the laboratory, but the present study found both males and females consumed smaller snow crabs.

Stable isotope analysis revealed subtle gender-specific diet differences in several regions, despite the lack in gender differences of diets from SCA. Males in the southern Chukchi were enriched in ^{13}C compared with mature and immature females within the same region, but given that the mean $\delta^{13}C$ value for males was within 1 ‰ (considered the range of natural variation, DeNiro and Epstein 1978) of mean $\delta^{13}C$ values for females in the same region, we suggest that these differences are likely of minor biological importance. Differences in mean isotope values were more variable between sexes in the Beaufort Sea, although not significant because of high variability in a low number of replicates.

4.3 Conclusions

Snow crab prey items in the Chukchi and Beaufort seas included common benthic taxa that occur across the study region. Frequency of occurrence of prey taxa differed regionally, with most separation of diets observed between the central and Canadian Beaufort regions. Neither size nor gender was a consistent factor explaining diet differences, and the few differences we found may need to be investigated further with larger sample sizes. Cannibalism was pronounced in the Chukchi Sea but not elsewhere, a pattern that may result from the locally high densities of small snow crabs in the Chukchi Sea relative to the Beaufort Sea. As suggested for other regions (Lovrich and Sainte-Marie 1997), we hypothesize that cannibalism may contribute to regulating recruitment in the Chukchi Sea via intraspecific predation that reduces cohort strength after settlement to the benthos. It may be more important than previously considered for fisheries managers to incorporate this source of mortality into assessments of snow crab population dynamics and estimations of sustainable yields for the Arctic Chukchi Sea population (NPFMC 2009). Given that no prey selectivity was apparent in the southern Chukchi Sea (where statistically tested), the present population of snow crabs seems to impact benthic prey fields equally. Should strong range shifts of large (> 80 mm CW) crabs or substantial increases of snow crab populations occur in the southern Chukchi Sea as some evidence suggests (Feder et al. 2005, Mueter and Litzow 2008, Bluhm et al. 2009), they would likely exert increased top down pressure and have the potential to restructure benthic food webs (e.g., Falk-Petersen et al. 2011, Dvoretsky and Dvoretsky 2015). Thus, continued monitoring of snow crab life history and population dynamics in the Pacific Arctic region is essential to detect future potential increases in snow crab abundances that may impact the benthic prey communities, and subsequently benthic food web structure. More detailed work on establishing relationships between snow crab diets and prey availability across the entire Alaska Arctic will allow a better assessment of how potential increases in snow crab populations in the Arctic may impact benthic communities. Conversely, changes in benthic community composition, as predicted with continued climate changes (Grebmeier 2012), may impact snow crabs as a potentially valuable commercial resource in the future.

Acknowledgements

We extend many thanks to the crews of the R/V *Norseman II*, F/V *Alaska Knight*, and R/V *Frosti* for their assistance during cruises and all cruise participants who were instrumental in sampling efforts. This study was made possible in part by samples collected in 2011 in the Beaufort Sea under BOEM Cooperative Agreement No. M10AC2004 "Beaufort Sea Marine Fish Monitoring in the Central Beaufort

Sea" (BeauFish), U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM), Alaska Outer Continental Shelf Region, Anchorage Alaska, as part of the BOEM Environmental Studies Program. Participation of KI and BB in the BeauFish field survey was supported by the Coastal Marine Institute (CMI, Award M11AC00003). Samples were also collected in the Beaufort Sea under the BOEM Agreement No. M12AC00011 “U.S.-Canada Transboundary Fish and Lower Trophic Communities Project” in 2012 and 2013. Samples in the Chukchi Sea were obtained with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior under Agreement No. 10-CIAP-010 and under BOEM Cooperative Agreement No. M12AC00009 “Arctic Ecosystem Integrated Survey (Arctic Eis)”. Some Chukchi Sea crab and infaunal prey samples were also collected through the 2012 Russian-American Long-Term Census of the Arctic (RUSALCA) cruise with support by the National Oceanic and Atmospheric Administration, NA08OAR4320870 CIFAR Amendment 2. The National Science Foundation Marine Ecosystem Sustainability in the Arctic and Subarctic (MESAS) IGERT (Award DGE-0801720) provided support for LD. Stable isotope analysis was made possible by the North Pacific Research Board (NPRB, Award 1227), the Robert and Kathleen Byrd award, Alaska Sea Grant, and the above CMI grant. We would also like to thank J. Grebmeier and L. Cooper (U. Maryland) for providing prey availability data, T. Howe, N. Haubenstock of the Alaska Stable Isotope Facility, and M. Clark for their assistance during isotope processing. We are grateful for assistance with taxonomic identifications by M. Hoberg (University of Alaska Fairbanks) and Ben Gray (UAF), and lab assistance by C. Lipka and C. Serratos (UAF).

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Table 1. Overall carapace width (CW) size ranges and number of stomachs analyzed for males, immature females, and mature females for each of the five study regions.

Region	Sex class	Size range (mm CW)	No. of Stomachs	No. Isotope samples
southern Chukchi	males	40-80	78	79
southern Chukchi	immature females	40-50	24	26
southern Chukchi	mature females	30-60	NA	33
northern Chukchi	males	40-80	101	79
northern Chukchi	immature females	40-50	10	10
northern Chukchi	mature females	30-60	NA	32
western Beaufort	males	30-70	26	24
western Beaufort	immature females	30-50	5	5
western Beaufort	mature females	30-60	3	3
central Beaufort	males	50-120	64	33
central Beaufort	immature females	60-70	3	3
central Beaufort	mature females	60	2	2
Canadian Beaufort	males	80-130	22	28

Table 2. Ranked biomass and abundance prey taxa for five stations from the 2012 RUSALCA cruise and for five carapace width (CW) size classes of snow crabs collected at close-by stations to the 2012 Arctic EIS cruise to the southern Chukchi Sea (see Fig. 1 for station locations) "—" indicates that prey taxa were absent at a station.

Station	**Polychaeta**	**Bivalvia**	**Crustacea**	**Sipuncula**	**Ophiuroidea**	**Echinoidea**	**Anthozoa**	**Ascidiacea**	**Nemertea**	**Other**
Biomass (g C m^{-2})										
CS8R	3	1	2	7	4	—	6	—	8	5
CS12R	4	1	2	—	—	—	3	—	5	6
CS17	4	2	6	5	7	10	9	3	8	1
CL1	1	2	4	8	5	7	—	—	6	3
CL3R	2	3	4	1	6	7	—	—	—	5
Abundance (individuals m^{-2})										
CS8R	3	2	1	8	5	—	6	—	7	4
CS12R	3	2	1	—	—	—	4	—	6	5
CS17	1	6	2	5	3	9	—	7	8	4
CL1	2	1	3	7	4	6	—	—	—	5
CL3R	2	1	3	6	5	6	—	—	—	4
Snow Crab CW size class										
40 mm	3	1	2	—	4	—	—	—	—	5
50 mm	1	2	3	—	4	—	—	—	—	5
60 mm	2	1	3	—	5	—	—	—	—	4
70 mm	1	2	2	—	—	—	—	—	—	3
80 mm	1	2	3	—	—	—	—	—	—	—

Table 3. PERMANOVA results comparing carapace width size classes (CW) and sex-age classes within study regions in the Chukchi and Beaufort Seas. Results shown indicate variance components explained by region, body size, and sex-age class for stomach contents analysis, as well as F-statistics and significance. Post-hoc comparisons are provided at the among-region and individual region level. Statistical details for differences among CW size classes (SIMPER analysis) in the southern Chukchi and central Beaufort Seas are provided in Appendix 1.

Source of variation	**df**	**SS**	**MS**	**Pseudo-F**	**P (based on 999 permutations)**
Stomach Contents Analysis- Region, CW, Sex-age as fixed variables					
Among regions	3	20333.0	6777.7	2.8	**0.001**
Among CW	9	27793.0	3088.2	1.3	0.056
Among Sex-age	1	1680.3	1680.3	0.7	0.718
Region*CW	13	42935.0	3302.7	1.4	**0.002**
Region*Sex-age	3	9085.7	3028.6	1.2	0.182
CW*Sex-age	4	10605.0	2651.2	1.1	0.344
Region*CW*Sex-age	2	3123.7	1561.9	0.6	0.874
Stomach Contents Analysis- post-hoc pairwise regions					
southern Chukchi- northern Chukchi					0.208
southern Chukchi- western Beaufort					0.281
southern Chukchi- central Beaufort					**0.001**
southern Chukchi- Canadian Beaufort					**0.025**
northern Chukchi- western Beaufort					0.338
northern Chukchi- central Beaufort					**0.001**
northern Chukchi- Canadian Beaufort					**0.008**
western Beaufort- central Beaufort					0.655
western Beaufort- Canadian Beaufort					**0.013**
central Beaufort- Canadian Beaufort					**0.001**
Stomach Contents Analysis- Individual region CW groups					
southern Chukchi	4	24572.0	6143.1	2.2	**0.001**
northern Chukchi	4	10109	2527.4	1.0	0.473
central Beaufort	7	21653.0	3093.3	1.7	**0.007**
western Beaufort	4	9717.5	2429.4	1.1	0.305
Canadian Beaufort	4	10150	2537.6	0.8	0.656

Table 4. PERMANOVA results for stable isotope analysis (SIA) comparing carapace width size classes (CW) and sex-age classes within study regions in the Chukchi and Beaufort Seas. Results shown indicate variance components explained by region, body size, and sex-age class, as well as F-statistics and significance. Post-hoc comparisons are provided at the regional and the sex-age levels.

Source of variation	**df**	**SS**	**MS**	**Pseudo-F**	**P (based on 999 permutations)**
SIA-Region, CW, *Sex-age as fixed variables*					
Among regions	4	0.61	0.15	7.1	**0.001**
Among CW	9	0.13	0.01	0.7	0.722
Among Sex-age	2	0.15	0.10	4.7	**0.034**
Region*CW	14	0.25	0.02	0.8	0.654
Region*Sex-age	6	0.24	0.04	1.9	0.056
Region*CW*Sex-age	4	0.06	0.02	0.7	0.658
SIA- post-hoc pairwise regions					
southern Chukchi-northern Chukchi					0.064
southern Chukchi-western Beaufort					0.084
southern Chukchi-central Beaufort					**0.009**
southern Chukchi-Canadian Beaufort					**0.001**
northern Chukchi-western Beaufort					0.137
northern Chukchi-central Beaufort					0.073
northern Chukchi-Canadian Beaufort					**0.002**
western Beaufort-central Beaufort					**0.002**
western Beaufort-Canadian Beaufort					**0.013**
central Beaufort-Canadian Beaufort					**0.001**
SIA-post-hoc pairwise within region					
southern Chukchi					
male-immature female					0.001
male-mature female					0.005
immature female-mature female					0.981
northern Chukchi					
male-immature female					0.848
male-mature female					0.547
immature female-mature female					0.724
western Beaufort					
male-immature female					0.140
male-mature female					0.055
immature female-mature female					0.056
central Beaufort					
male-immature female					0.937
male-mature female					0.064
immature female-mature female					0.094

Table 5. Mann-Whitney U-tests comparing ranked prey biomass and abundance *in situ* to ranked importance (based on frequency of occurrence [%]) of snow crabs within the southern Chukchi Sea.

Source of variation	**df**	**U**	**P-value**
Polychaeta (biomass)	1	2.32	0.13
Polychaeta (abundance)	1	1.22	0.27
Bivalvia (biomass)	1	0.12	0.73
Bivalvia (abundance)	1	0.12	0.73
Crustacea (biomass)	1	0.97	0.32
Crustacea (abundance)	1	1.04	0.31
Ophiuroidea (biomass)	1	0.05	0.83
Ophiuroidea (abundance)	1	0.29	0.59
Echinoidea (biomass)	1	3.75	0.05
Echinoidea (abundance)	1	3.75	0.53
Anthozoa (biomass)	1	3.71	0.05
Anthozoa (abundance)	1	2.22	0.14
Ascidiacea (biomass)	1	1.00	0.32
Ascidacea (abundance)	1	1.00	0.32
Sipuncula (biomass)	1	5.53	**0.02**
Sipuncula (abundance)	1	5.54	**0.02**
Nemertea (biomass)	1	5.58	**0.02**
Nemertea (abundance)	1	3.72	0.05
Other prey (biomass)	1	0.20	0.67
Other prey (abundance)	1	0.20	0.66

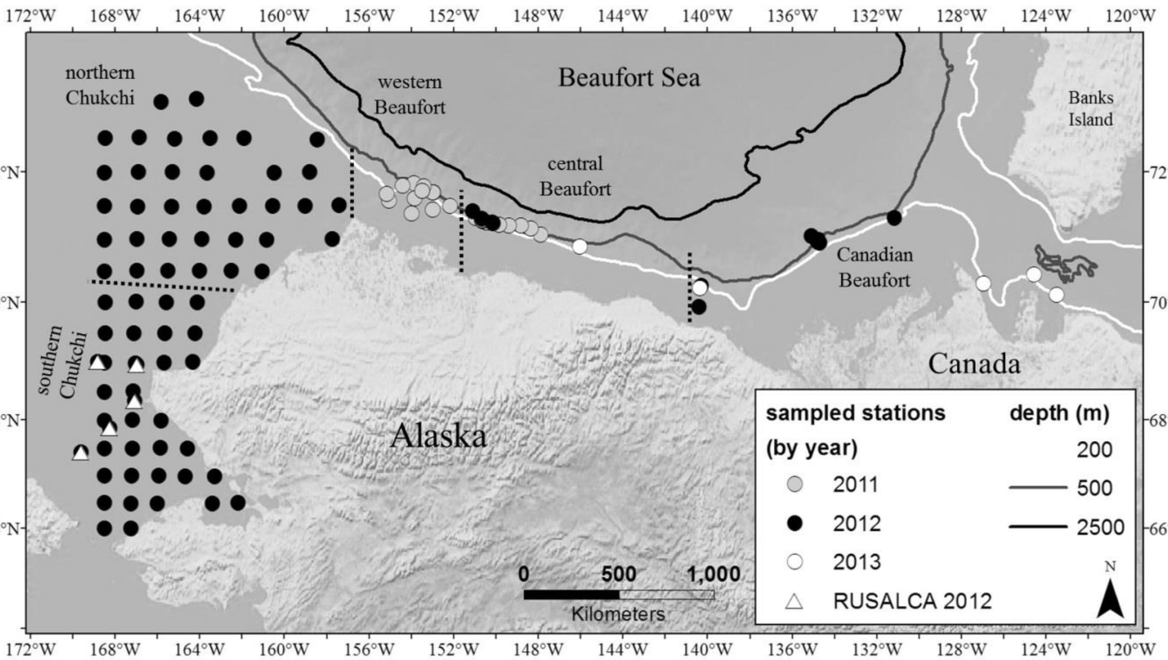

Figure 1. Map of station locations in the Chukchi and Beaufort seas where snow crab collections occurred. Stations are shaded by year of collections. White triangles represent RUSALCA stations where macrofauna were collected for prey availability analysis. Regions are delineated by black dotted lines.

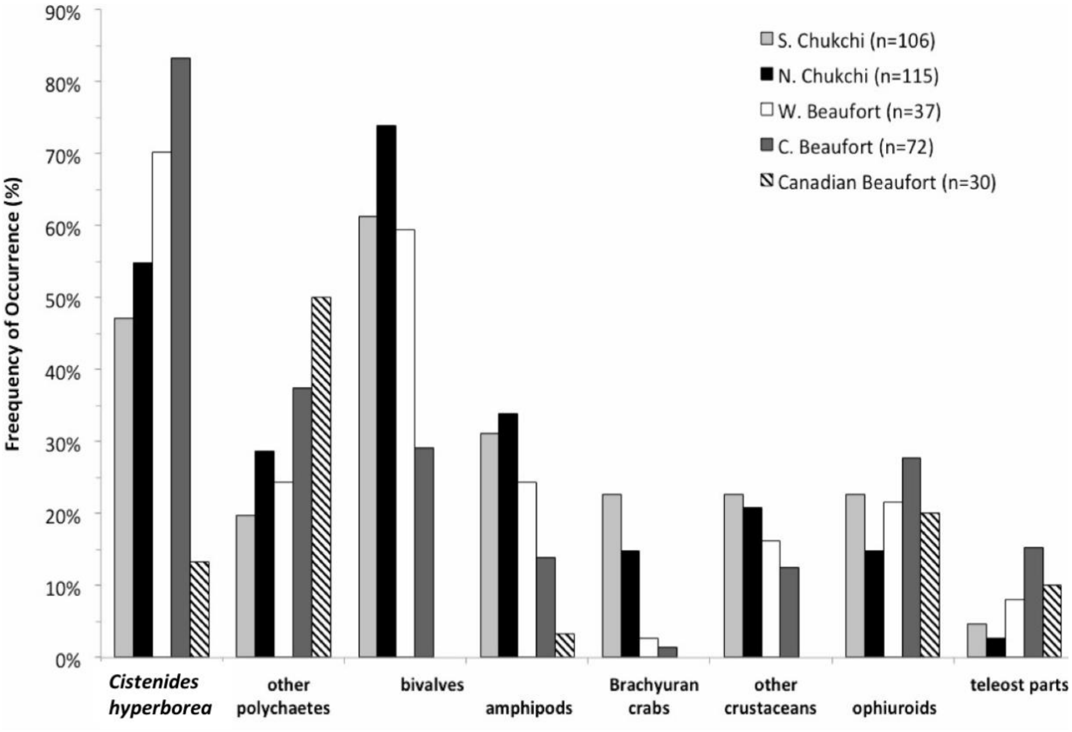

Figure 2. Frequency of occurrence (%) data for the most common prey taxa categories by regions in the Chukchi and Beaufort Seas. Sample sizes for each region are indicated in parentheses in the legend.

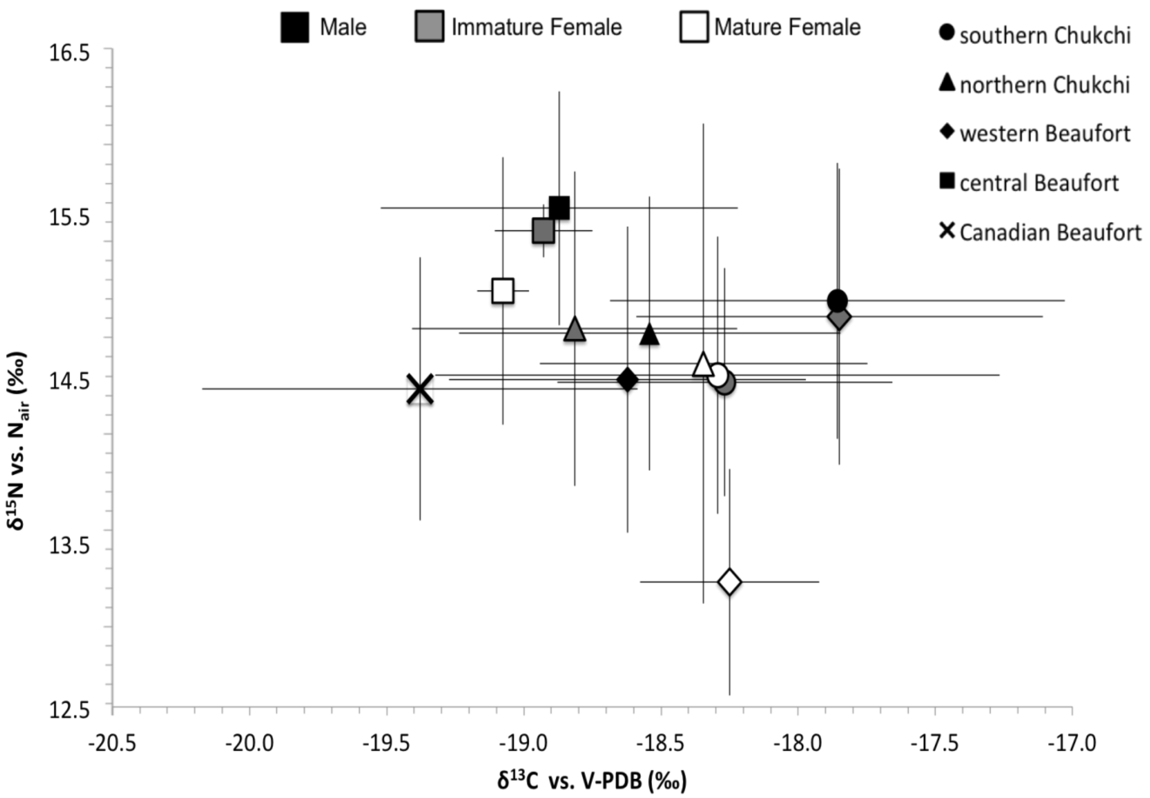

Figure 3. Mean δ^{13}C and δ^{15}N stable isotope values for males and immature and mature females for five regions: southern and northern Chukchi Sea and western, central, and Canadian Beaufort Sea. Error bars are ±1 S.D.

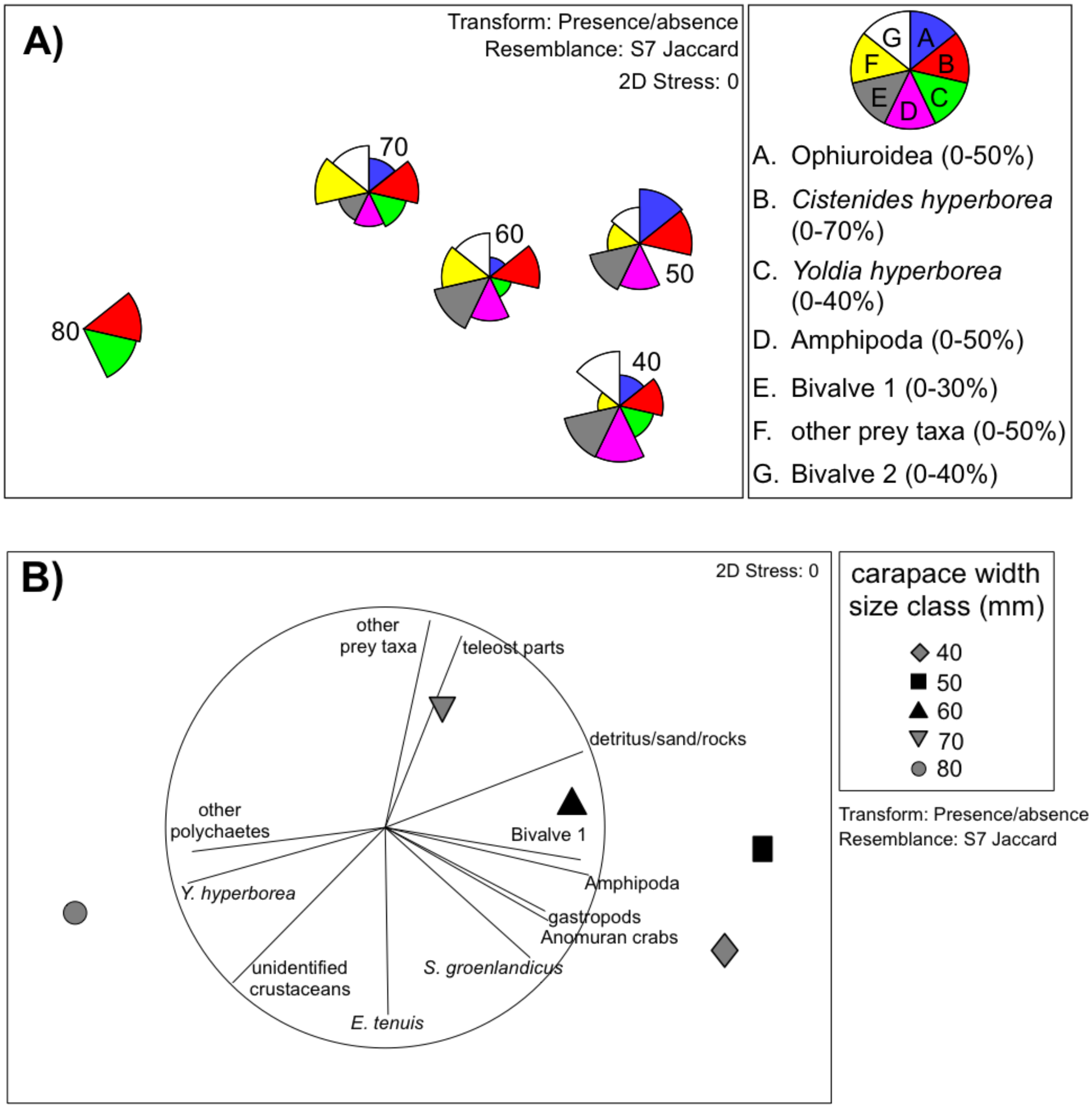

Figure 4. MDS plots for snow crabs in the southern Chukchi Sea showing A) seven prey taxa contributing to differences among size classes (carapace width size classes are represented numerically) and their frequency of occurrence (FO) within diets for each size class (FO minimum to maximum range indicated in parentheses). Pie pieces are proportional within each specified taxa to the range of FO occurring among size classes. B) Prey taxa that contributed to dissimilarities in the diets among various carapace width size classes as indicated in SIMPER analysis. Distances among data points are proportional to the degree of dissimilarity among size classes and overlaid directional lines indicate prey taxa that contribute to these dissimilarities.

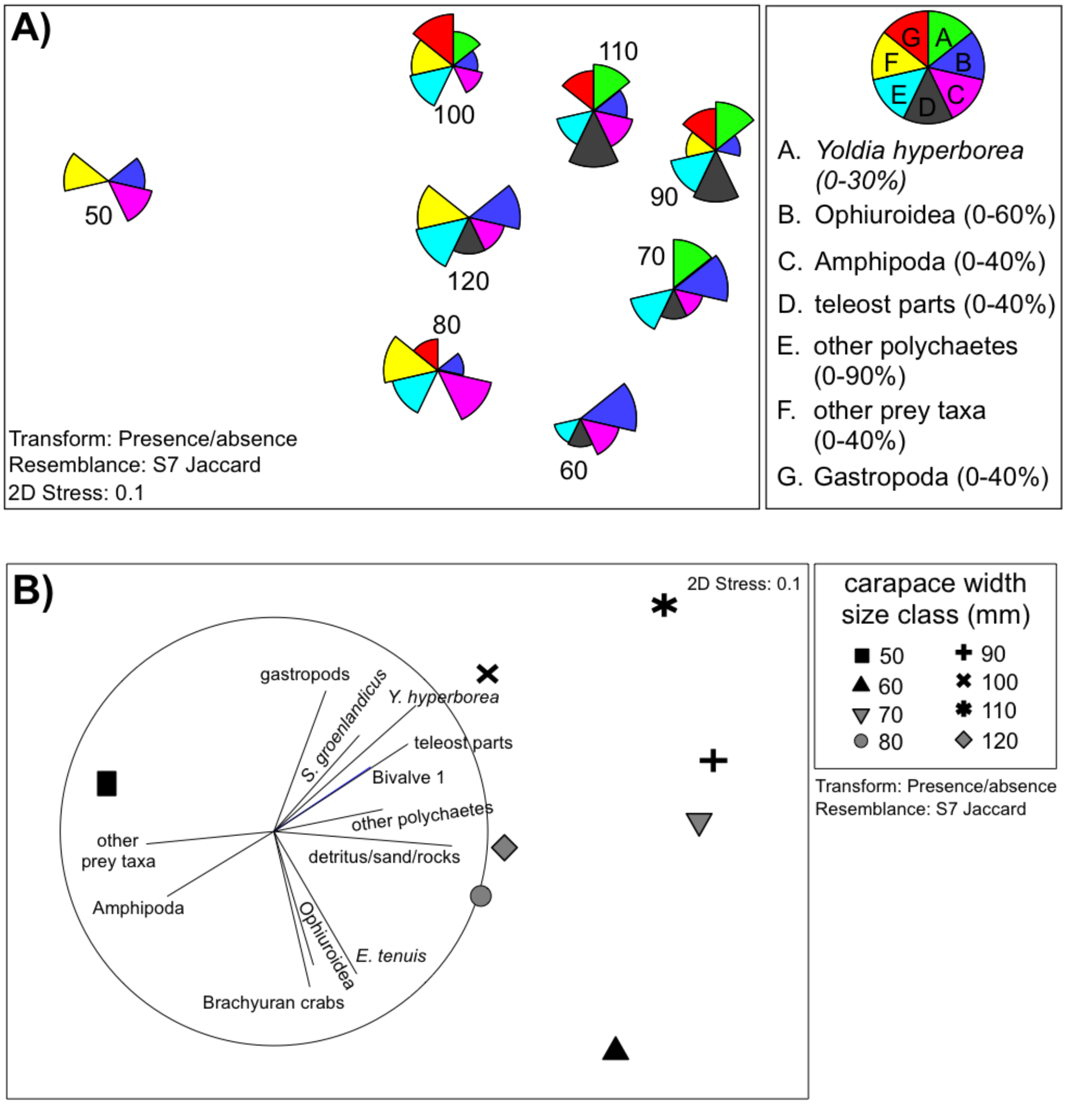

Figure 5. MDS plots for snow crabs in the central Beaufort Sea showing A) seven prey taxa contributing to differences among size classes (carapace width size classes are represented numerically) and their frequency of occurrence (FO) within diets for each size class (FO minimum to maximum range indicated in parentheses). Pie pieces of each specified taxa are proportional to the range of FO occurring among size classes. B) Prey taxa that contributed to dissimilarities in the diets among various carapace width size classes as indicated in SIMPER analysis. Distances among data points are proportional to the degree of dissimilarity among size classes and overlaid directional lines indicate prey taxa that contribute to these dissimilarities.

Objective (4)

Assess crab population dynamics and the potential for harvestable biomass

New estimates of length-weight relationships, size-at-maturity, fecundity, and biomass of snow crab, *Chionoecetes opilio,* in the Arctic Ocean off Alaska[4]

Abstract

Snow crabs (*Chionoecetes opilio*) were identified as a potential future target fisheries species in the Fishery Management Plan for the Fish Resources of the Arctic Management Area (Arctic FMP) in 2009, but a moratorium currently prohibits commercial fishing in federal waters of the Arctic Ocean off Alaska. One problem of the current Arctic FMP is the limited data on which critical snow crab population and biomass estimates are based. Collaborative research efforts in the Chukchi and Beaufort seas over the past decade have yielded a much richer database on Arctic snow crabs. Here, we generated new estimates of stock biomass and abundance to re-calculate sustainable yield of snow crab in the Alaskan Arctic, length-weight relationships, size-at-maturity, and fecundity. Although snow crabs were more abundant in the Chukchi Sea, harvestable biomass of male snow crabs only occurred in the Beaufort Sea because no crabs larger than the minimum marketable size (≥ 100 mm carapace width, based on Bering Sea metric) occurred in the Chukchi Sea during the study period. Our estimates for biomass and sustainable yield in the Beaufort Sea are lower than previous estimates in the Arctic FMP. Length-weight relationships were

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[4] In preparation for publication: Divine LM, Mueter F, Kruse GH, Bluhm BA, Iken K. New estimates of biomass, abundance, maximum sustainable yield, length-weight relationships, size-at-maturity, and fecundity of snow crab, *Chionoecetes opilio,* in the Arctic Ocean off Alaska. Prepared for: tbd.

generally similar for male and female snow crabs between the Chukchi and Beaufort seas. Size-at-maturity was slightly smaller, and fecundity was similar, for Chukchi snow crabs than for snow crabs occurring in other geographic regions; low sample sizes in the Beaufort prevented size-at-maturity and fecundity analyses. Our results expand overall understanding of Arctic snow crab dynamics and inform management of the snow crabs in the Alaskan Arctic in light of potential future fisheries and other, non-fishing activities.

Key words: Fishery Management Plan for the Fish Resources of the Arctic Management Area (Arctic FMP), Beaufort Sea, Chukchi Sea, sustainable yield

Introduction

Snow crab *Chionoecetes opilio* are widely distributed across sub-Arctic and Arctic waters, with lucrative commercial fisheries occurring in the North Atlantic (eastern Canada and Greenland), Bering Sea, and Sea of Japan. Although minimum legal size is 78 mm CW, minimum marketable size in the Bering Sea is 100 mm CW; thus, harvest is limited to only males ≥ 100 mm carapace width (CW) in an attempt to protect female reproductive potential (Zheng and Kruse 2006, Turnock and Rugolo 2012). In 1999, the Eastern Bering Sea (EBS) fishery was declared overfished after a period of declining snow crab biomass and abundance (Turnock and Rugolo 2012). Additionally, a northward contraction of the center of snow crab distribution in the EBS in response to changing oceanographic conditions was identified shortly after overfishing was recognized (Zheng et al. 2001, Orensanz et al. 2004). The combination of the biomass decline, a distribution shift in the EBS snow crab stock, and high abundances of snow crabs in the northern Bering Sea (NPFMC 2009, Kolts et al. 2015), have raised fisheries concerns about the possibility of this species moving further out of EBS fishing grounds and northward into Arctic waters. In response to a potential future fishery in the Alaskan Arctic, the Fishery Management Plan for the Fish

Resources of the Arctic Management Area (Arctic FMP) was developed by the North Pacific Fisheries Management Council (NPFMC 2009). Authors of the Arctic FMP had to rely on limited available Arctic snow crab population data and applied life history metrics estimated from snow crab populations from other regions to evaluate total and harvestable biomass in the Chukchi and Beaufort seas.

Exploitable snow crab biomass is currently presumed to be low in the Alaskan Arctic, although snow crabs are dominant members of benthic communities with respect to biomass and abundance in the Chukchi Sea and in the western Beaufort Sea (Bluhm et al. 2009, Rand and Logerwell 2011, Ravelo et al. 2014, 2015). The potential commercial exploitation of Arctic snow crab requires detailed knowledge of their stock structure and life history in the Arctic. However, snow crab populations in the Chukchi and Beaufort seas have not been historically monitored with any regularity due to the lack of federal monitoring programs and challenges of sampling the vast, seasonally ice-covered shelves and slopes. In the Chukchi Sea, snow crabs contribute significantly to overall invertebrate biomass, even at small maximum sizes (i.e., 74 mm CW, Frost and Lowry 1983, Paul et al. 1997; 94 mm CW, Gross 2015). Limited available data suggest that snow crab abundance has increased on the Chukchi shelf by at least an order of magnitude over the last few decades (Feder et al. 2005) although individual snow crab body sizes remain small. Abundance estimates in the Beaufort Sea have increased because recent deeper sampling yielded more and larger crabs than on the shelf (Logerwell and Rand 2010, Bluhm et al. 2015) and the maximum size of snow crabs collected in the Beaufort Sea has increased from 75 mm carapace width (CW) recorded in the 1970s (Frost and Lowry 1983) to 119 mm CW in the 2000s (Rand and Logerwell 2011). Thus, marketable-sized crabs do occur in the Beaufort Sea, either as a new development since the 1970s or due to higher sampling efforts in the 2000s.

A clear understanding of life history, maturation processes, population structure, and fecundity is essential for effective management of snow crab stocks (Comeau and Conan 1992, Sainte-Marie et al. 1995), including the development of sustainable harvest limits (NPFMC 2009). Snow crab life history and growth has been best studied in geographic regions where snow crabs are commercially exploited (e.g., Gulf of St. Lawrence: Watson 1970, Haynes et al. 1976, Comeau and Conan 1992, Sainte-Marie et al. 1995, Comeau et al. 1998; Bering Sea: Haynes et al. 1976, Otto 1998, Orensanz et al. 2007, Ernst et al. 2012). Snow crabs undergo a series of molts during which they exhibit discrete increases in body size (Hartnoll 1982). Somatic growth for males and females is similar at small sizes (i.e., 3-10 mm CW, estimated ages 0+ to 4 years, Comeau et al. 1998), but males molt more frequently and molt increments are larger at later stages, resulting in larger maximum sizes for males relative to females (Alunno-Bruscia and Sainte-Marie 1998, Burmeister and Sainte-Marie 2010, Dawe et al. 2012). Individuals undergo a final, terminal molt to maturity at an estimated age of 7+ years after settlement (for Canadian Atlantic regions), but size at terminal molt is highly variable among individuals and sexes (Conan and Comeau 1986, Comeau and Conan 1992, Comeau et al. 1998, Sainte-Marie et al. 1995, 2008, Burmeister and Sainte-Marie 2010). In cold waters (< 0°C) snow crabs may exhibit slower growth rates, have a smaller growth increment per molt, or skip a molt, all of which can result in smaller terminal sizes (Burmeister and Sainte-Marie 2010, Dawe et al. 2012). Skip-molting is more common in later instars, shortly before the terminal molt, and especially females at low temperatures may be forced to skip-molt if they do not reach the physiological threshold to accomplish the energetically costly female terminal molt (Dawe et al. 2012). Males, in turn, may skip-molt late in their adolescent development to eventually reach larger terminal sizes, which will increase their life-time fitness (Sainte-Marie et al. 2008, Dawe et al. 2012). All of this complicates the application of growth models to Arctic snow crab populations.

Size-at-maturity is a critical determinant of reproductive output and rate of population growth in brachyuran crabs (Stearns 1976, Hines 1982). Male crabs exhibit an allometric increase in chela height relative to body size during the terminal molt (Conan and Comeau 1986), and this relationship is used to determine maturity status for males. However, gonad development occurs prior to terminal molt and males may be sexually mature prior to exhibiting a change in chela allometry (Sainte-Marie et al. 1995). For example, males in the Gulf of St. Lawrence reach size of 50% physiological maturity at 34 mm CW based on presence of spermatophores inside the vas deferens (Comeau and Conan 1992), but reach 50%

morphometric maturity at 57 mm CW based on chela allometry (Watson 1970). Moreover, size-at-maturity varies with latitude. For instance, based on chela allometry males mature at a minimum of 65 mm CW in the eastern Bering Sea (Somerton 1981), compared with minimum sizes of ~ 40 mm CW in the Chukchi Sea (Barber et al. 1994). For females, maturity is indicated by a marked increase in the size of the abdominal flap to accommodate an egg clutch after their terminal molt (Watson 1970, Moriyasu et al. 1987, Alunno-Bruscia and Sainte-Marie 1998). Temperature dependence of size-at-maturity may be reflected in a latitudinal trend, where size-at-maturity in female snow crabs based on abdominal flap size decreases from 60-67 mm CW in the southeastern Bering Sea to 50-52 mm CW in the northern Bering Sea (Somerton 1981, Otto 1998, Ernst et al. 2005, Armstrong et al. 2008) but then remains similar around 50 mm CW in the northern Chukchi Sea in 1976 (Jewett 1981). However, the mean CW at 50% maturity of females collected during 1990-1991 (Paul et al. 1997) and in the 2000s (Bluhm et al. 2015) in the Chukchi Sea was smaller, estimated at 46 mm. In general, though, while size-at-maturity is strongly temperature-driven, it does typically occur over a range of sizes within a geographic region (Dawe et al. 2012).

Female fecundity (i.e., number of fertilized eggs per clutch) and female lifetime fecundity (i.e., number of clutches produced in a lifetime) are important metrics in understanding distribution patterns in crab stocks and their changes over time (Armstrong et al. 2008). In the Bering Sea, female fecundity is scaled to body size, with larger females producing larger egg clutches (Orensanz et al. 2007, Kolts et al. 2015). In response to cold annual mean temperatures (≤ ~1 °C) in the northern Bering Sea, females shift from an annual to a biennial breeding cycle (Rugolo et al. 2005, Kolts et al. 2015). For the Alaskan Arctic, it is unclear whether mature females breed annually or biennially and, if biennial breeding occurs, what proportion of mature females are on a biennial breeding schedule. Virtually no mature females with fertilized egg clutches have been collected in the Beaufort Sea to date (Bluhm et al. 2015), indicating zero to minimal local reproduction in this region.

The goal of the present study was to provide new information on high Arctic snow crab life history and distribution in the Chukchi and Beaufort seas, using a synthesis of available data collected over the past decade. Specifically, we estimated (1) regional biomass, abundance, and sustainable yield for snow crabs in the Chukchi and Beaufort seas, (2) individual length-weight relationships for snow crabs in the Chukchi and Beaufort seas, (3) size-at-maturity for males and females in the Chukchi Sea only, and (4) fecundity of females in the Chukchi Sea only, due to low sample sizes in the Beaufort Sea. We used these data to revise total and harvestable biomass estimates originally published for snow crabs in the Arctic FMP (NPFMC 2009).

2. Methods

2.1 Snow crab collections

This project used a combination of snow crab data collected from 19 surveys, 12 in the Chukchi Sea and 7 in the Beaufort Sea between 2004 and 2015 (Table 3.1, Fig. 3.1). New samples and/or existing data were used in various combinations to address project objectives (e.g., subsets of data were used for various calculations and analyses as appropriate), depending on data or availability of crabs for new measurements. A vast majority of crabs were collected with a plumb staff beam trawl (PSBT, modified from Gunderson and Ellis 1986, details on towing methods in Norcross et al. 2015; Table 3.1). The PSBT has an effective 2.26 m opening and a net with square mesh of 7 mm and a 4 mm cod end liner. Tow duration lasted from 1-6 min at speeds ranging 1-1.5 kts. Crabs were also collected using an 83-112 Eastern bottom trawl (EBT, Table 3.1), which is the standard net for the Alaska Fisheries Science Center (AFSC) bottom trawl surveys in the Bering Sea. The EBT has a 25.3 m headrope and 34.1 m footrope. During the Ocean Explorer survey in the Beaufort Sea in 2008 and the Arctic Eis 2012 survey (Table 3.1), the EBT was fitted with a net mesh of 102 mm, with 89 mm intermediate and cod end liners (see Rand and Logerwell 2011 for information on lined or unlined tows during 2008 Ocean Explorer cruise). During the Arctic Eis cruise, the cod end had a 32 mm liner (Goddard et al. 2012). Tow duration for the EBT ranged from 5 to 15 min at an approximate speed of 3 kts.

To eliminate gear bias in the size composition estimate of the snow crab population in the Chukchi Sea, we compared the size frequencies of crabs between the PSBT and EBT based on snow crab CW data from 33 paired trawls taken during the Arctic Eis 2012 cruise (Britt et al. 2013, Table 3.1). Observed sizes were summarized as the number of crabs per km^2 and binned into 1 mm size bins for each gear type. The effectiveness of the two nets for sampling snow crabs in their path is unknown (gear selectivity) and is likely to differ among crab sizes (size selectivity). Assuming each trawl is fully size selective over some range of observed sizes (CW), the size selectivity of the two trawl types can be estimated under the following assumptions. Selectivity follows a logistic model of the form:

$$\text{selectivity} = \frac{1}{1 + e^{b(x-a)}}$$

where x is the carapace width, parameter a corresponds to size at 50% selectivity, and b corresponds to the steepness of the curve. We also assumed that the EBT has full selectivity for large crabs (large mesh size) and selectivity may decrease with decreasing CW ($b > 0$), and the PSBT has full selectivity for small snow crabs (small mesh size) and selectivity may decrease with increasing CW ($b < 0$).

Estimated size selectivity can be used to estimate the "true" size distribution of crabs in the Chukchi Sea by dividing the observed numbers at a given size by the estimated selectivity at that size. We simultaneously estimated the parameters of the two selectivity curves by minimizing the weighted sum of squared differences between the predicted number of crabs at size *k* from the PSBT and the predicted number of crabs at size *k* from the EBT. Because the variability in numbers at size was not constant and increased with the number of crabs (N_k) in size bin *k*, we applied appropriate weights to the squared differences before summing across size bins. We assumed that variance increases linearly with N_k based on the expected mean-variance relationship for Poisson-distributed count data. We then weighted the squared difference for each size bin by $1/ N_k$, where N_k values were computed from a smoothed length-frequency distribution estimated by minimizing the unweighted sum of squares. If the number of crabs in a given size bin was estimated to be less than 1 it was set equal to 1. This selectivity analysis was used to determine the size threshold at which snow crabs were representatively caught with both gears for biomass and abundance assessments.

Snow crabs collected from all trawls were rinsed and counted, bulk weight per station recorded using spring or digital hanging scales, and during some cruises, carapace width (body size) was measured to the nearest 0.1 mm using digital Vernier calipers. Crabs were either frozen whole or preserved in formalin (RUSALCA 2009 only) for transport to the home laboratory. Crabs were then thawed, blotted dry, and individually weighed to the nearest 0.1 g. When necessary, crabs with missing limbs were weighed with remaining limbs attached, then limbs were removed and weighed, and added to the body weight for a total individual weight.

2.2 Biomass, abundance, and sustainable yield

Biomass and abundance at each station were estimated from area swept by the trawl. For the EBT, area swept was determined by multiplying the distance towed by the mean net spread. For the PSBT, the net width was assumed to be fixed at 2.257 m (Gunderson and Ellis 1986), and area swept was equal to the net swath multiplied by the distance towed. All estimates were standardized to 1 km^2 for an estimate of catch per unit effort (CPUE). Because we compiled multiple years and cruises where stations were sampled with varying frequency over the study period, we aggregated all sample stations in 1° latitude x 1° longitude grid cells and summed all samples within each grid cell in the Chukchi Sea (for a total of 44 grid cells, Fig. 3.1). We then averaged data within a grid cell for an average estimate of biomass or abundance per unit effort per grid cell. This mean CPUE was multiplied by the total survey area in the US Chukchi Sea (145,200 km^2) for an estimate of total biomass or abundance. Total survey area was bounded by the outer periphery of all sampled stations (MATLAB, V. 7.10.0 Natick, MA, Fig. 3.1). We did not aggregate data from multiple cruises in the Beaufort Sea by grid cells because most station locations did not overlap temporally, but rather divided the survey area into two depth strata: shallow stations were all sampled locations < 100 m depth, and deep stations were all stations > 100 m depth. We then aggregated total biomass and abundance for each depth stratum in the Beaufort Sea for a total survey area of 65,002 km^2. We acknowledge that both temporal and spatial biases are not completely resolved, but assume that aggregating data in these ways alleviated some potential biases.

Estimates obtained here were considered pristine, or unfished, biomass for comparison with previous estimates from the Arctic FMP (NPFMC 2009). For the comparison, we determined the equilibrium biomass following Thompson (1992) as:

$$B(F|r) = \left[\left(\frac{h}{M+F}\right)\left(1+\frac{1}{(M+F)d}\right)\right]^{\frac{1}{r}} ,$$

where F is the instantaneous fishing mortality, r is the amount of resilience implied by the stock recruitment relationship, h is the scale parameter in Cushing’s (1971) stock-recruitment relationship, M is the instantaneous natural mortality rate, and d is the difference between the age-at-maturity and the age intercept of the linear weight-at-age equation (Thompson 1992, NPFMC 2009). As this stock has not been historically fished, F was set equal to 0. To determine the amount of biomass available to future potential fishing harvest based on our new biomass estimates, we determined sustainable yield as the product of F and equilibrium biomass:

$$Y(F|r) = F \cdot B(F|r)$$

We then obtained an estimate of the instantaneous fishing mortality that maximizes sustainable yield as:

$$F_{MSY}(r) = \left(\frac{M}{2(1-r)}\right)\left(1-\frac{2-r}{M*d}+\sqrt{\left(\frac{(2-r)}{M*d}\right)^2+\frac{4-6r}{M*d}+1}\right)-M .$$

The biomass at which a maximum sustainable yield (MSY) can be obtained was calculated as:

$$B_{MSY} = B\mathit{ratio}(F_{MSY}(r)|r) \cdot B_0 ,$$

where B*ratio* is the ratio of equilibrium biomass to unfished (pristine) biomass (B_0). Finally, the maximum sustainable yield was estimated as:

$$MSY = Y\mathit{ratio}(F_{MSY}(r)|r) \cdot B_0 ,$$

where Y*ratio* is the ratio of sustainable yield (Y(F|r)) to B_0. We compared our estimates of unfished and equilibrium biomass and maximum sustainable yield to values put forth in the Arctic FMP (NPFMC 2009).

2.3 Length-weight relationships

To investigate the individual crab length-weight relationships, we log-transformed wet body mass (g) and size (mm CW) for all individual males and females collected. The length-weight relationship was estimated from the log-transformed linear regression as:

$$\log M_b = b \cdot \log CW + a$$

where M = mass, *a* is the intercept, and *b* is the slope of the linear function. Analysis of covariance (ANCOVA) was performed to determine if the size relationships differed significantly between the Chukchi and Beaufort seas for males, immature females, and mature females. Females were separated into immature and mature status because mature female growth is disproportionately allocated to reproduction rather than somatic growth (Alunno-Bruscia and Sainte-Marie 1998). Males were treated as one group because of uncertainties in differentiating between immature and mature males.

Size frequency distributions (SFD) were established at 1 mm CW increments separately for the Chukchi and Beaufort seas from all size data available, and pooled across years, to characterize the size ranges of male and female crabs. Assuming that these pooled data are representative of the population, we attempted a mixed model analysis for observed SFD histograms to identify modal peaks that may be interpreted as instars or ages (Kolts et al. 2015). Unfortunately, clear peaks in the size frequency distributions did not occur and precluded our ability to make estimates of numbers-at-age. This may be due to temporal variability and/ or because skip-molting causes some bias in age-at-size relationships in cold water environments (Dawe et al. 2012).

2.4 Size-at-maturity

For male snow crabs from the Chukchi Sea, size-at-maturity was determined based on a relationship between the proportion of males exhibiting large rather than small chela relative to body size (Conan and Comeau 1986). Sample sizes were too low to determine size-at-maturity for either sex in the Beaufort Sea. To determine a breakpoint in the allometric relationship for male size-at-maturity estimates, observed male CW and chela height (CH) were plotted against several published regression equations (i.e., from the Bering Sea, Kolts et al. 2013 and Newfoundland, Comeau et al. 1998, data not shown here) to determine the existing relationship that best fit our data. The northern Bering Sea data presented the best fit for male snow crab data in the Chukchi Sea; thus, mature males were distinguished from juvenile and adolescent males by using a dividing line of $CH = 0.191 \cdot CW$ (Kolts et al. 2013). Female maturity was determined as the carapace width at which the abdominal flap covers the entire ventral side of mature females (Paul et al. 1997), as well as those visibly carrying an egg clutch. This was done for the Chukchi Sea only, as very few mature females were recovered from the Beaufort Sea during the study period. Size-at-maturity was determined by fitting males and females separately to a logistic curve to obtain a likelihood estimate of the proportion of mature crabs by size.

2.5 Fecundity

Fecundity was estimated as the number of eggs per clutch taken from 306 mature females collected at random during the 2009 and 2012 RUSALCA, 2010 COMIDA, 2010 CSESP, and 2012 Arctic Eis cruises in the Chukchi Sea. ‘Egg clutch’ refers to the total number of fertilized eggs, or embryos, being carried by a female. Total egg clutch was removed from the pleopods, 250 eggs were sub-sampled, dried at 60 °C to a constant weight, and dry weight of the sub-sample determined (Stichert 2009). Remaining eggs were also dried as described above and total dry weight obtained. Fecundity was determined by dividing the weight of the total egg mass by the average dry weight of the eggs in the sub-sample and multiplying by the number of eggs in the sub-sample (250). The logarithm (log) of total number of eggs was plotted against log-transformed carapace width for each crab, and linear regression determined the relationship between body size (CW, independent variable) and number of eggs in a clutch (dependent variable). We did not attempt to characterize the developmental stage of eggs to judge whether reproduction was annual or biennial (see Kolts et al. 2015). However, data from Atlantic Canada, Greenland, and the nearby northern Bering Sea suggest that breeding is likely biennial over much of our study area (Moriyasu & Lanteigne 1998, Burmeister 2002, Kolts et al. 2015).

3. Results

3.1 Biomass, abundance, and sustainable yield

Our estimates of total (pristine) snow crab biomass in the Beaufort Sea survey area were approximately four times that of Chukchi total biomass (B_0= 15,656 mt and 3,461 mt, respectively, Table 3.2). We estimated pristine harvestable biomass (males ≥ 100 mm CW) in the Beaufort Sea as B(F|r)= 1,722 mt. With an unfished biomass of 1,722 mt, and holding all other Arctic FMP parameters constant (M= 0.23, d= 8.00, and F= 0.36), we estimated sustainable yield to be Y(F|r)= 1,255 mt and biomass at maximum sustainable yield to be B_{MSY}= 272 mt in the Beaufort Sea. We did not estimate B_{MSY} for the Chukchi Sea because no males ≥100 mm CW occurred. Maximum sustainable yield in our Beaufort Sea study area was MSY= 97 mt (Table 3.2). We estimated a mean abundance CPUE in the Chukchi Sea of 387,691 individuals km^{-2} with a total abundance of 56,292,775,896 individuals for the entire Chukchi Sea survey area. Abundance was much lower in the Beaufort Sea, with an estimated 47 individuals km^{-2}, and a total of 3,055,863 individuals for the entire survey region.

3.2 Size composition and length-weight relationships

Gear selectivity analysis showed that both trawl gears had similar selectivity for snow crabs ≥ 30 mm CW, with the exception that the PSBT had higher selectivity for crabs 30 mm to 42 mm CW (selectivity = 1.0 compared with selectivity 0.5 – 1.0 for EBT, Fig. 3.2, Table 3.3). The EBT had a selectivity of 0.4 for crabs 30 mm CW, but quickly increased and reached a selectivity of 0.5 by 32 mm CW, with selectivity near or at 1.0 for sizes ≥ 41 mm CW. Due to the high abundances of smaller snow crabs caught in the PSBT but not the EBT, we chose 30 mm CW as a lower threshold to achieve comparable selectivity between gear types.

A total of 4,733 male and immature and mature female snow crabs ≥ 30 mm CW were individually measured and/or weighed across the Chukchi and Beaufort seas between 2004 and 2015 (Fig. 3.3 and 3.4). Although males were overall much less abundant in the Beaufort Sea than in the Chukchi Sea, Beaufort males reached larger sizes (up to 120 mm CW, Fig. 3.3B), approximately 27 mm larger than the largest male collected in the Chukchi Sea (93 mm CW, Fig. 3.3A). Mature female snow crabs were also considerably less abundant in the Beaufort Sea compared with the Chukchi Sea, but also reached larger maximum sizes (82 and 72 mm CW in the Beaufort and Chukchi seas, respectively, Fig. 3.4B). Immature females in the Chukchi Sea ranged from 4 to 58 mm CW and mature females ranged from 21 to 72 mm CW (overlapping by 37 mm CW, Fig. 3.4A). In the Beaufort Sea, immature females ranged from 16 to 70 mm CW and mature females ranged from 37 to 82 mm CW (overlapping by 33 mm CW, Fig. 3.4B).

Length-weight relationships were similar between the Chukchi and Beaufort seas for males (ANCOVA, $p= 0.72$, Fig. 3.5A, B). Length-weight relationships also were similar among immature and mature females between the Chukchi and Beaufort seas (ANCOVA, $p= 0.63$ for both, Fig. 3.5C-F). However, females in the Chukchi Sea had heavier body masses at a given CW than Beaufort Sea females (ANCOVA, $p< 0.0001$ for both immature and mature females). When considering immature versus mature female length-weight relationships within each region, we found contrasting patterns. Mature females in the Chukchi Sea achieved heavier body masses at a given size than immature females of the same size (ANCOVA, $p< 0.0001$, Fig. 3.5C, E), but the opposite pattern occurred in the Beaufort (ANCOVA, $p< 0.001$, Fig. 3.5D, F), where immature females were heavier at a given size than mature females. However, low sample sizes in the Beaufort Sea require cautious interpretation of the biological significance of the difference observed in this region.

3.3 Size-at-maturity

For Chukchi crabs, we estimated that 50% of male snow crabs reach reproductive maturity at 62 mm CW, based on morphometric allometry with chela height (Fig. 3.6A). Female snow crabs in the Chukchi Sea achieved 50% size-at-maturity at 46 mm CW based on allometry of the abdominal flap or the presence of an egg clutch (Fig. 3.6B). Size-at-maturity could not be estimated for the Beaufort Sea because of low sample sizes.

3.4 Fecundity

A total of 306 mature females, ranging from 38 to 78 mm CW (Table 3.4), were collected for fecundity estimates in the Chukchi Sea. Egg production scaled to body size (Linear regression, $r^2 = 0.50$, $p < 0.0001$, Fig. 3.7). Mean number of eggs per 1-mm bin CW ranged from 7,092 eggs (38 mm CW) to 49,164 eggs (78 mm CW) (Table 3.4).

4. Discussion

This study improved knowledge of standing stock and population structure of snow crabs in the Chukchi and Beaufort seas. Snow crabs occurred across the Chukchi shelf but were found only in a localized portion of the western Beaufort shelf and along the central Beaufort shelf break and upper slope. Our estimates of total biomass and sustainable yield of snow crabs in the Alaskan Arctic were considerably lower than previous estimates (NPFMC 2009), likely due to inclusion of more sampled stations for more coverage of the study regions. Both males and females in the Beaufort Sea reached larger sizes than conspecifics in the Chukchi Sea, even though there was considerable overlap in the size range of females between the seas. Despite size range differences, length-weight relationships were similar between the Chukchi and Beaufort seas for males, but not females. Our direct estimates of size-at-maturity for males and females in the Chukchi Sea found males mature at larger sizes than females.

4.1 Biomass, abundance, and sustainable yield

Estimated total snow crab biomass in this study was much lower in both the Chukchi and Beaufort seas compared with previous estimates from the Arctic FMP (see Table 3.2). The Arctic FMP also estimated Chukchi total snow crab biomass to be more than double that of the Beaufort Sea (66,491 mt and 29,731 mt, respectively; NPFMC 2009). The Arctic FMP used a total of 96 sampling stations in the Chukchi and 26 sampling stations in the Beaufort seas. The present study, in contrast, used 320 sampling stations in the Chukchi and 197 sampling stations in the Beaufort Sea. This improved region coverage in the Chukchi by 33% (145,200 km^2 versus 98,803 km^2) and in the Beaufort by 90% (65,002 km^2 versus 6,280 km^2) compared with the Arctic FMP region coverage. This lower total (pristine) biomass, which were 50 to 95% lower than Arctic FMP estimates for the Chukchi and Beaufort seas, respectively, perpetuated into lower harvestable biomass estimates for the Beaufort Sea, although harvestable biomass in the Chukchi Sea remained zero since no male crabs larger than the marketable 100 mm CW were caught. Harvestable biomass in the Beaufort Sea (1,722 mt) was approximately 26% of the previously estimated 6,571 mt in the Arctic FMP and our estimate of maximum sustainable yield (97 mt) was about 79% lower than the Arctic FMP-calculated MSY of 453 mt (see Table 3.2). Our results underscore the need for precautionary management regarding commercial fishing activities in the Arctic Management Area. In this region, snow crab are an important prey species for marine mammal species and removal of snow crab biomass via a commercial fishery may have negative impacts on these species.

Although our results indicate much lower biomass, we estimated higher mean CPUE values for snow crabs in the Chukchi Sea (387,691 individuals km^{-2}) than a previous estimate that used Arctic Eis EBT trawl data only (212,000 individuals km^{-2}, Goddard et al. 2012). The higher abundances we observed were possibly due to large numbers of very small (30- 40 mm CW) crabs across the Chukchi

Sea, which may indicate large numbers of young juvenile crabs that settled in the area over the study period. There are many questions surrounding larval drift and settlement in the Chukchi Sea from adjacent areas (see *Fecundity* discussion below), but the presence of high abundances of juvenile crabs suggests that this region may be a settlement location for snow crabs. Abundance in the Beaufort Sea, including small crabs, was much lower than in the Chukchi Sea, with only 47 individuals km^{-2}. For comparison, a previous abundance estimate for the western Beaufort Sea found between 800 (unlined EBT) and 99,600 (lined EBT) individuals km^{-2}, depending on whether a net liner was used (Rand and Logerwell 2011); no comparative estimate for total survey area was available. The use of a liner during that cruise presumably increased the number of small (< 30 mm CW) crabs that were retained in the trawl relative to unlined trawls, but the PSBT that was used in most cruises compiled in the present study also had a high selectivity for these small crabs; thus, we argue that catches in our study represent the true abundances. The low numbers of total crabs recovered from the Beaufort Sea, compared with the adjacent Chukchi Sea, suggest that little local production occurs in that region and that crabs may migrate from adjacent areas to the Beaufort near or after the terminal molt.

4.2 Size distributions and length-weight relationships

Snow crabs in the Chukchi Sea had a smaller maximum size (maximum size of 93 mm CW) than conspecifics in other geographic locations, except the adjacent north-central Bering Sea (90 mm CW, Kolts et al. 2015). The maximum size of 119 mm CW found in the Beaufort Sea (this study, also see Rand and Logerwell 2011) was more similar to the maximum size observed in the Gulf of St. Lawrence, Canadian Atlantic (120 mm CW, Sainte-Marie and Gilbert 1998) and 160 mm CW off the coast of western Greenland (Burmeister and Siegstad 2008). In the Pacific, maximum reported size in the Okhotsk Sea is 100 mm CW (Yanagimoto et al. 2004), and ~130 mm CW in the eastern Bering Sea (Turnock and Rugolo 2012). Thus, maximum size of snow crabs in the Beaufort Sea was similar to maximum sizes in these other regions (except for even larger crabs in Greenland). The consistently small crab sizes observed in the Chukchi Sea (and northern Bering Sea, Kolts et al. 2015) suggest that maximum size may be restricted in this region. One possible reason for smaller maximum size at least in the northeastern part of the Chukchi Sea is the low bottom temperatures from persistent winter water that occurs on the shelf for a majority of the year (< -1°C, Weingartner et al. 2005). Similarly, it has been suggested that body size in adult crabs may be limited by the persistently cold bottom temperatures in the northern Bering Sea (Kolts et al. 2015). Temperature is a principal factor regulating size at terminal molt in snow crabs, and temperatures below 1°C can inhibit a positive energy balance in snow crabs reared in the lab (Foyle et al. 1989, Thompson and Hawryluk 1990). Low temperatures may also result in a higher frequency of skipped molting (Dawe et al. 2012), slowed growth, smaller growth increments per molt, and a shift to a biennial reproductive cycle (Kolts et al. 2015).

Cold bottom water temperatures (< 0 °C) also prevail on the Beaufort shelf, but a marked transition occurs at about 200 m depth, where warmer Atlantic water (up to ~0.5 °C) persists (Crawford et al. 2012). In the Beaufort Sea, Logerwell et al. (2011) reported a strong association between snow crabs and cold waters (< -1.5 °C) on the upper Beaufort Sea slope; however, temperature measurements in that study were only shown to 140 m, which is above the warmer Atlantic layer that starts at ~ 200 m depth and where most crabs occur. A majority of the large female crabs and mature males collected in the Beaufort Sea during the present study were found in waters around 0.5 °C around 200 m depth (Bluhm et al. 2015, Ravelo et al. 2015), possibly capitalizing on the warmer Atlantic water conditions where they are able to grow to comparable sizes as snow crabs in other regions of more moderate temperature regimes. This is consistent with observations of very large male crabs at greater depth (500-600 m) associated with soft substrates and warmer water temperatures along the Newfoundland slope, where they encounter a rich prey spectrum and energetically favorable temperature conditions to obtain large body sizes (Dawe and Colbourne 2002, Dawe et al. 2012). It also is possible that mature males migrate out of the shallow Chukchi and into deeper regions of the Beaufort Sea, similar to the ontogenetic size-related migrations they undertake in the Bering Sea (Orensanz et al. 2004, Ernst et al. 2005) and the Canadian Atlantic (Dawe and Colbourne 2002, Biron et al. 2008).

4.3 Size-at-maturity

Size-at-morphometric maturity for males in the Chukchi Sea was larger with 62 mm CW in our study compared with a previous estimate of 35 mm CW for Chukchi males based on presence of spermatophores (Paul et al. 1997). The smaller size-at-maturity based on spermatophore presence is explained by the fact that male snow crabs develop testes during their adolescence, before the terminal molt (Sainte-Marie et al. 1995). But, aside from differences in methodology for determining maturity state, this discrepancy in size-at-maturity in the Chukchi Sea may also be due to an actual increase in size-at-maturity in the region over the last 2-3 decades. As noted earlier, snow crab size-at-maturity is, among others, a function of temperature conditioning during early ontogeny (Orensanz et al. 2007, Sainte-Marie et al. 2008, Burmeister and Sainte-Marie 2010). Although fall and winter temperatures across the shelf are condensed to a narrow temperature range near-freezing (Woodgate et al. 2005), water temperatures show dramatic interannual differences and can span from below -1˚C to ≥ 6 ˚C (e.g., Day et al. 2013, Blanchard and Feder 2014). A generally increasing temperature trend (Shimada et al. 2006, Woodgate et al. 2006) may account for the observed increase in size-at-maturity in snow crabs on the Chukchi shelf.

Comparisons of size-at-maturity using allometric CH:CW ratios yields high variability across geographic locations. In the Gulf of St. Lawrence males are morphometrically mature at 40 mm CW (Sainte-Marie and Hazel 1992). Males in the southeastern Bering Sea and the Barents Sea achieve morphometric maturity at 100 mm CW (Turnock and Rugolo 2012, Dvoretsky and Dvoretsky 2011). Males in the north-central Bering Sea south of St. Lawrence Island and in the Chirikov Basin are morphometrically mature at 59 mm and 51 mm CW, respectively (Kolts et al. 2015), distinctly smaller than in our Chukchi Sea study area just to the north. Possibly, the persistent cold pool in the northern Bering Sea provides colder year-round temperatures than on most of the Chukchi Sea shelf (Wyllie-Echeverria and Wooster 1998), depressing male maximum size in the northern Bering Sea (Dawe et al. 2012).

We found more agreement with earlier studies in size-at-maturity for females in the Chukchi Sea. Females reached 50% size-at-maturity at 46 mm CW, identical to a previous estimate in the northeastern Chukchi Sea from over two decades ago (Paul et al. 1997), indicating size-at-maturity has been conserved in this region. Our estimate was also similar to reported size-at-maturity for females from the southeastern Bering Sea, Gulf of St. Lawrence, and Sea of Japan (50 mm CW for all regions; Ito 1967, Watson 1970, Jewett 1981, Orensanz et al. 2007). Several investigators suggest that female snow crabs tend to be smaller at maturity at the northern limit of their distribution due to reduced bottom temperatures at northern limits (Jewett 1981, Somerton 1981, Paul et al. 1997, Dawe et al. 2012, Kolts et al. 2015). Clinal variation in size-at-maturity is well established in the eastern Bering Sea ranging from 55°N to 65°N (Zheng et al. 2001, Ernst et al. 2005, Orensanz et al. 2007) and in the Gulf of St. Lawrence, Canada (Sainte-Marie and Gilbert 1998), and further supported by the range of mature females collected in the northern Bering Sea (Kolts et al. 2015). In the northern Bering Sea, mature females ranged from 40 to 68 mm CW south of St. Lawrence Island and from 49 to 59 mm CW north of St. Lawrence Island in the Chirikov Basin (Kolts et al. 2015). Female size-at-maturity in the present study for the Chukchi Sea was slightly smaller (46 mm) compared with those the Bering Sea findings, contrary to this regional comparison for male crab size-at-maturity.

4.4 Fecundity

Estimates of fecundity (number of fertilized eggs per clutch) in our study were slightly lower compared with previous estimates for the Chukchi Sea (Jewett 1981) and with other regions. For example, a 55 mm CW Chukchi Sea female in our study would have a mean fecundity of 23,223 fertilized eggs. A 55 mm CW female in the southeastern Chukchi Sea was reported as carrying a mean of 28,600 fertilized eggs (Jewett 1981), and about 29,560 eggs in the northeastern Chukchi Sea (Paul et al. 1997). The same sized female in the Canadian Atlantic would carry about 24,470 fertilized eggs (Haynes et al. 1976), a southeastern Bering Sea female would have about 26,640 fertilized eggs (Jewett 1981), and a female in the north-central Bering Sea would have 24,390 eggs (see curves and equations for all areas in

Fig. 11 of Kolts et al. 2015). A 55 mm CW female in the Sea of Japan is expected to carry a mean of 30,404 fertilized eggs (Kon and Sinoda 1992). Thus, while our fecundity estimates were lowest among these comparisons, egg production for females in the Chukchi Sea seems to be around the same overall magnitude as in other regions. However, an important question that still remains is the survival rate of snow crab larvae during the pelagic stages and how much, if at all, females in the Chukchi Sea contribute to local production in the Chukchi Sea. The presence of clutch-bearing females in the Chukchi Sea indicates that at least some local production occurs in the region, but the dependence on larval supply from the Bering Sea is still unknown.

Larval advection has been postulated as an important source of crabs in the Chukchi and Beaufort seas (Clement et al. 2005, Hu and Wang 2010, Bluhm et al. 2015). This seems supported by the fact that genetically, snow crab in the Bering, Chukchi and Beaufort seas are considered a panmictic population, with strong gene flow among these regions (Hardy et al. 2011, Albrecht et al. 2014). Further, advection of zooplankton (incl. meroplankton) from the Bering Sea into the Chukchi Sea is well documented (e.g., Grebmeier et al. 2006, Hopcroft et al. 2008, 2010). The presence of mature females with egg clutches in the Chukchi Sea, however, warrants further investigation to evaluate the contributions of larval advection versus local production. In this context, it will be important in future studies to determine if females in the Chukchi Sea are on annual or biennial breeding cycles. This may be resolved by relating the stage of egg clutches to the state of ovaries (i.e., empty and spent in an annually breeding female versus plump and developing in a biennially breeding female, Orensanz et al. 2007). Annually breeding females will likely produce close to three times more eggs over their lifetime than a biannually breeding female, reducing the possible contribution of local reproduction if biennial breeding is prevalent, as has been found for the northern Bering Sea (Kolts et al. 2015). In addition, influx into the Chukchi Sea snow crab population may also not be limited to larval advection. The conspicuous lack of adult snow crabs in the range of 45-60 mm CW in the northern Bering Sea may suggest significant adult migration of these crabs into the southern Chukchi Sea, which could then contribute to local reproduction in the region (Kolts et al. 2015).

Summary and conclusions

Our results are intended to inform the management of the Alaskan Arctic snow crab stock and to expand our understanding of Arctic snow crab life history parameters and distribution trends in light of potential future fisheries or other, non-fishing activities. The lower total and harvestable biomass estimates presented here for the Chukchi and Beaufort seas compared with previous estimates from the Arctic FMP highlight the need to compile a large dataset that encompasses as much of the region of interest as possible. Biomass and abundance estimates presented here may be further improved with inclusion of molting probabilities (prevalence of skip-molting) and accurate size-at-age data, should those become available in the future. We found generally similar length-weight relationships in snow crabs between sexes and seas. Both size-at-maturity and fecundity estimates were within similar ranges as for snow crabs occurring in other geographic localities, albeit on the lower end. Our estimate of fecundity could be improved if information became available regarding the percentage of females on an annual versus biennial reproductive schedule. Ultimately, the results of the present study support continued precautionary management and continuation of the moratorium on commercial harvest of Alaskan Arctic snow crab stocks. Specifically, there are many unknowns surrounding snow crab distribution and life history in these regions. Although we were able to re-estimate biomass and abundance, and provide new length-weight relationships, size-at-maturity, and fecundity data, we were unable to make reliable growth and natural mortality estimates. Knowledge of these key population parameters as estimated directly from the existing stock is necessary to improve population modeling. The presence of large male snow crabs in the Beaufort, but not the Chukchi Sea, continues to remain puzzling, although we propose the likely role of temperature control as this has been proposed as a principal controlling mechanism for many life history processes of snow crab. Continued monitoring with the intent of augmenting the temporal coverage of snow crab size frequency distributions, biomass, and abundance, as well as investigations into the larval dispersal and migratory connectivity of snow crabs occurring in the Bering, Chukchi, and

Beaufort regions, will greatly facilitate improved management of snow crabs as a potential future fishery resource.

Acknowledgements

We extend many thanks to the crews and all cruise participants of all cruises listed in Table 1, who were instrumental in sampling efforts during cruises. In particular, we are indebted to the many data providers including A. Blanchard (UAF), L. Cooper (UMCES), K. Dunton (UT Austin), J. Grebmeier (UMCES), S. Jewett (UAF), B. Konar (UAF), R. Lauth (NOAA), and L. Logerwell (NOAA). This study was made possible in part by samples collected in 2008 in the Beaufort Sea under funding provided by the US Department of the Interior's Mineral Management Service (MMS), Alaska Region (Interagency Agreement M07PG13152 and AKC-058) 2011 in the Beaufort Sea under BOEM Cooperative Agreement No. M10AC2004 "Beaufort Sea Marine Fish Monitoring in the Central Beaufort Sea" (BeauFish), U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM), Alaska Outer Continental Shelf Region, Anchorage Alaska, as part of the BOEM Environmental Studies Program. Participation of KI and BB in the BeauFish field survey was supported by the Coastal Marine Institute (CMI, Award M11AC00003). Samples were also collected in the Beaufort Sea under the BOEM Agreement No. M12AC00011 "U.S.-Canada Transboundary Fish and Lower Trophic Communities Project" in 2012-2014. Samples in the Chukchi Sea were obtained with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior under Agreement No. 10-CIAP-010 and under BOEM Cooperative Agreement No. M12AC00009 "Arctic Ecosystem Integrated Survey (Arctic Eis)". Some Chukchi Sea crab samples were also collected through the Russian-American Long-Term Census of the Arctic (RUSALCA) cruise and as such, this publication is the result in part of research sponsored by the Cooperative Institute for Alaska Research with funds from the National Oceanic and Atmospheric Administration under cooperative agreements NA13OAR4320056 and NA08OAR4320870 with the University of Alaska. Snow crab data also were provided by the Arctic Marine Biodiversity Observing Network (AMBON) program in 2015, funded through the NOS Integrated Ocean Observations Systems with contributions from NOAA, BOEM and Shell Industry (award number NA14NOS0120158). Snow carb data provided during the 2014 and 2015 Arctic Nearshore Impact Monitoring in Development Area (ANIMIDA) program was funded through BOEM M13PC00019.

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Table 3.1. Cruise data showing the timing of sampling, project name, gear type used, and data provided for the current study. PSBT= plumb staff beam trawl, EBT= Eastern bottom trawl. Major funding sources indicated by superscripts.

Month/ Year	Project	Gear Type	Data Provided
Chukchi Sea			
Aug 2004	RUSALCA-1 [a]	PSBT	Biomass, abundance, size frequency
Aug 2007	Oscar Dyson [a]	PSBT	Biomass, abundance
Aug 2008	Oshoru Maru IPY [b]	PSBT	Biomass, abundance
Aug 2009	RUSALCA-2 [a]	PSBT	Biomass, abundance, size frequency, fecundity
Aug 2009	COMIDA [c]	PSBT	Biomass, abundance
Aug 2010	COMIDA [c]	PSBT	Biomass, abundance, size frequency, fecundity
Sept 2010	CSESP [d]	PSBT	Biomass, abundance, size frequency
Aug-Sept 2010	AKMAP [e]	PSBT	Biomass, abundance, size frequency
Sept 2011	AKMAP [e]	PSBT	Biomass, abundance, size frequency
Aug 2012	RUSALCA-3 [a]	PSBT	Biomass, abundance, size frequency, fecundity
Aug-Sept 2012	Arctic Eis [c]	PSBT, EBT	Biomass, abundance, size frequency, fecundity, size-at-maturity
Aug-Sept 2015	AMBON [a,c,d]	PSBT	Biomass, abundance, size frequency
Beaufort Sea			
Aug-Sept 2008	Western Beaufort Fish Survey [c]	EBT	Biomass, abundance
Aug-Sept 2011	BeauFish Survey [c,f]	PSBT	Biomass, abundance, size frequency
Sept 2012	Transboundary [c]	PSBT	Biomass, abundance, size frequency
Aug-Sept 2013	Transboundary [c]	PSBT	Biomass, abundance, size frequency
Aug-Sept 2014	Transboundary [c]	PSBT	Biomass, abundance, size frequency
Aug 2014	ANIMIDA [c]	PSBT	Biomass, abundance, size frequency
Aug 2015	ANIMIDA [c]	PSBT	Biomass, abundance, size frequency

Major funding sources: [a] NOAA: National Oceanographic and Atmospheric Administration; [b] Japanese Funding,

[c] BOEM: Bureau of Ocean Energy Management (in 2008 as Minerals Management Service), [d] Oil Industry (Shell Oil, Concoco Phillips, and/or Statoil), [e] DEC: Department of Environmental Conservation, [f] CMI: Coastal Marine Institute.

Table 3.2. Estimates of total and harvestable biomass in the Chukchi and Beaufort seas as determined in the Arctic FMP (NPFMC 2009) and based on the revised estimates (this study) for snow crabs. B_0= pristine or unfished biomass, B(F|r)= equilibrium fished biomass, Y(F|r)= equilibrium yield, F_{MSY}= Fishing mortality at maximum sustainable yield (MSY), B_{MSY}= biomass at MSY, mt= metric tons.

Parameter	**Arctic FMP**	**This study**
Total B_0 (Chukchi Sea)	66,491mt	3,461 mt
Total B_0 (Beaufort Sea)	29,731mt	15,656 mt
Harvestable B_0 (Chukchi Sea)	0 mt	0 mt
Harvestable B_0 (Beaufort Sea)	6,571 mt	1,722 mt
B(F|r)	2,891 mt	3,527 mt
Y(F|r)	1041 mt	1,255 mt
F_{MSY}	0.36	0.36
B_{MSY}	1041 mt	272 mt
MSY	453 mt	97 mt
B_{MSY}/B_0	0.19	0.16
MSY/B_0	0.06	0.06

Table 3.3. Parameters used to establish selectivity for EBT and PSBT by minimizing the difference between the EBT and PSBT in the predicted proportions of snow crabs in each width bin. Parameter *a* is crab size (mm CW) at 50% selectivity, and parameter *b* is the steepness of the curve.

Parameters	EBT	PSBT
a	31.32	120.00
b	-0.32	0.57

Table 3.4. Mean eggs per clutch scaled to snow crab body size (carapace width, CW) and proportion of female snow crabs at each CW as determined from female size-at-maturity in the present study for the range of mature females observed in the Chukchi Sea (38 to 78 mm CW).

CW (mm)	mean # eggs per clutch	proportion mature
38	7,092	0.19
39	8,231	0.22
40	9,505	0.25
41	8,917	0.29
42	13,258	0.33
43	12,489	0.37
44	12,307	0.41
45	13,188	0.46
46	14,765	0.50
47	16,167	0.55
48	15,592	0.59
49	16,339	0.63
50	17,387	0.67
51	20,363	0.71
52	21,282	0.75
53	22,380	0.78
54	21,700	0.81
55	23,223	0.83
56	24,441	0.86
57	27,881	0.88
58	26,138	0.90
59	16,105	0.91
60	36,477	0.93
61	34,044	0.94
62	31,611	0.94
63	33,720	0.95
64	31,923	0.96
65	42,597	1.00
66	36,267	1.00
67	37,342	1.00
68	38,416	1.00
69	39,491	1.00
70	40,566	1.00
71	41,641	1.00

72	42,716	1.00
73	43,790	1.00
74	44,865	1.00
75	45,940	1.00
76	47,015	1.00
77	48,090	1.00
78	49,164	1.00

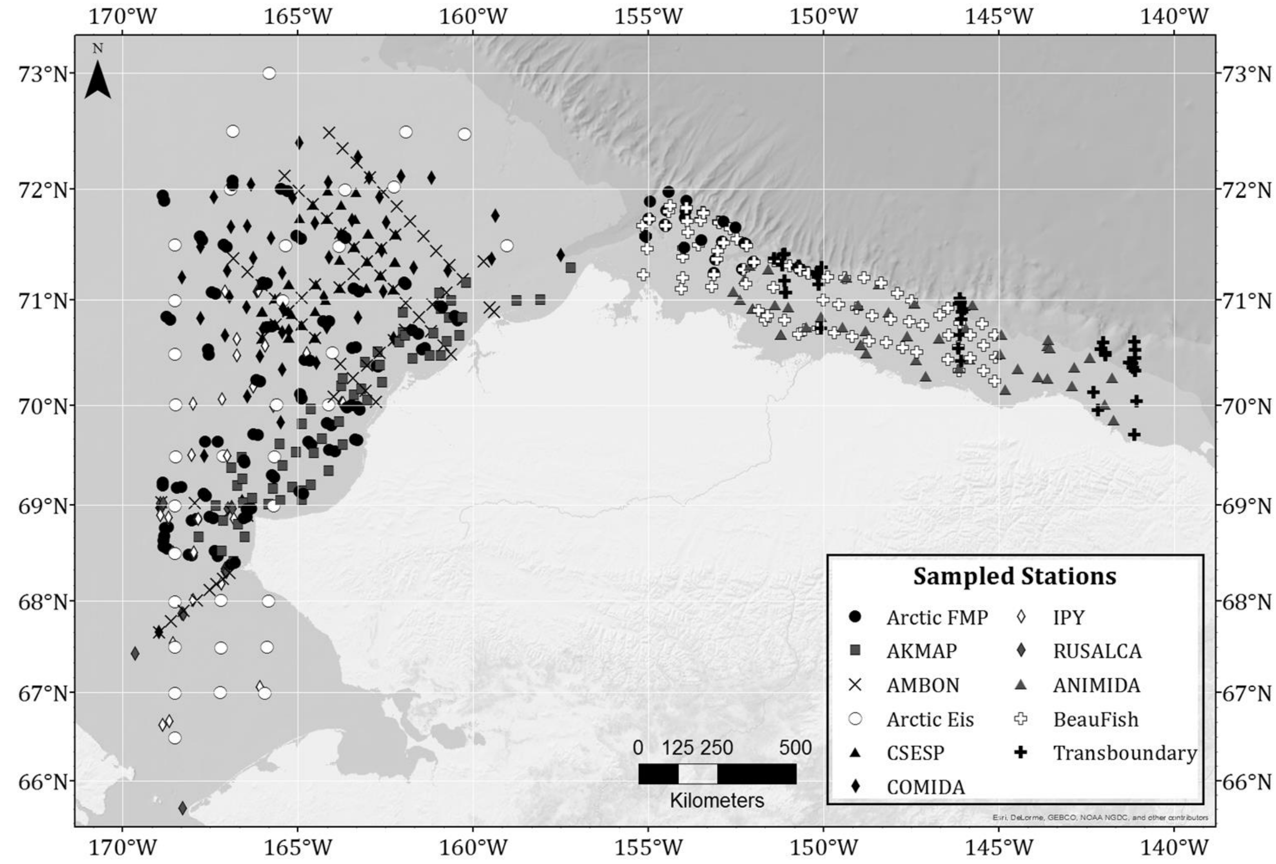

Figure 3.1. Stations sampled on the Alaska Chukchi and Beaufort Sea shelves from 2004 to 2015. Stations denoted as black circle data points occurring in the Chukchi and Beaufort seas are stations that contributed to biomass estimates in the Arctic FMP (Barber et al. 1994, NPFMC 2009, Rand and Logerwell 2011). White gridded lines at 1°latitude and 1°longitude are provided as reference for station groupings that were pooled at this level for the Chukchi region to account for temporal and spatial variability in area coverage.

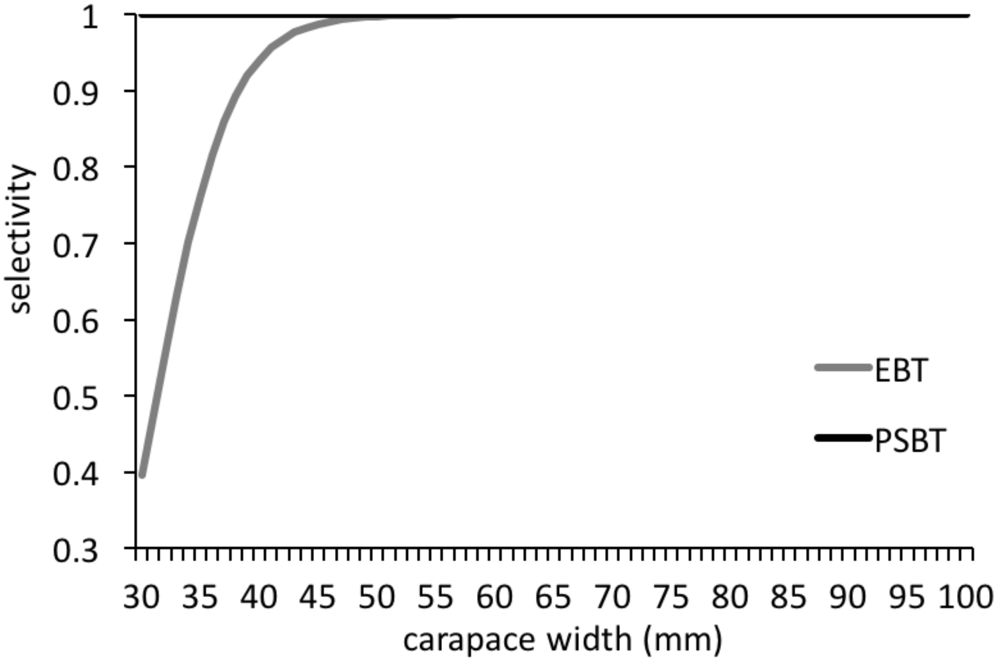

Figure 3.2. Selectivity for two gear types: the Eastern Bottom Trawl (EBT) and the Plumb Staff Beam Trawl (PSBT) during the Arctic Eis 2012 bottom trawl cruise for the range of snow crab carapace widths captured.

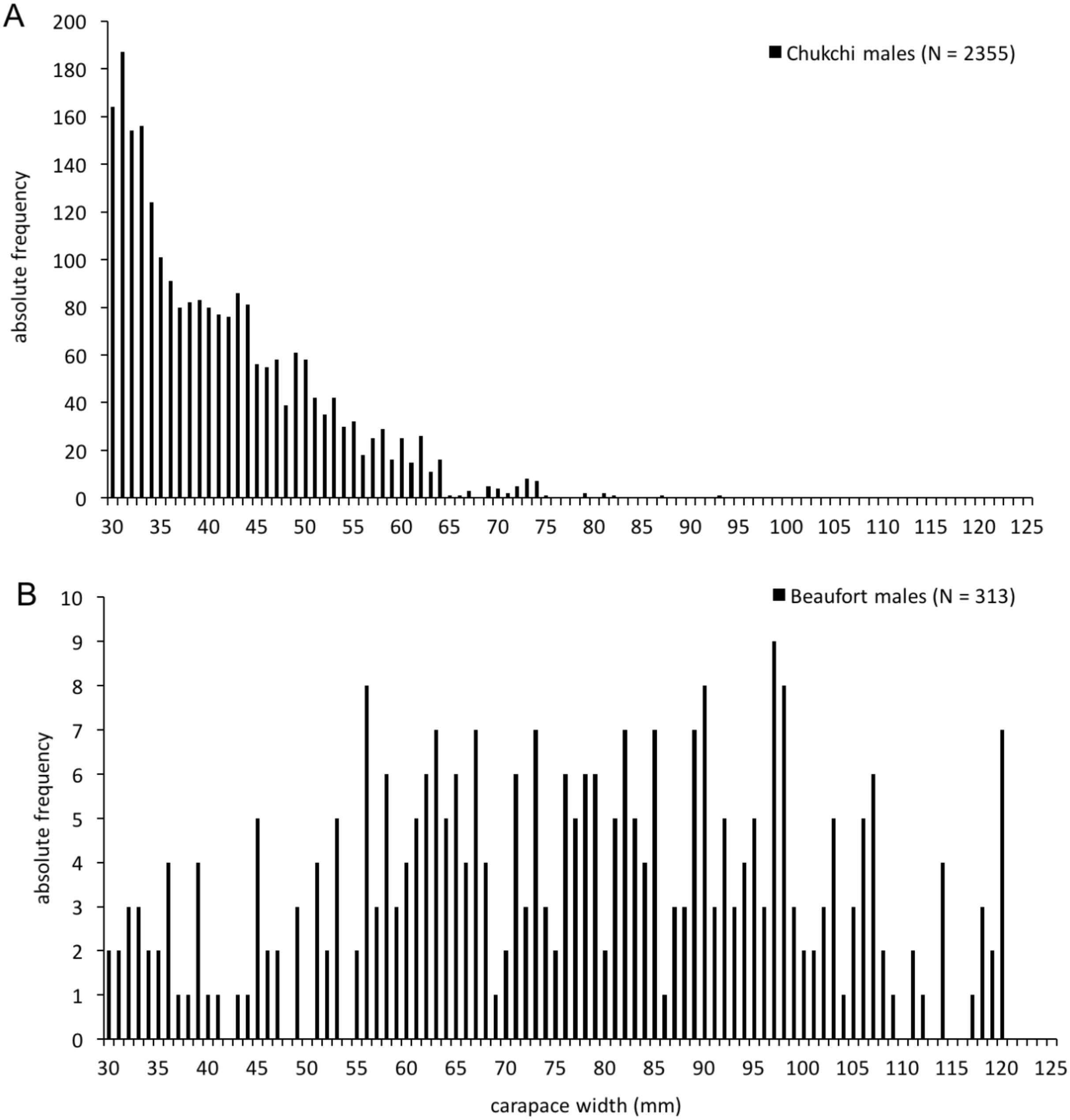

Figure 3.3. Size frequency distributions for males ≥ 30 mm CW in the A) Chukchi collected from 2004 to 2015 and B) Beaufort Seas collected from 2008 to 2015. Note the different scales of the y-axes.

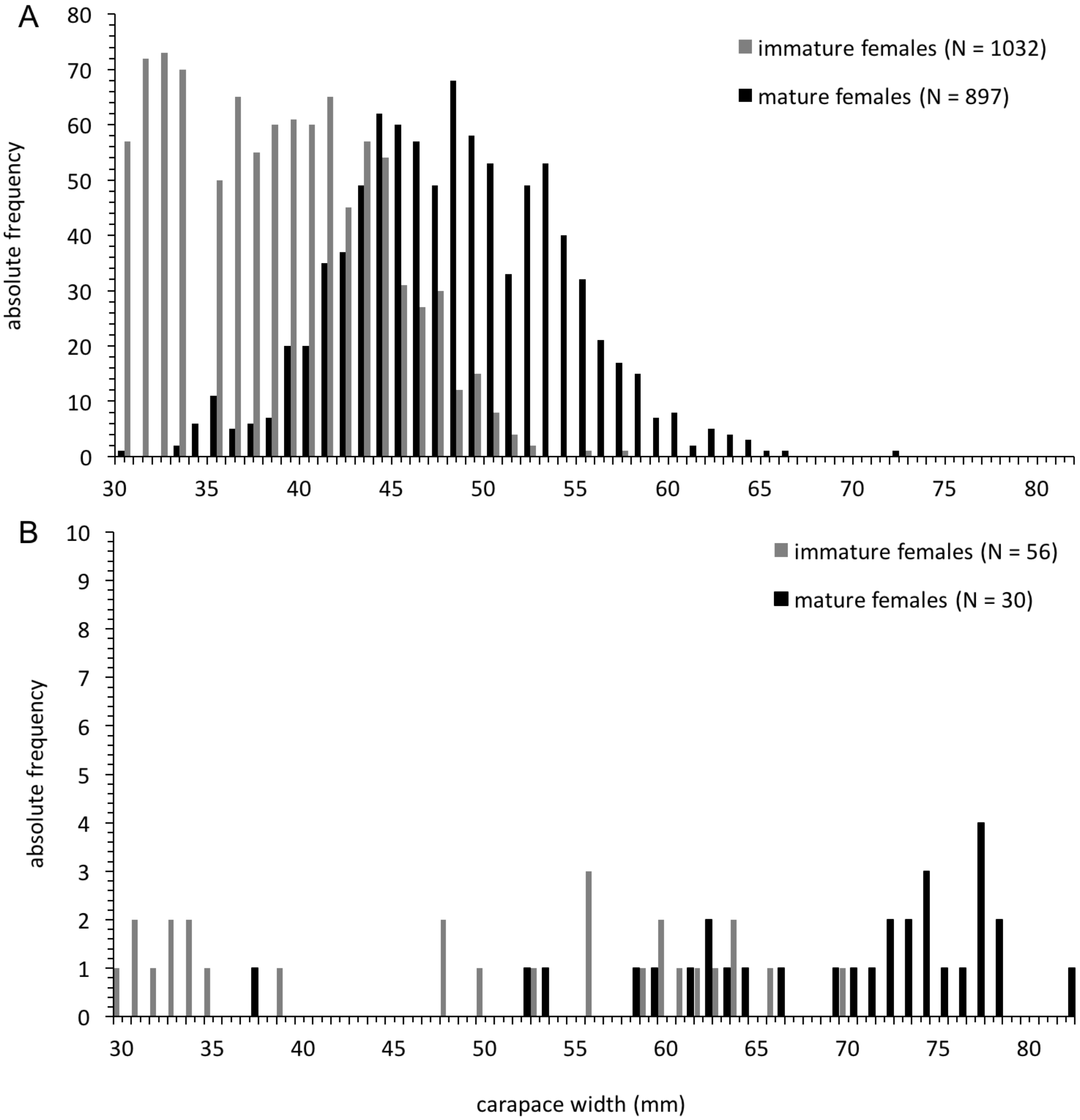

Figure 3.4. Size frequency distributions for immature and mature females ≥ 30 mm CW (A) in the Chukchi Sea collected from 2004 to 2015, and (B) immature and mature females collected in the Beaufort Sea from 2008 to 2015. Note the different scales of the y-axes.

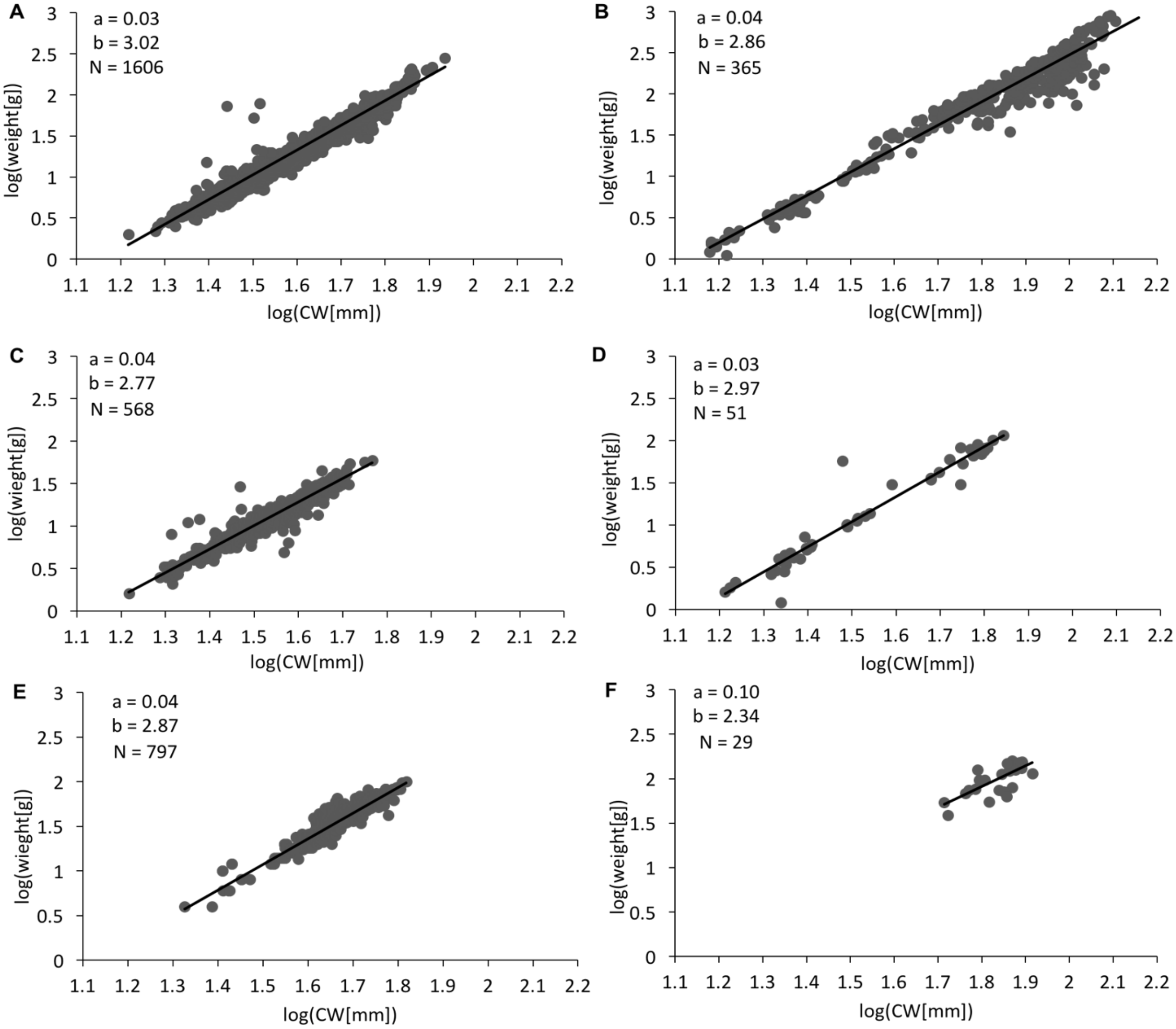

Figure 3.5. Linear regressions showing the length-weight relationships of A) Chukchi Sea males, B) Beaufort Sea males, C) Chukchi immature females, D) Beaufort Sea immature females, E) Chukchi mature females and F) Beaufort Sea mature females (estimated from snow crabs collected from 2004 to 2015). Parameters (*a* and *b*) and sample sizes (N) are presented in the respective figures.

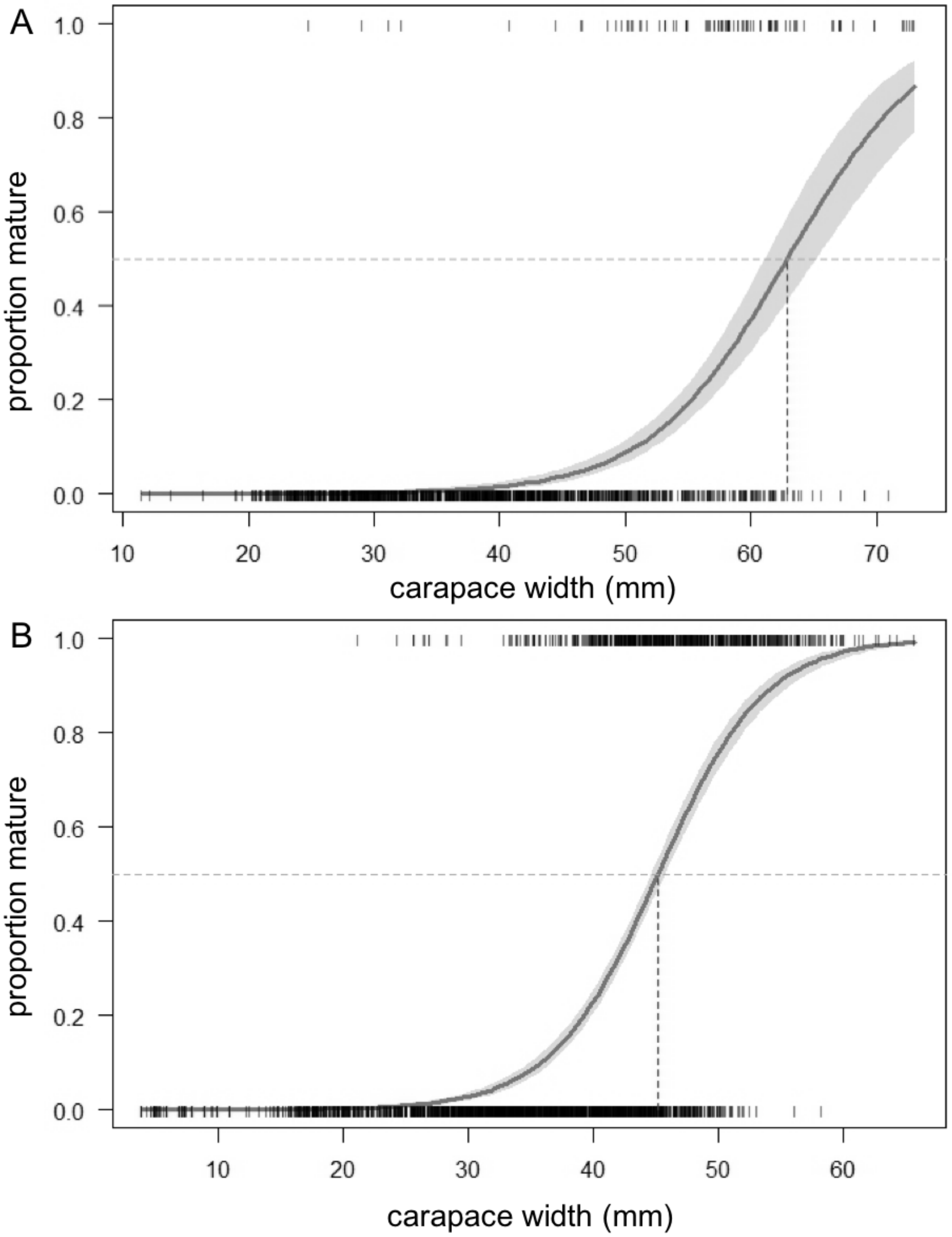

Figure 3.6. Size-at-maturity (dark gray solid lines) with 95% confidence intervals (light gray shaded areas) for (A) males and (B) females estimated from snow crabs collected in the Chukchi Sea. Size at which 50% of all crabs are mature is denoted at the intersection of the gray dashed lines. Short black lines at top and bottom of graphs indicates individual snow crabs that are either mature (top lines) or immature (bottom lines).

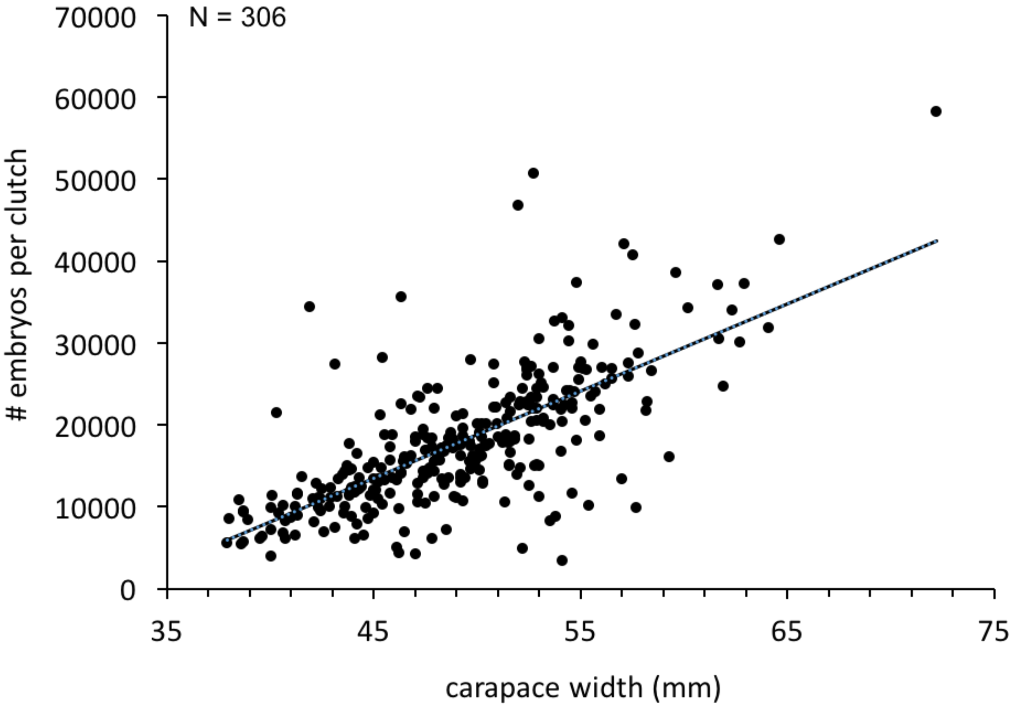

Figure 3.7. Fecundity as number of eggs plotted against body size (carapace width) per mature female snow crab collected from the Chukchi Sea from 2009 to 2012. Number of embryos in a clutch= 1,063.7 · CW – 34,379, r^2= 0.50 (linear regression fit), p< 0.0001.

Appendix G.

Saffron cod population structure

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Date
August 31, 2017

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
C	Carbon
N	Nitrogen
ACW	Alaska Coastal Water
BCSW	Bering Chukchi Summer Water
MW	Melt Water
CWW	Chukchi Winter Water
SIA	Stable Isotope Analysis

Authors: A.J. Gharrett, N. Sme

List of Oral and Poster Presentations

Sme, N. and A.J. Gharrett. Population genetic structure of Saffron Cod. Arctic Eis PI Meeting. June 2014. Juneau, Alaska.

Proposed Objectives and Study Chronology

The saffron cod is abundant in Alaskan Arctic waters and an important component of the Arctic ecosystem (Wolotira 1985). However, the species is little studied, especially in North American waters. It is a commercially valuable species in Asia and its potential commercial value (NPFMC 2009) and importance as prey for several marine mammals (Bluhm and Gradinger 2008) dictate a need to learn more about the species. The geographic structure of populations, or, for continuously distributed species, the scale of a species' basis for production is important to both conservation and management and to understanding responses to anthropogenic disturbances. That geographical scale is often referred to as its intrinsic scale and is related to the scale of lifetime dispersal of a species. The extent of dispersal of a species determines the amount of genetic divergence that occurs over geographical distance. Consequently, the geographic elements of management should focus on intrinsic structure as determined by genetic divergence as well as by practical geographic features. Here we describe work that will provide information about the genetic structure of saffron cod and will enhance our understanding of the biology and life history of the species. To accomplish those objectives we will: (1) develop genetic markers for saffron cod, (2) determine geographic scale of genetic divergence, which will include evaluation of reference collections distal to the Arctic and Bering Sea collections, (3) describe the genetic population structure and seascape genetics of saffron cod in the Pacific sector of the subarctic and Arctic oceans, with a particular focus on the Chukchi Sea, and (4) ensure that saffron cod in the Alaskan Arctic does not also include the congener nawaga (*E. nawaga*). This work will produce two manuscripts that will be submitted for publication. The first manuscript (below) addresses objectives (1) and (4). Specifically, it describe the genetic markers that were developed for population study of saffron cod and its differences from nawaga and other cods northern Pacific Ocean cods [Pacific cod (*Gadus macrocephalus*), walleye pollock (*G. chalcogrammus*), Pacific tomcod (*Microgadus proximus*), Arctic cod (*Boreogadus saida*)]. The second manuscript will address objectives (2) and (3) and is expected to be N. Sme’s M.S. thesis. It will be submitted to Bureau of Ocean and Energy Management (BOEM) upon completion.

A version of this report was submitted to Fishery Bulletin and is currently in revision as:

Noel Sme, Sarah Lyon, Michael Canino, Natalia Chernova, Jason R. O’Bryhim, Stacey L. Lance, Kenneth L. Jones, Franz Mueter, and Anthony J. Gharrett (In revision). The first Identification of saffron cod (*Eleginus gracilis*) and its distinction from several other gadid species by microsatellite differences. Fishery Bulletin.

Abstract

Nine microsatellite loci were isolated in saffron cod (*Eleginus gracilis*) for potential population genetic applications. The loci amplified reliably with PCR, produced only one or two microsatellite bands, and had no apparent homozygote excess in northwestern Alaska *E. gracilis* samples. A collection of *E. gracilis* sampled in the Gulf of Alaska (GOA) near Kodiak Island did not reliably amplify at one locus and had allele frequency profiles that produced a principal components analysis (PCA) cluster distinct from the northwestern Alaska collection. There was genetic divergence between the northwest Alaska and GOA *E. gracilis* collections ($G'_{ST} = 0.313$, $D_{chord} = 0.078$, $P < 10^{-6}$) and differences in their expected average heterozygosities over their shared loci (0.859 and 0.689, respectively). We then tested the microsatellite primers on five other gadid species endemic to the northern Pacific Ocean, Bering Sea, and Arctic Ocean for cross-species amplification. Not all nine loci amplified reliably in *E. nawaga*, *Microgadus proximus*, *Boreogadus saida*, *Gadus macrocephalus*, or *G. chalcogrammus*. Reliable loci varied in microsatellite size profiles and produced distinct PCA clusters and accurate genotype assignments that allowed accurate species identification. The identifications supported the systematic classification based on previous morphological and genetic studies and separated the two geographically-separated collections of *E. gracilis*.

1. Introduction

The saffron cod (Eleginus gracilis) is a gadid distributed from the northern Gulf of Alaska, around the Pacific Rim into the Sea of Okhotsk and into the Arctic Ocean abutting the North Pacific Ocean (Cohen et al., 1990, Mecklenburg et al., 2016). Mature fish, which generally exceed 20 cm and may grow to more than 50 cm, are eaten by indigenous Alaskans and in Asia and have potential for commercial harvest in North America (Cohen et al., 1990; NPFMC, 2009; Love et al., 2016;). Saffron cod is an important component of the Arctic ecosystem (Wolotira, 1985; Copeman et al., 2016; Love et al., 2016). It is a significant prey item for several marine mammals (Bluhm and Gradinger, 2008). Because it is thought to compete for food with Arctic cod (Boreogadus saida), it may have a competitive advantage as sea ice changes occur in response to climate change (Love et al., 2016). The species is little studied, especially in North American waters, but its position in the food web, potential population responses to warming and reduction of sea ice in the Arctic, and proposed offshore oil and gas development make learning more about the species imperative.

The distributions of several other gadid species – Arctic cod (B. saida), Pacific cod (Gadus macrocephalus), walleye pollock (Gadus chalcogrammus), and Pacific tomcod (Microgadus proximus) – overlap with that of E. gracilis, and nawaga (Eleginus nawaga) from the western Arctic Ocean is a congener of *E. gracilis*. Small gadids of several species are very similar morphologically and often present challenges for identification.

The morphological bases of Gadiform taxonomy, including the subfamily Gadinae to which all of the species in our study belong, have been described (e.g., Schultz and Welander, 1935; Svetovidov, 1948; Cohen, 1989), as have the phylogenetic relationships among Gadiform families (e.g., Roa-Varón and Ortí, 2009) and within Gadinae (Teletchea et al., 2006). Questions remain about the relationships among *E. gracilis*, *E. nawaga*, and *M. proximus* (e.g., Carr et al., 1999; Roa-Varón and Ortí, 2009). Moreover, the modern geographic separation between *E. eleginus* and *E. nawaga*, if any exists, is unknown.

Genetic analyses of a species can provide insight into several facets of its biology, including population structure, life history (e.g. Kamin et al., 2014), and recent demographic history (e.g. Harpending et al., 1998). Population genetic information can be obtained from geographically-based surveys of microsatellite variation. Microsatellites have benefits as compared to other classes of molecular markers in that they are often highly polymorphic in fishes (de Woody et al. 2000) and are relatively inexpensive to apply. Consequently, microsatellite markers were isolated from and developed for *E. gracilis*. Here we (1) examine their variability in two *E. gracilis* collections from geographically separated areas; (2) determine their cross-reactivity with other northern Pacific and Arctic ocean gadids and the ability of suites of these loci to accurately distinguish among them; and (3) evaluate differences in the allele profiles among *M. proximus*, *E. nawaga*, and the two collections of *E. gracilis*.

2. Materials and methods

2.1 Samples and DNA isolation

Samples of muscle tissue of *E. gracilis*, *E. nawaga*, *M. proximus*, *G. macrocephalus*, *G. chalcogramma*, and *B. saida* were collected for analysis and comparison (Table 1). Tissue samples were preserved in a DNA preservative solution (Seutin et al., 1991) or 95% ethanol and stored in the lab at -20°C. Total cellular DNA was isolated with Puregene^{TM} or Qiagen DNeasy^{TM} kits (Qiagen, Valencia, CA) following manufacturer's instructions.

2.2 Microsatellite discovery

An Illumina paired-end shotgun library was prepared by shearing 1 µg of DNA from a single *E. gracilis* Chukchi Sea individual with a Covaris S220 focused ultrasonicator (**Covaris, Inc.,** Woburn, MA). The standard protocol for the Illumina TruSeq DNA Library Kit (Illumina, Inc., San Diego, CA) and a multiplex identifier adaptor index were used (see e.g. Stoutamore et al., 2012). An Illumina HiSeq System was used to sequence 100 bp paired-end reads. The program *PAL_FINDER_v0.02.03* (Castoe et al., 2012) analyzed $5*10^6$ of the resulting sequences to identify reads that had di-, tri-, tetra-, penta-, and hexanucleotide repeat motifs. The data are archived in the NCBI Sequence Read Archive (SRA) under accession number SAMN06333955. Once positive reads were identified, oligonucleotide primers were designed with the program Primer3 (version 2.0.0). To avoid issues with copy number of primer sequences in the genome, loci for which the primer sequences occurred only once or twice in the 5 million reads were selected. Forty-eight presumed loci from *E. gracilis* that met this criterion were chosen for primer design.

The 48 primer pairs were tested with DNA from 8 *E. gracilis* individuals. The polymerase chain reactions (PCR) were conducted over two 10°C spans of annealing temperatures (65-55°C or

58-48°C) with touchdown thermal cycling profiles (Don et al., 1991). The results (not presented) were analyzed with GeneMapper version 3.7 (Applied Biosystems). Eighteen primer pairs were then selected for evaluation with larger sample sizes.

2.3 Microsatellite analysis

Target sequences of the 18 primer pairs amplified with a touchdown PCR strategy reduced non-target bands in the product spectrum (Don et al., 1991). All reactions contained ~1 unit Taq polymerase, 1X PCR buffer (50 mM KCl_2, 10 mM Tris-HCl pH 9.0, 0.1% Triton X 100; Promega™, Madison, WI), 0.5 µM deoxyribonucleotide triphosphates, and 0.025 to 0.1 µM DNA template. Fluorescent primers labeled with an IRDye® infrared dye (10 µg/ml; IDT, Coraleville, IA) were included in the reactions. The amplification profiles for each locus were: denaturation at 95 °C for 5 min; 20 touchdown cycles at 95 °C for 30 s, annealing temperatures ranging from 62-52 °C (touchdown) for 30 s (decreased 0.5 °C per cycle), and 72 °C for 30 s; then 15 cycles of 95 °C for 30 s, the lowest annealing temperature (55°C) for 30 s, and 72 °C for 30 s, and a final extension at 72 °C for 5 min.

Approximately 1 µl of amplified PCR product and stop buffer (95% formamide, 0.1% Bromophenol Blue) was loaded onto a 0.25 mm 6% acrylamide gel (PAGE-PLUS™, Amresco®, Solon, OH) and fragments were separated in 1X TBE buffer (0.09 M Tris-Borate, 2 mM EDTA, pH 8) at 1500 V with a LI-COR 4300 DNA Analyzer™ (Lincoln, NE). Electrophoresis times varied from 2 to 3 hours depending on allele sizes of the PCR product. The image of the PCR product was analyzed with SAGA™ v.3.1 (LI-COR) software. Two individuals scored each gel separately and discrepant samples in recorded allele size were genotyped a second or third time.

2.4 Data analysis

Two collections of *E. gracilis* (one from the Chukchi Sea and another from near Kodiak Island, Alaska) were examined separately (Table 1). Collections of *B. saida* from the Chukchi Sea were combined for analysis as a single species as were collections of *M. proximus* (Prince William Sound and Puget Sound), and of *G. macrocephalus* (Puget Sound and Unimak Pass) (Table 1).

Allele frequencies and expected unbiased heterozygosities were estimated and genotype frequencies were tested for departures from Hardy-Weinberg expectations with GENEPOP V.4.5.1 (Rousset, 2008). Significance of multiple tests was confirmed with sequential Bonferroni tests (Rice, 1989) and false discovery rate (FDR; Benjamini and Hochberg, 1995) corrections. Genotypes of individuals that produced deviations from Hardy-Weinberg expectations or apparent principal components analysis (PCA) outliers were reconfirmed by additional genotyping.

Two commonly used genetic distances that are not strongly influenced by the numbers of alleles at a locus, but that are based on very different algorithms were used. The standardized genetic differentiation measure G'_{ST} (Hedrick, 2005), based on ratios of heterozygosities adjusted to account for the amount of genetic variation observed at each locus, was estimated with the program SMOGD (Crawford, 2010). Estimates of chord distances (Cavalli-Sforza and Edwards, 1967), a geometric measure, were made with PHYLIP (Felsenstein 2005).

Principal components analysis was used to contrast the genetic compositions of species groups (SYTAT v.13 software; SYSTAT Software Inc., Richmond, CA). Correlation matrix-based PCA standardizes variables so that each variable has a similar scale; it was used to contrast which alleles occurred in each species. Covariance matrix-based PCA applies the observed variances so that the scale of variation is included in the analysis; it was used to contrast allele frequency profiles. Loci missing from a collection or a species did not contribute to the PCA score.

Assignment tests (GeneClass2; Piry et al., 2004) were used to evaluate the robustness of the differences among species groups. The tests removed each individual from the species groups before assignment. The tests applied the criterion of Rannala and Mountain (1997).

3. Results

Only genotypes from loci that could be reliably interpreted were analyzed in each species. Nine loci both amplified reliably and had no apparent homozygote excess in *E. gracilis* (Table 2; Supplemental Table 1). However, not all that were reliable in *E. gracilis* amplified consistently and produced just 1 or 2 bands in all sets of samples. Most notably, Elgr38 did not reliably amplify Gulf of Alaska (GOA) *E. gracilis* samples, nor was it reliable in *E. nawaga*. In addition, only 7 of the 9 loci worked well in *M. proximus* and only 5 in either *G. chalcogramma* or *B. saida*. Most notably, Elgr38 did not reliably amplify in the Gulf of Alaska (GOA) *E. gracilis* samples nor was it reliable in *E. nawaga*. In addition, only 7 of the loci worked well in *M. proximus* and only 5 in each of *G. chalcogramma* and *B. saida*. Of the loci that did not amplify reliably for a species group, several did produce bands. Only the loci that could be reliably interpreted were analyzed in each species.

3.1 Comparisons among gadid collections

Differences in allele size ranges differentiated species and species groups (Table 2, Supplemental Figure 1). For example, alleles at Elgr38 averaged much larger for *B. saida* and *G. chalcogrammus* than for the others; alleles at Elgr31 averaged larger for *B. saida* and alleles at Elgr23 averaged larger for *G. macrocephalus* and *G. chalcogramma*. The divergences in allele frequency size ranges were reflected in values of D_{chord} and G'_{ST} (Table 3), all of which were significant (adjusted pairwise homogeneity tests $P < 10^{-6}$). The estimate of G'_{ST} between the two *E. gracilis* collections was smaller than values of all other gadid pairs; whereas the estimate of D_{chord} was smaller than all but three of the gadid comparisons, even though different suites of microsatellite loci were used. To provide a comparison of the extent of divergence between the two *E. gracilis* collections, values of G'_{ST} and D_{chord} were estimated for the species pair *Sebastes aleutianus* and *S. melanostictus* from data in Gharrett et al. (2005), $G'_{ST} = 0.551$ and $D_{chord} = 0.064$. The estimate of G'_{ST} between the *E. gracilis* pair was lower (0.313) but the estimate of D_{chord} was higher (0.078) than that between *S. aleutianus* and *S. melanostictus*, presumably because different algorithms were applied; D_{chord} has a geometric basis and G'_{ST} is based on ratios of heterozygosities adjusted to account for the amount of genetic variation observed at each locus (Hedrick, 2005).

Individual-based principal components analysis (PCA) of allelic compositions (correlation matrix) and allele frequency profiles (covariance matrix) produced both species- and collection-specific clusters (Figure 1). The plot of the first and second components of the correlation-based PCA separated individual species more clearly, but separation of the two *E. gracilis* collections was not as strong. The covariance-based PCA clearly separated the two *E. gracilis* collections, but the other species were not separated quite as well. The first five components of the correlation-based analysis accounted for 10.6% and the first two components accounted for 5.1% of the overall variation in allelic composition. In contrast, the first five components of the covariance-based PCA accounted for 24.3% and the first two for 14.1% of the overall variation in allelic frequencies. Nevertheless, sufficient variation existed to separate these species and the two *E. gracilis* collections.

A series of four tests was needed to estimate assignments of individuals because not all loci could be used for all species groups (Supplemental Table 2). The tests were: (1) all individuals were assigned based on the three loci all groups had in common – Elgr14, Elgr23, and Elgr31; (2) the individuals scored in (1) as Chukchi Sea *E. gracilis* (CSC), GOA *E. gracilis* (GSC), *E. nawaga* (NAW), *M. proximus* (PTC), and *G. macrocephalus* (PCO) were assigned based on Elgr7, Elgr11, Elgr13, Elgr14, Elgr23, and Elgr31; (3) the individuals scored in (2) as CSC, GSC, or NAW were tested based on Elgr7, Elgr11, Elgr13, Elgr14, Elgr23, Elgr31, Elgr44, and Elgr45; and (4) the individuals scored in (1) as PTC, PCO, *G. chalcogrammus* (WPO), or *B. saida* (ACO) were tested at Elgr14, Elgr23, Elgr31, and Elgr38. The results of (3) and (4) assigned each individual to its own group except for 1 CSC (96.7% of the total) and 1 ACO (98.1% of the total) (Table 4).

Previous molecular studies recognized *G. macrocephalus*, *G. chalcogrammmus*, and *B. saida* as distinct species (Coulson et al., 2006, Carr et al., 2008) but the systematic relationships among *E. gracilis*, *E. nawaga*, and *M. proximus* are still unresolved (Mecklenburg et al., 2016). Differences in the allele frequency profiles are easier to see in plots that include only those four groups (Table 2, Supplemental Figure 2). The *M. proximus* and *E. nagawa* distributions clearly differ from those of the 2 *E. gracilis* collections at Elgr07 and Elgr11. *M. proximus* also differs at Elgr13 and Elgr31 and has a substantially higher number of large alleles. The numbers of observed alleles (Table 2) in the GOA *E. gracilis* collection are relatively lower than those of the others and several are more abundant (Supplemental Figure 2), which is consistent with the somewhat lower heterozygosity (Table 2) of the GOA *E. gracilis*.

4. Discussion

Eight of the nine microsatellites that were evaluated for two *E. gracilis* collections amplified reliably, were variable, (heterozygosities 0.537 to 0.933), and had no apparent homozygote excess, indicating low null allele frequencies. The single exception, Elgr38, amplified reliably in the Chukchi Sea collection of *E. gracilis* but not in the GOA collection. At the other loci, the two collections had similar allele size ranges but differed substantially in allele frequencies (G'_{ST} = 0.313, D_{chord} = 0.078, $P < 10^{-6}$). The observed differences were similar to those between two cryptic rockfish species that had overlapping ranges, *S. aleutianus* and *S. melanostictus*, although they were estimated with different suites of loci. In the PCA plots, individuals from the two collections were mostly distinct from each other, particularly in the analysis of the covariance matrix, which focuses on the allele frequencies rather than allele composition. It is also notable that the PCA analyses included frequency differences of the other gadids analyzed, so differences between the 2 *E. gracilis* collections were evident against the background variation from other species.

Assignment tests placed all but one saffron cod in the group from which it originated. Not all nine microsatellite loci amplified reliably in all of the other gadid species analyzed and some had an excess of homozygotes, most likely as a consequence of null alleles; those loci were not used for assignment tests. Nevertheless, where comparisons were possible, all of the other gadids differed in microsatellite composition ($P < 10^{-6}$) from both *E. gracilis* collections and each other. The correlation matrix-based PCA, in particular, clustered individuals according to species or species geographic groups. The PCA analyses turned out to be valuable in analyzing a large set of putative *E. gracilis* samples because the analysis revealed outliers that, when compared to the other gadids, enabled detection of individuals misidentified as *E. gracilis*. Two notable instances were 14 aberrant genotypes included in a collection of *E. gracilis* from the Chukchi Sea and another 15 in a collection of *E. gracilis* from Prince William Sound. In both instances it was possible to reexamine the individual specimens; the former were re-identified as *B. saida* and the latter as *M. proximus* (Table 1). Both sets of re-identified individuals were included with their correct species in the analyses presented here (designated as '+' and 'x', respectively in Figure 1). Assignment tests correctly reassigned all of the other gadids except one Arctic cod.

In these analyses, the two *E. gracilis* collections, *M. proximus*, and *E. nawaga* collections were all distinct from each other ($P < 10^{-6}$). Their divergences mostly exceeded those observed between *S. aleutianus* and *S. melanostictus* (Gharrett et al. 2005) and each of the collections clustered separately in PCAs. It is notable that misidentified Prince William Sound *M. proximus* individuals were collected at the same site with *E. gracilis*, but were genetically distinct from them. Clearly, some field identifications, even by trained personnel, are challenging (c.f. Teletchea, 2009). It is unlikely that they represent two sympatric populations of a single marine species that are so strongly different genetically. While it could be argued that the genetic differences between *E. nawaga* and both *E. gracilis* collections could result from divergence over the large distance that separates them, the very large divergences in allele frequencies, as well as similar differences in allele size ranges at Elgr11 and Elgr14, are more consistent with their being distinct species. More complete knowledge of the modern Arctic distributions of the two *Eleginus* species, and location of the historic contact zone between them, would contribute to resolving their systematic status, as would independent data, such as mitogenomic sequences of *E. nawaga* and *E. gracilis*, coupled with morphological characters (Teletchea, 2009).

5. Acknowledgements

We thank the captains and crews of the F/V Alaska Knight and the F/V Bristol Explorer. A special thanks to the numerous Arctic Eis scientists that aided in sample collection. E. Munk (NOAA Kodiak), A. Whiting (Native Village of Kotzebue), P. Moran (NOAA Juneau), and R. Heintz (NOAA Juneau), M. Canino (NOAA Seattle), and M. Arimitsu (USGS Juneau) kindly provided some of the samples.Other samples were provided by This study was funded in part by the Bureau of Ocean and Energy Management (BOEM) Award # M12AC00009 and in part with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, U.S. Fish and Wildlife Service, U.S. Department of the Interior (contracts #s: 10-CIAP-010; F12AF00188).

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Table 1: Gadid species, number of samples (*n*), date of collection, and collection locations in this study.

Species	Scientific name	Geographic region	Date	*n*	latitude	longitude
Saffron cod	*Eleginus gracilis*	Chukchi Sea	9/2011	30	66.91 N	162.55 W
		Gulf of Alaska	6-7/2013	41	57.73 N	152.51 W
Nawaga	*Eleginus nawaga*	Barents Sea	7/2013	81	69.04N	57.87 E
Pacific tomcod	*Microgadus proximus*	Puget Sound	3/1997-8/1999	8	47.71N	122.52 W
		Prince William Sound*	7/2012	15	60.87 N	147.19 W
Pacific cod	*Gadus macrocephalus*	Puget Sound	3/2013	5	48.40 N	124.41 W
		Unimak Pass	3/2013	8	54.45 N	164.99 W
Walleye pollock	*Gadus chalcogramma*	SE Bering Sea	9/2015	6	55.67 N	163.33 W
Arctic cod	*Boregadus saida*	Chukchi Sea	4/2012	39	66.90 N	162.59 W
		Chukchi Sea*	4/2012	14	66.90 N	162.59 W

Table 2: Microsatellite properties of northern Pacific rim and Arctic gadid species for microsatellite loci designed for *Eleginus gracilis*. Sample sizes for each species (n), the numbers of different allele observed (n_a), the range of allele sizes, the average and standard error of allele sizes, expected heterozygosities (H_e), and inbreeding coefficients (F_{is}) are given . 'dna' means did not reliably amplify.

		Elgr07						Elgr11					
species	n	n_a	range	mean	SE	H_e	F_{is}	n_a	range	mean	SE	H_e	F_{is}
Chukchi Sea *E. gracilis*	30	10	127 - 175	155.7	1.2	0.867	-0.016	12	208 - 272	222.1	1.7	0.833	0.043
GOA *E. gracilis*	41	7	151 - 179	160.6	0.5	0.683	-0.054	8	204 - 260	214.0	1.3	0.634	-0.117
E. nawaga	81	14	115 - 183	133.7	0.7	0.815	-0.028	21	240 - 336	274.7	1.4	0.877	0.043
M. proximus	22	1	123	123.0	0.0	0.000	-	17	248 - 340	285.8	3.0	0.727	0.230[a]
G. macrocephalus	14	2	115 &131	128.7	1.1	0.286	-0.130	18	192 - 204	202.9	0.6	0.286	-0.072
G. chalcogrammus	6	2	131 &135	133.3	0.6	0.833	-0.667	dna	-	-	-	-	-
B. saida	53	dna	-	-	-	-	-	dna	-	-	-	-	-

		Elgr31						Elgr38					
species	n	n_a	range	mean	SE	H_e	F_{is}	n_a	range	mean	SE	H_e	F_{is}
Chukchi Sea *E. gracilis*	30	6	191 - 211	197.1	0.7	0.833	-0.103	9	112 - 144	127.5	1.1	0.867	-0.026
GOA *E. gracilis*	41	4	191 - 203	194.8	0.5	0.659	-0.015	dna	-	-	-	-	-
E. nawaga	81	11	179 - 231	204.4	0.8	0.864	-0.052	dna	-	-	-	-	-
M. proximus	22	14	215 - 267	240.5	2.0	0.955	-0.027	6	120 - 140	127.9	0.8	0.727	0.068
G. macrocephalus	14	18	223 - 299	263.3	3.7	1.000	-0.034	6	128 - 160	141.9	1.9	0.786	0.037
G. chalcogrammus	6	10	215 - 267	241.7	4.8	1.000	-0.035	7	236 - 276	258.0	4.4	0.833	0.039
B. saida	53	37	223 - 543	355.6	7.6	0.962	0.005	37	252 - 448	348.6	6.3	0.566	0.422[c]

Table 2 (continued).

	Elgr13						Elgr14					
species	n_a	range	mean	SE	H_e	F_{is}	n_a	range	mean	SE	H_e	F_{is}
Chukchi Sea *E. gracilis*	12	230 - 286	251.1	1.3	0.867	0.007	14	322 - 378	347.6	1.7	0.800	0.101
GOA *E. gracilis*	10	226 - 286	254.3	1.4	0.805	0.006	9	330 - 370	345.7	1.1	0.829	-0.007
E. nawaga	19	214 - 286	243.8	1.3	0.926	-0.009	12	318 - 362	329.4	0.7	0.790	-0.010
M. proximus	19	242 - 338	284.5	3.7	0.909	0.040	11	326 -370	340.3	1.6	0.682	0.217
G. macrocephalus	14	250 - 346	314.7	4.3	1.000	-0.093	4	314 - 346	325.6	0.9	0.143	0.667[b]
G. chalcogrammus	dna	-	-	-	-	-	10	330 - 418	364.7	7.2	1.000	-0.035
B. saida	12	206 - 318	250.8	1.0	0.830	-0.064	19	290 - 366	325.5	1.7	0.811	0.121

	Elgr44						Elgr45					
species	n_a	range	mean	SE	H_e	F_{is}	na	range	mean	SE	H_e	F_{is}
Chukchi Sea *E. gracilis*	14	212 - 264	240.9	1.7	0.867	0.057	13	205 - 265	218.8	1.6	0.867	0.0085
GOA *E. gracilis*	7	228 - 272	247.1	1.1	0.537	0.161[a]	4	209 - 221	213.0	0.4	0.683	0.0145
E. nawaga	14	216 - 268	238.4	1.1	0.840	0.079	17	189 - 269	224.5	1.2	0.864	0.0471
M. proximus	dna	-	-	-	-	-	6	197 - 217	204.9	0.8	0.955	-0.077
G. macrocephalus	dna	-	-	-	-	-	dna	-	-	-	-	-
G. chalcogrammus	dna	-	-	-	-	-	dna	-	-	-	-	-
B. saida	dna	-	-	-	-	-	dna	-	-	-	-	-

	Elgr23					
species	n_a	range	mean	SE	H_e	F_{is}
Chukchi Sea *E. gracilis*	15	142 - 202	170.5	1.8	0.933	-0.027
GOA *E. gracilis*	4	162 - 190	168.1	0.4	0.683	-0.181
E. nawaga	17	138 - 214	168.1	1.1	0.926	-0.019
M. proximus	13	138 - 206	161.6	2.4	0.909	-0.044
G. macrocephalus	17	154 - 286	215.0	5.0	0.929	0.034
G. chalcogrammus	11	186 - 318	246.7	12.6	1.000	-0.017
B. saida	23	138 - 258	191.6	2.3	0.660	0.309[c]

[a]$P < 0.05$; [b]$P < 0.01$; [c]$P < 0.001$

Table 3: Estimates of pairwise chord distances (D_{chord}; above the diagonal) and G'_{ST} (below the diagonal); all were significant (adjusted probabilities; $P < 10^{-6}$). Average unbiased expected heterozygosity (H_e) is in italics on the diagonal.

Collection	**A**	**B**	**C**	**D**	**E**	**F**	**G**
A. Chukchi Sea *E. gracilis*	*0.859*	0.078^a	0.076^a	0.138^a	0.189^b	0.218^d	0.076^d
B. GOA *E. gracilis*	0.313	*0.689*	0.130^a	0.183^b	0.245^b	0.296^e	0.0950^e
C. *E. nawaga*	0.414	0.680	*0.863*	0.093^b	0.137^c	0.158^e	0.069^e
D. *M. proximus*	0.603	0.779	0.565	*0.733*	0.182^b	0.228^d	0.088^e
E. *G. macrocephalus*	0.877	0.963	0.822	0.721	*0.633*	0.204^d	0.092^e
F. *G. chalcogrammus*	0.868	0.893	0.739	0.582	0.449	*0.933*	0.087^e
G. *B. saida*	0.599	0.680	0.584	0.781	0.681	0.607	*0.766*

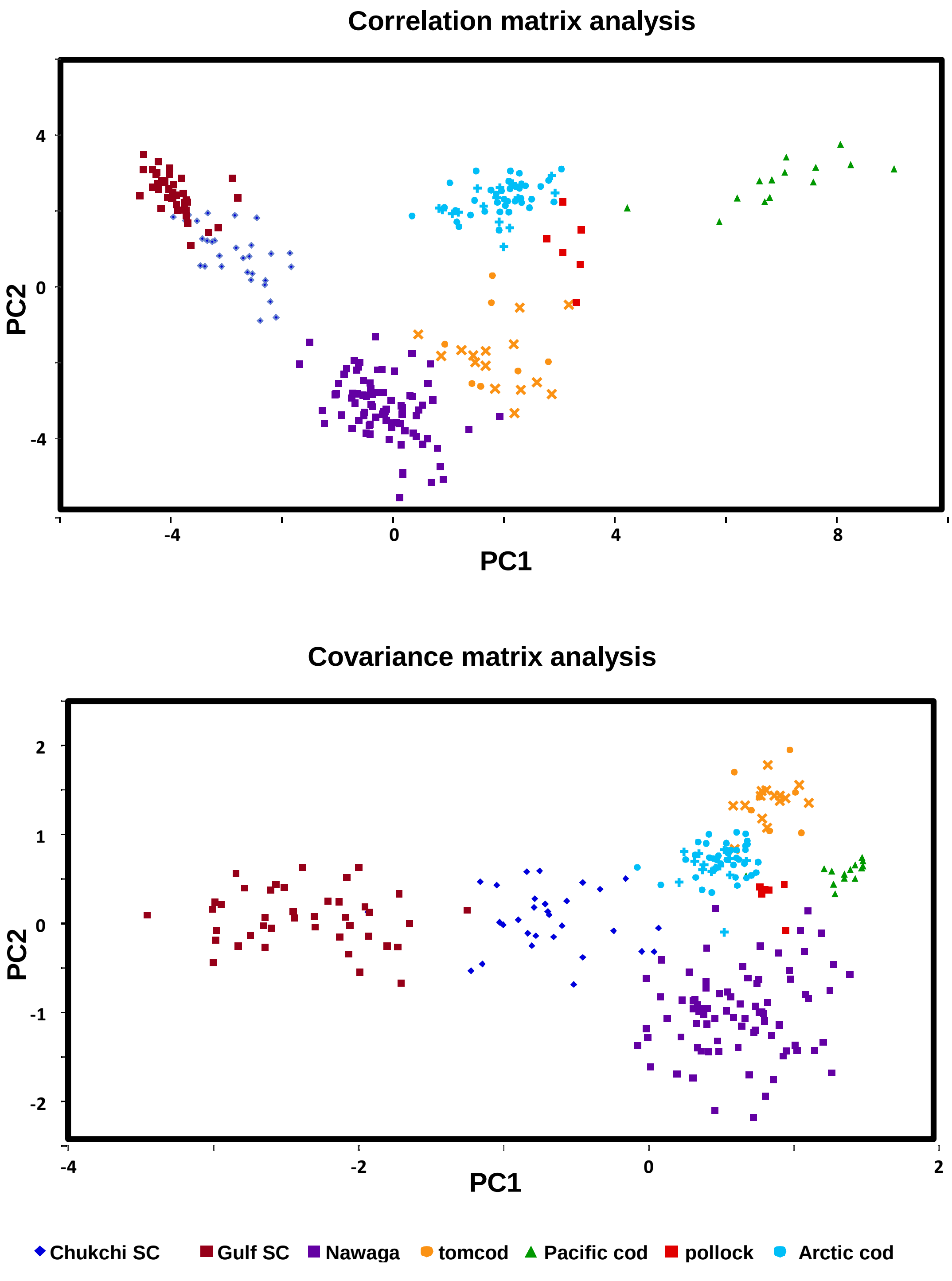
^{a} 8 loci; ^{b} 7 loci; ^{c} 6 loci; ^{d} 5 loci; ^{e} 4 loci for both D_{chord} and G'_{ST} estimates

Table 4: Summary of a series of tests (Piry et al. 2004) that assigned each individual to the species groups – Chukchi saffron cod (CSC); GOA saffron cod (GSC); nawaga (NAW); Pacific tomcod (PTC); Pacific cod (PCO); walleye Pollock (WPO); and Arctic cod (ACO) – in the remaining data (Supplementary Table 2).

		Assigned to:						
n	Species group	CSC	GSC	NAW	PTC	PCO	WPO	ACO
30	CSC	29	1[a]	0	0	0	0	0
41	GSC	0	41	0	0	0	0	0
81	NAW	0	0	81	0	0	0	0
23	PTC	0	0	0	23	0	0	0
14	PCO	0	0	0	0	14	0	0
6	WPO	0	0	0	0	0	6	0
53	ACO	0	0	0	0	0	1[b]	52

[a] 83% GSC/ 17% CSC

[b] 55% PCO/ 44% WPO/ 1% ACO



Correlation matrix analysis

Covariance matrix analysis

Figure 1: Allele composition (correlation-matrix) and allele frequency profiles (covariance-matrix) principle component analyses of walleye pollock (*G. chalcogramma*), Pacific cod (*G. macrocephalus*), Arctic cod (*Boreogadus saida*), Pacific tomcod (*M. proximus*), nawaga (*E. nawaga*), and Chukchi Sea and Gulf of Alaska saffron cod (SC *E. gracilis*) microsatellite data. The symbols '+' and '×' denote individuals provide in *E. gracilis* collections that were later reidentified as arcic cod and Pacific tomcod, respectively.

Supplemental Tables and Figures

The oligonucleotide primer sequences, repeat motifs of the microsatellite loci and estimated expected heterozygosities for Eleginus gracilis are presented in Supplemental Table 1.

Details of the series of assignment tests for the collections of gadids that were analyzed are presented in Supplemental Table 2.

The allele frequencies at 9 microsatellite loci for all 7 gadid collections are plotted in a bar graph to demonstrate graphically the differences in allele compositions (Supplemental Figures 1A and 1B).

The allele frequencies at 9 microsatellite loci are plotted for the 4 gadid collections that are presumably most closely related (Supplemental Figure 2) to accentuate their differences in allele frequency compositions.

Supplemental Table 1: Locus characteristics for 9 polymorphic microsatellite loci developed for *Eleginus gracilis*.

Locus		**Primer Sequence**	**Repeat motif**	n	H_E	F_{is}
Elgr7	F:	5' TCCTCTCTCTGAACACAACACTCC 3'	TCTG	30	0.853	-0.016
	R:	5' ACCAGAGCGGACGAAGGC 3'				
Elgr11	F:	5' AATGCTCCTATTTCAATAGCCC 3'	ATCT	30	0.833	0.043
	R:	5' ATAGTTGCAGCTTTCGCAGG 3'				
Elgr13	F:	5' TGCTGATAGCTGAAGATGGC 3'	TCTG	30	0.867	0.007
	R:	5' ATTTGCTCAGCAGAACATGG 3'				
Elgr14	F:	5' GTGTATTCAAAGCAACGCCG 3'	TCTG	30	0.800	0.101
	R:	5' CAAGCAACACACATCTTCAGTCC 3'				
Elgr23	F:	5' AAGAAGGTATTACCCTGTATAATTGCC 3'	TCTG	30	0.933	-0.027
	R:	5' CCACCTTCAACACGCAGG 3'				
Elgr31	F:	5' TTTGGCAGTCACGTGTGC 3'	AAAG	30	0.833	-0.103
	R:	5' GAGGCAAGAACAGCATCTGG 3'				
Elgr38	F:	5' CAAACCTGGCTCAGGAACG 3'	TCTG	30	0.867	-0.026
	R:	5' GGAAAGAGGAGATCCCTGTGG 3'				
Elgr44	F:	5' TGGCTCATGGTAGAATCGCC 3'	TCTG	30	0.867	0.057
	R:	5' TGGAAAGCCAAAGTTGTACTGC 3'				
Elgr45	F:	5' GAGCACGCGTTTAGCTCC 3'	AGTG	30	0.867	0.009
	R:	5' TTTAAATGGTCGACCTATCACC 3'				

Supplemental Table 2: Results of assignment tests: A. All specimens were tested with Elgr14, Elgr23, and Elgr31. B. Individuals scored as Chukchi saffron cod (CSC), GOA saffron cod (GSC), nawaga (NAW), Pacific tomcod (PTC), or Pacific cod (PCO) in A. were tested at Elgr7, Elgr11, Elgr13, Elgr14, Elgr23, and Elgr31. C. Individuals scored as CSC, GSC, or NAW in B. were tested at Elgr7, Elgr11, Elgr13, Elgr14, scored as CSC, GSC, or NAW in B. were tested at Elgr7, Elgr11, Elgr13, Elgr14, Elgr23, Elgr31, Elgr44, and Elgr45. D. Individuals scored as PTC, PCO, walleye pollock (WPO), or Arctic cod (ACO) in A. were tested at Elgr14, Elgr23, Elgr31, and Elgr38.

A		Assigned to:						
n	Species group	CSC	GSC	NAW	PTC	PCO	WPO	ACO
30	CSC	19	5	6	0	0	0	0
41	GSC	5	36	0	0	0	0	0
81	NAW	9	1	70	1	0	0	0
23	PTC	0	0	0	23	0	0	0
14	PCO	0	0	0	1	11	0	2
6	WPO	0	0	0	3	1	2	0
53	ACO	0	0	0	0	2	1	50

B

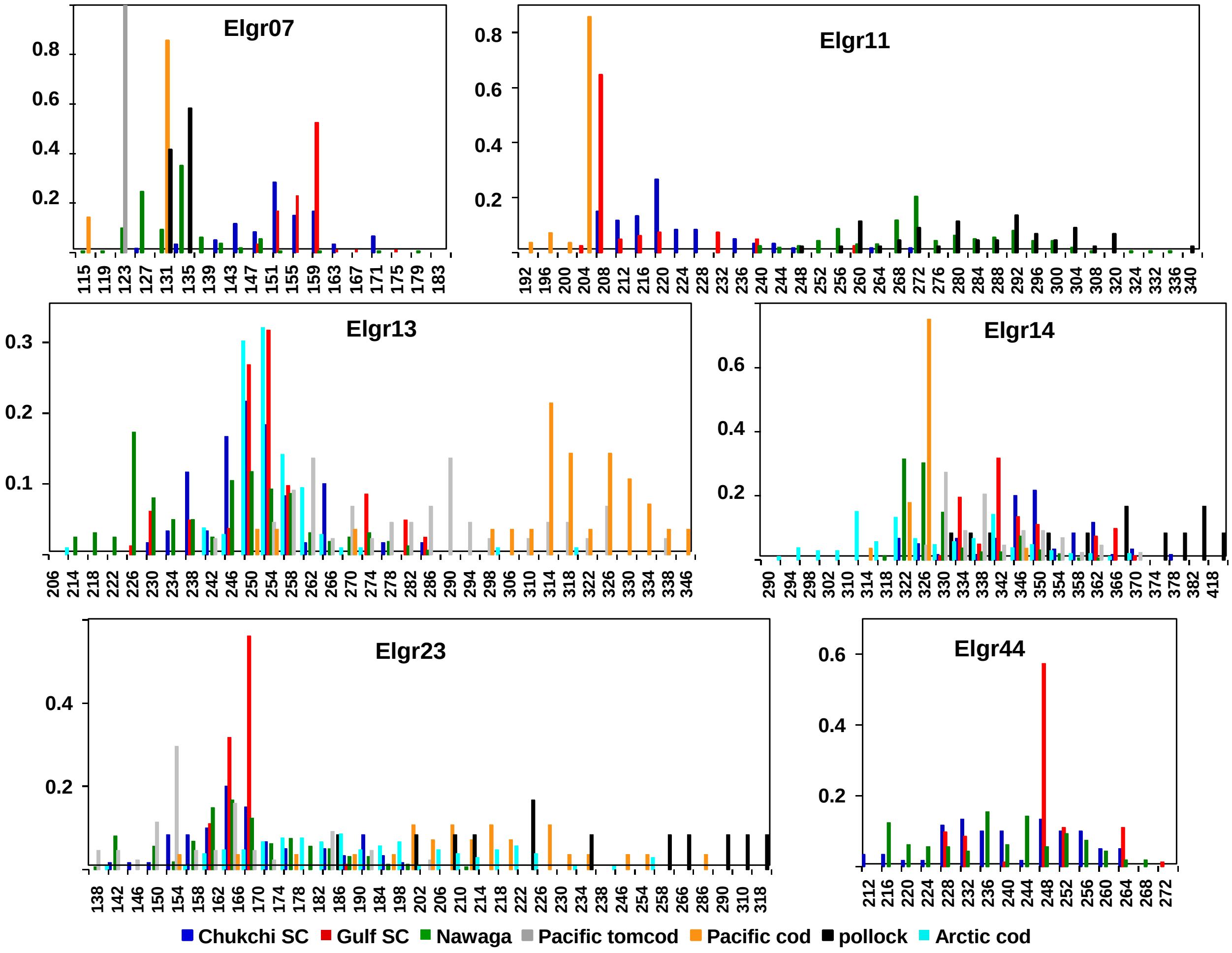
		CSC	GSC	NAW	PTC	PCO
30	CSC	28	2	0	0	0
41	GSC	1	40	0	0	0
81	NAW	0	0	81	0	0
23	PTC	0	0	0	23	0
12	PCO	0	0	0	0	12

C

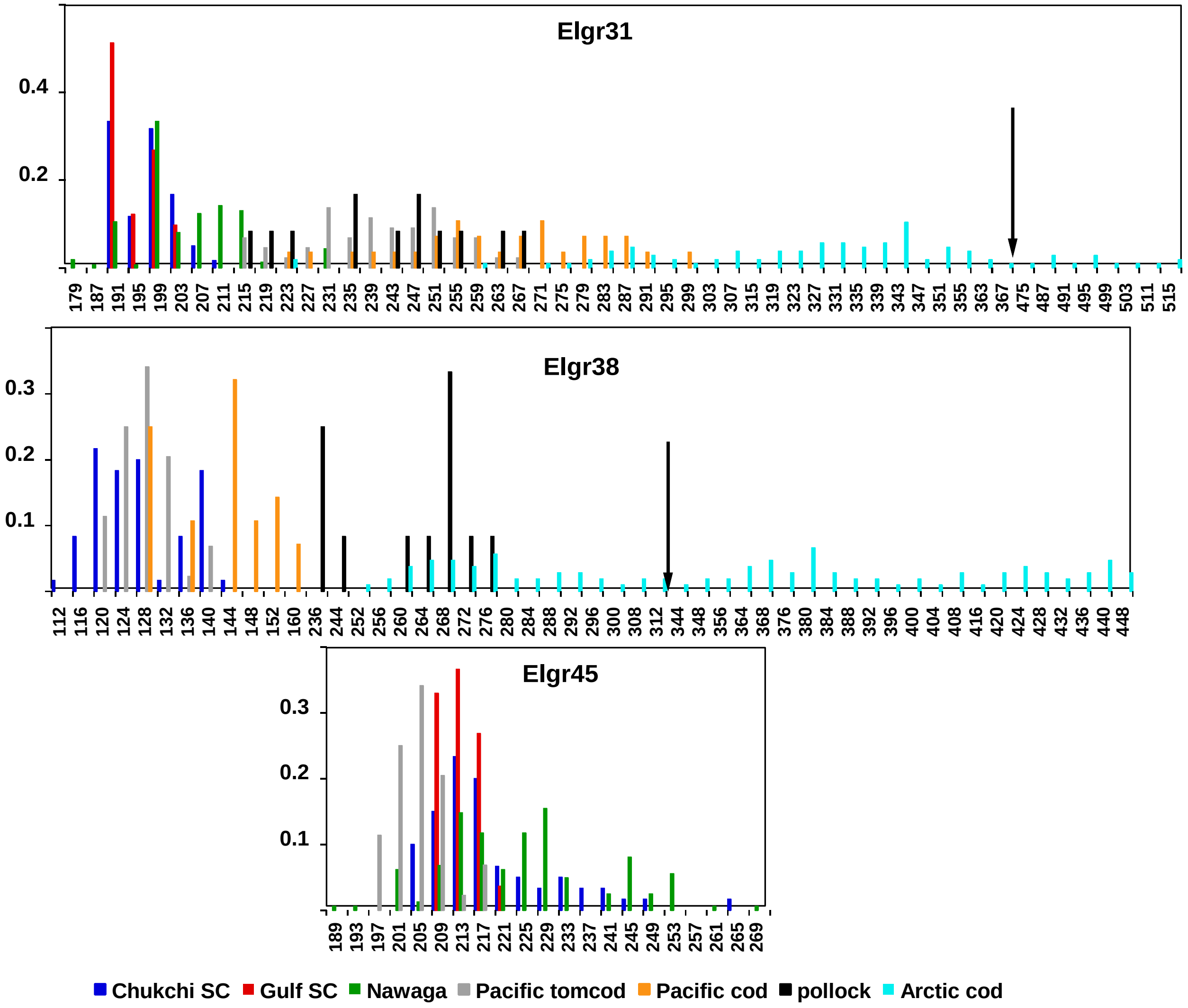
		CSC	GSC	NAW
30	CSC	30	1	0
41	GSC	0	41	0
81	NAW	0	0	81

D

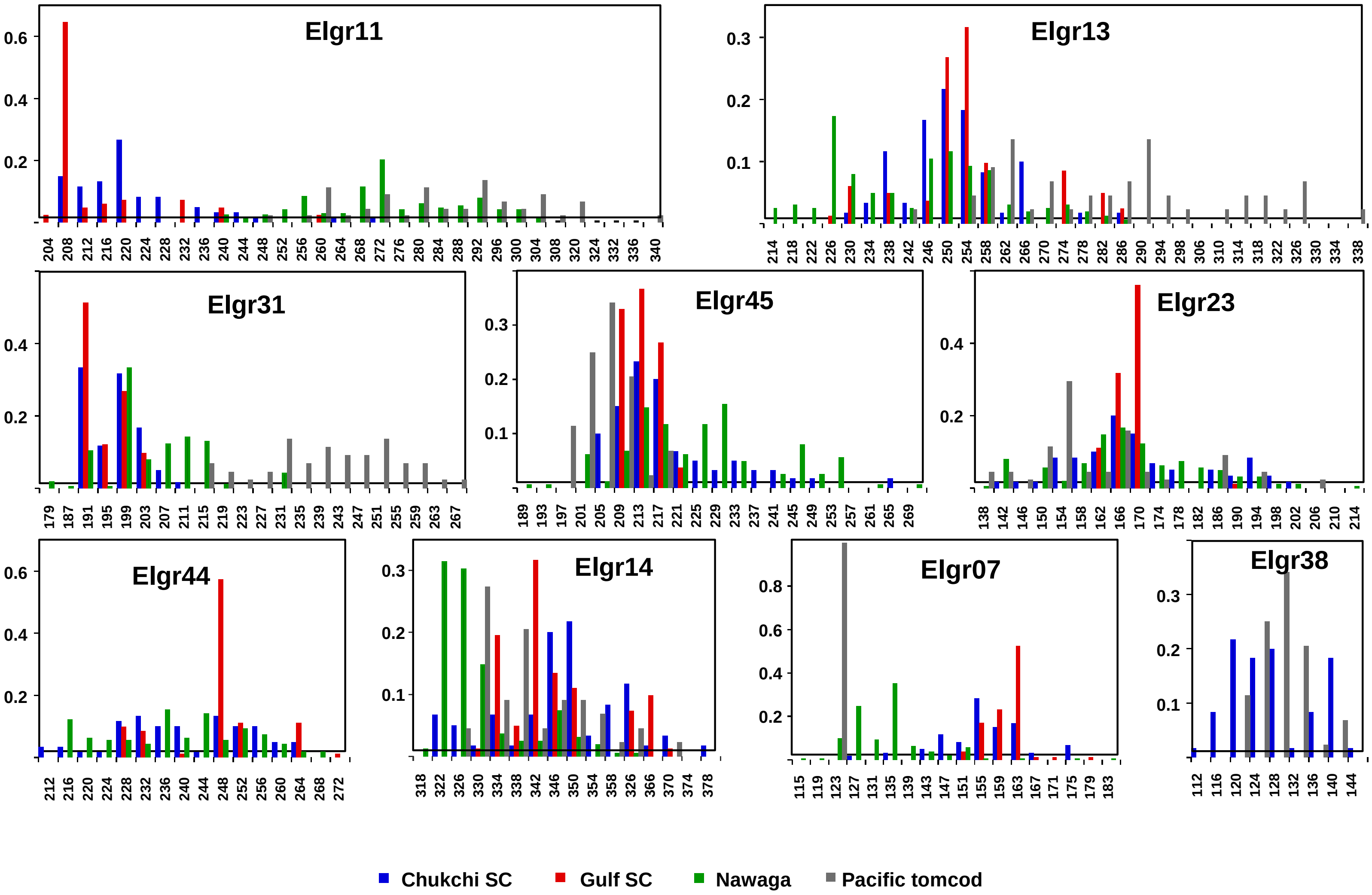
		PTC	PCO	WPO	ACO
23	PTC	23	0	0	0
14	PCO	0	14	0	0
6	WPO	0	0	6	0
53	ACO	0	0	52	1



Supplemental Figure 1: Microsatellite allele frequency plots of walleye pollock (*G. chalcogramma*), Pacific cod (*G. macrocephalus*), Arctic cod (*Boreogadus saida*), Pacific tomcod (*M. proximus*), nawaga (*E. nawaga*), and Chukchi Sea and Gulf of Alaska saffron cod (SC *E. gracilis*). Arrows indicate large breaks in the x-axis scale.



Supplemental Figure 1 (continued).



Supplemental Figure 2: Microsatellite allele frequency plots of Pacific tomcod (*M. proximus*), nawaga (*E. nawaga*), and Chukchi Sea and Gulf of Alaska saffron cod (SC *E. gracilis*).

Appendix H.

Results of the 2012 Chukchi Sea bottom trawl survey of bottomfishes, crabs, and other demersal macrofauna

Authors
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September 12, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

ADFG	Alaska Department of Fish and Game
AFSC	Alaska Fisheries Science Center
Arctic Eis	Arctic Ecosystem Integrated Survey
ASG	Alaska Sea Grant
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
JISAO	Joint Institute for the Study of the Atmosphere and Ocean
NOAA	National Oceanic and Atmospheric Administration
NSB	North Slope Borough
PMEL	Pacific Marine Environmental Laboratory
SFOS	School of Fisheries and Ocean Sciences
UAF	University of Alaska Fairbanks
USFWS	US Fish and Wildlife Service
UW	University of Washington

List of Oral and Poster Presentations

Lauth, R, Kotwicki, S, Britt, L, and Norcross, B. 2016. Differences in catch and size selectivity between two bottom trawls used in Arctic surveys of fishes, crabs and other demersal macrofauna. Arctic Eis Workshop. Alaska Marine Science Symposium, Anchorage, Alaska.

1. ABSTRACT

The results of the 2012 Chukchi Sea bottom trawl survey of bottomfishes, crabs, and other dermersal macrofauna are presented. The 2012 survey was only the fourth Chukchi Sea survey conducted by the National Marine Fisheries Service or its predecessor, the Bureau of Commercial Fisheries, since 1959. Seventy-one survey stations were successfully completed during the bottom trawl survey. The survey area extended north and east from the Bering Strait to Barrow Canyon, bounded to the west by the U.S.-Russia Maritime Boundary and east to the 10-m bathymetry limit along the Alaska coastline. Demersal populations were sampled by trawling at stations centered within 55.56 × 55.56 km (30 × 30 nautical miles) grid cells covering the survey area. Survey results presented in this report include biomass in metric tons (t), abundance numbers, and catch-per-unit-effort (CPUE; kg/ha and no./ha) for all taxa identified during the survey. Size composition and CPUE distribution plots are presented for the most abundant fish and invertebrate species. Appendices provide station data, summarized catch data by station, species listings, and biomass and population data for the sampled populations. Funding for this survey was provided in part by the Bureau of Ocean Energy Management (BOEM) Arctic Ecosystem Integrated Survey (Arctic Eis) contract agreement number M12PG00018.

2. INTRODUCTION

As part of an interagency agreement between the Bureau of Ocean Energy Management (BOEM), University of Alaska Fairbanks (UAF) and National Oceanic and Atmospheric Administration (NOAA)/National Marine Fisheries Service (NMFS), the Alaska Fisheries Science Center's (AFSC) Resource Assessment and Conservation Engineering Division (RACE) conducted a bottom trawl survey of the Chukchi Sea to assess the distribution of bottomfishes, crabs, and other demersal macrofauna from 9 August to 24 September 2012. Prior to 2012, demersal trawl surveys of the Chukchi Sea region were conducted by the Bureau of Ocean Fisheries in 1959 and the NMFS in 1976 and 1990. Results from previous surveys are summarized in: Alverson and Wilimovsky (1966); Wolotira et al. (1977); and Barber et al. (1994). The 2012 survey was the first of these surveys to use standard AFSC/ RACE bottom trawl survey techniques (Stauffer 2004) to conduct a basin-wide systematic survey of the Chukchi Sea within U.S. territorial waters. Moreover, it was part of a much larger multidisciplinary survey, the Arctic Ecosystem

Integrated Survey (Arctic Eis), that involved government and university scientists. The primary objective of Arctic Eis was to gather baseline scientific data (e.g., oceanography, plankton, fish, and larval distributions) as a foundation for responsibly guiding and mitigating future economic development activities in the Arctic region and for long-term monitoring of climate change effects to the Arctic marine ecosystem.

3. METHODS

Standard trawl operations and catch sampling procedures were based on the RACE eastern Bering Sea bottom trawl survey methods described in detail by Wakabayashi et al. (1985) and Stauffer (2004). A brief summary of these procedures is described below.

3.1 Survey area and Station Selection

The 2012 Chukchi Sea bottom trawl survey region extended north of the Bering Strait to Barrow Canyon and the 100 m isobath, bounded to the west by the U.S.-Russia Maritime Boundary and to the east by the 10 m isobath along the Alaska coastline (Fig. 1). A systematic sampling design was based on a 55.6 km (30 nautical mile (nmi)) square grid pattern with the planned trawl stations located at the approximate center of each grid cell, resulting in a total of 73 sampling locations.

3.2 Vessel

Survey efforts were conducted aboard the 43.5 m FV Alaska Knight, a twin-engine, houseforward, commercial stern trawler with Kort nozzles allowing for suitable control of the vessel at slow trawling speeds (3.0 knots).

3.3 Net Design

The bottom trawl used for sampling was an 83-112 Eastern trawl, which has a 25.3 m (83 ft) headrope and a 34.1 m (112 ft) footrope (Fig. 2a). Survey trawls were towed behind 816 kg, 1.8 × 2.7 m, steel V-doors and 54.9 m (30 fathoms) paired bridles (Fig. 2b). Each lower bridle had a 61 cm chain extension connected to the lower wing edge to improve bottom-tending characteristics. The footrope was fished without roller gear and consisted of a wrapped 0.8 cm (5/16 in.) chain to maximize bottom contact (Fig. 2a). The body of the net was constructed from nylon with stretched mesh sizes 10.2 cm (4 in.) in the wings and body and 8.9 cm (3.5 in.) in the intermediate and codend. The codend also had a liner of 3.2 cm (1.25 in.) mesh. Survey nets used by the AFSC are constructed in rigorous compliance with the regional protocols detailed in Stauffer (2004).

3.4 Scientific equipment

Surface and bottom water temperatures, as well as temperature and depth profiles, were recorded at 3-second intervals at each station using a Sea-Bird SBE-39 datalogger (Sea-Bird Electronics Inc., Bellevue, WA) attached to the headrope of the trawl. A bottom contact sensor (inclinometer/accelerometer) provided data used to assess the bottom tending performance of the net and to determine when the footrope was in contact with the seafloor. Marport Deep Sea technologies, Inc. acoustic net mensuration sensors were used to monitor and record net height and net width during fishing operations for bottom depth and area swept calculations. Net width was measured as the distance between two sensors attached immediately forward of the connection of the upper breastline to the bridle, and net height was measured from the headrope to the seafloor bottom. Bottom depth was obtained by adding net height to the depth of the headrope. Trawl warps (wire out) were determined by the standardized scope table for the eastern Bering Sea shelf bottom trawl survey (Stauffer 2004) using painted marks on wires that were calibrated with an Olympic Model 750-N cable meter. table 1 lists the specific models, versions, serial numbers, and RACE numbers for sampling and data recording equipment used on the survey.

3.5 Trawl Operations

Samples were collected by bottom trawling at each station for a target fishing time of 15 minutes at a speed of 1.54 msec-1 (3 knots). When possible, the tow was conducted near the center of a 55.6 × 55.6 km grid cell, and the vessel maintained a constant heading during the tow. 2 If the seafloor appeared to be untrawlable at the specified location, the area was surveyed for a trawlable site within the same grid square. Any hauls that sustained significant gear damage or contained excessive mud were re-sampled immediately following the unsuccessful haul.

3.6 Catch Sampling Procedures

Total catches weighing less than 1,150 kg (2,500 lb) were placed directly onto a sorting table and the catch was sorted and enumerated in its entirety. larger catches were weighed in aggregate and subsampled before sorting. Catches were sorted to the lowest taxonomic level practicable (Stevenson and Hoff 2009; Mecklenburg et al. 2002). Fishes and invertebrates that could not be identified at sea were preserved and brought to Seattle for further identification. Catch weights and numbers by taxon were either obtained directly or by subsampling and extrapolating the proportion in the subsample to that of the entire catch weight. Unusual fish or invertebrate species (e.g., large skates, large sculpins, sharks, or octopus) were completely sorted from the catch. All *Chionoecetes* and *Paralithodes* species were sorted, weighed and enumerated. Carapace length or carapace width, sex, maturity, shell condition, and egg condition were recorded from a representative sample of each of these crab species. Random subsamples of each fish species retained for length measurements were chosen to represent the sex and size composition in the catch. The greater the size range of a fish species in the sample, the greater the number of individuals retained in the random subsample for length measurements, up to a maximum of 300 specimens per species per haul. The sex of each fish was determined and then fish were measured to the nearest centimeter (fork or total length).

3.7 Catch Data Analysis

The catch sampling data were used to estimate: 1) catch per unit effort (CPUE); 2) biomass; 3) population abundance, and 4) population abundance by size class. A brief description of the procedures used for these analyses follows, for a detailed description see Wakabayashi et al. (1985). Catch per unit effort was calculated for every species at each station where it occurred by dividing the catch weight (kg) or catch number by the area swept; area swept (hectares) was computed as the distance towed multiplied by the mean net width (Alverson and Pereyra 1969). Mean catch per unit effort (CPUE) for each species was calculated in kilograms per hectare (1 ha = 10,000 m2) and number of fish per hectare for the survey area. Biomass and population abundance were derived by multiplying the mean CPUE by the total survey area (216,015 km^2). For estimated population abundance by size class, the proportion of fish at each length interval, weighted by CPUE, was expanded to the survey population.

3.8 Scientific Personnel

Table 2 lists the scientific personnel participating in the survey and their professional affiliations.

3.9 Additional Research Projects

A gear comparison study was conducted to evaluate the catch and size composition of bottom fishes, crabs, and other epibenthic macrofauna caught in the 83-112 Eastern trawl and the plumb staff beam trawl (PSBT) (Britt et al. 2013). The results indicate the 83-112 Eastern trawl is ideal for broader basin-wide surveys monitoring changes of larger and more mobile or patchily distributed fishes and crabs. Likewise, the PSBT is better suited for monitoring changes of small sized or juvenile fishes and crabs, as well as superficial benthic infauna, within and between localized areas. In addition to the standard data, samples were collected for other researchers from AFSC, University of Alaska (UAF), Alaska Sea Grant (ASG), Pacific Marine Environmental laboratory (PMEL), and North Slope Borough (NSB) (table 3). For more information on the status of samples collected please contact the Principal Investigator listed in the table.

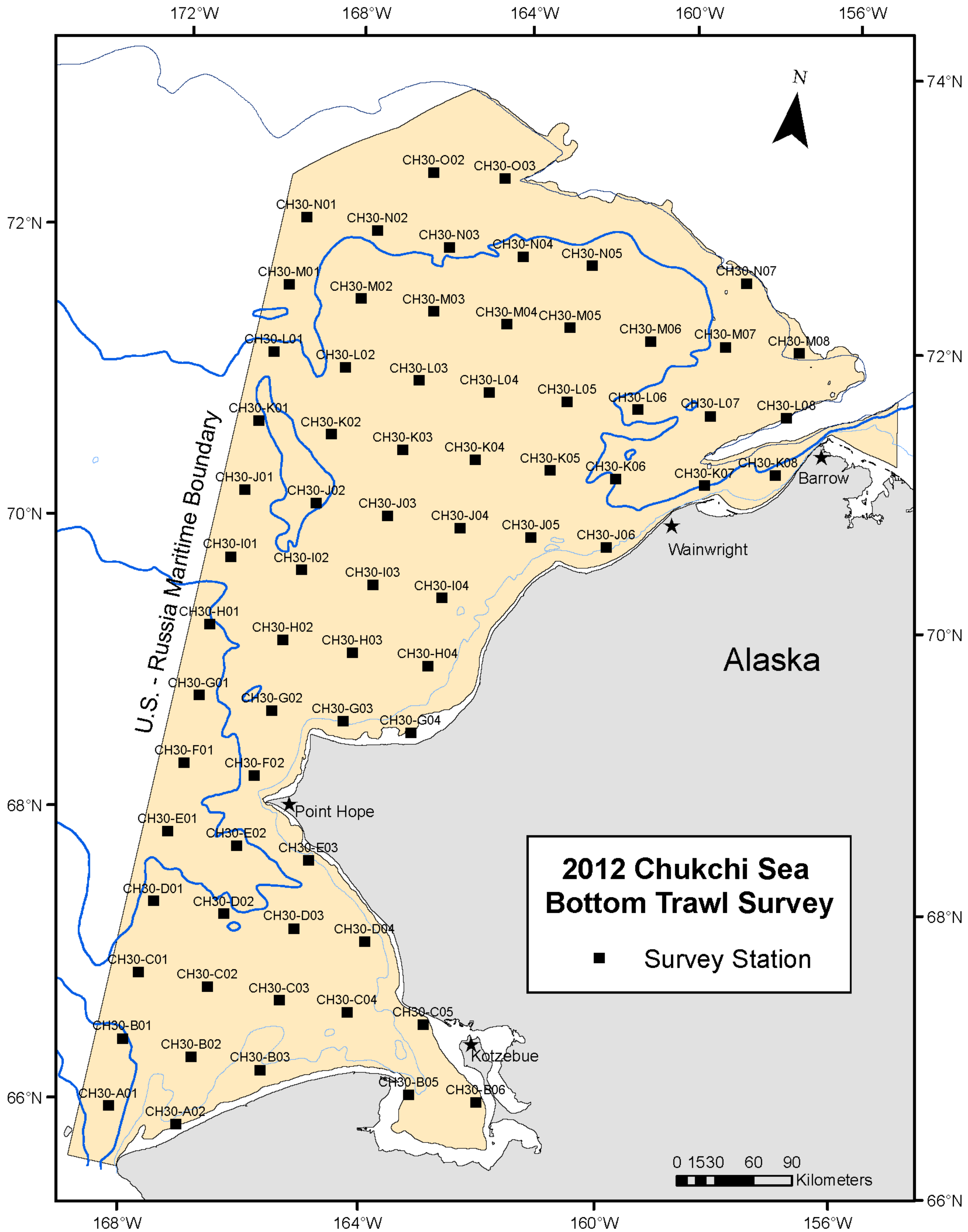


Figure 1.--Station locations for the 2012 Chukchi Sea bottom trawl survey.

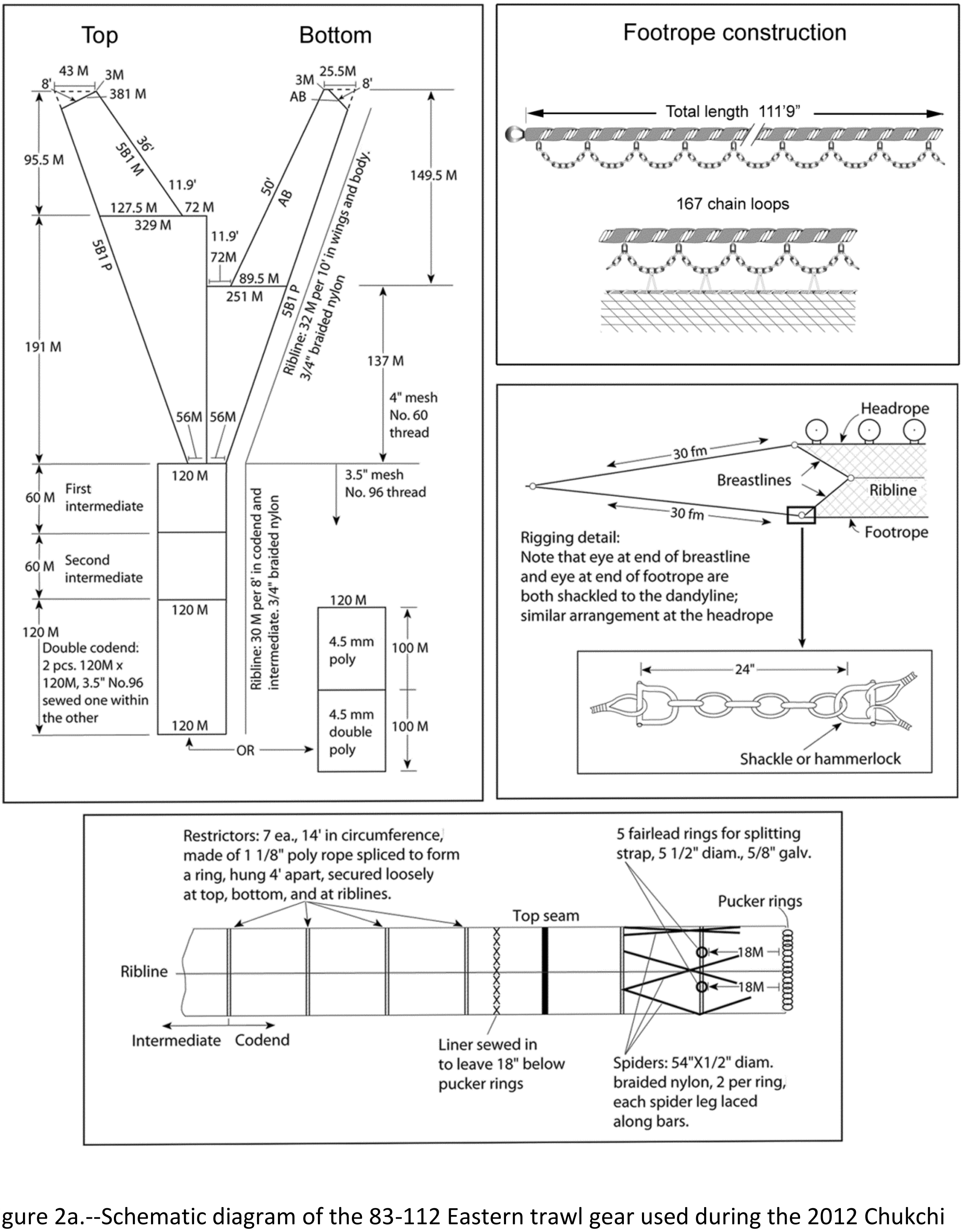


Figure 2a.--Schematic diagram of the 83-112 Eastern trawl gear used during the 2012 Chukchi Sea bottom trawl survey.

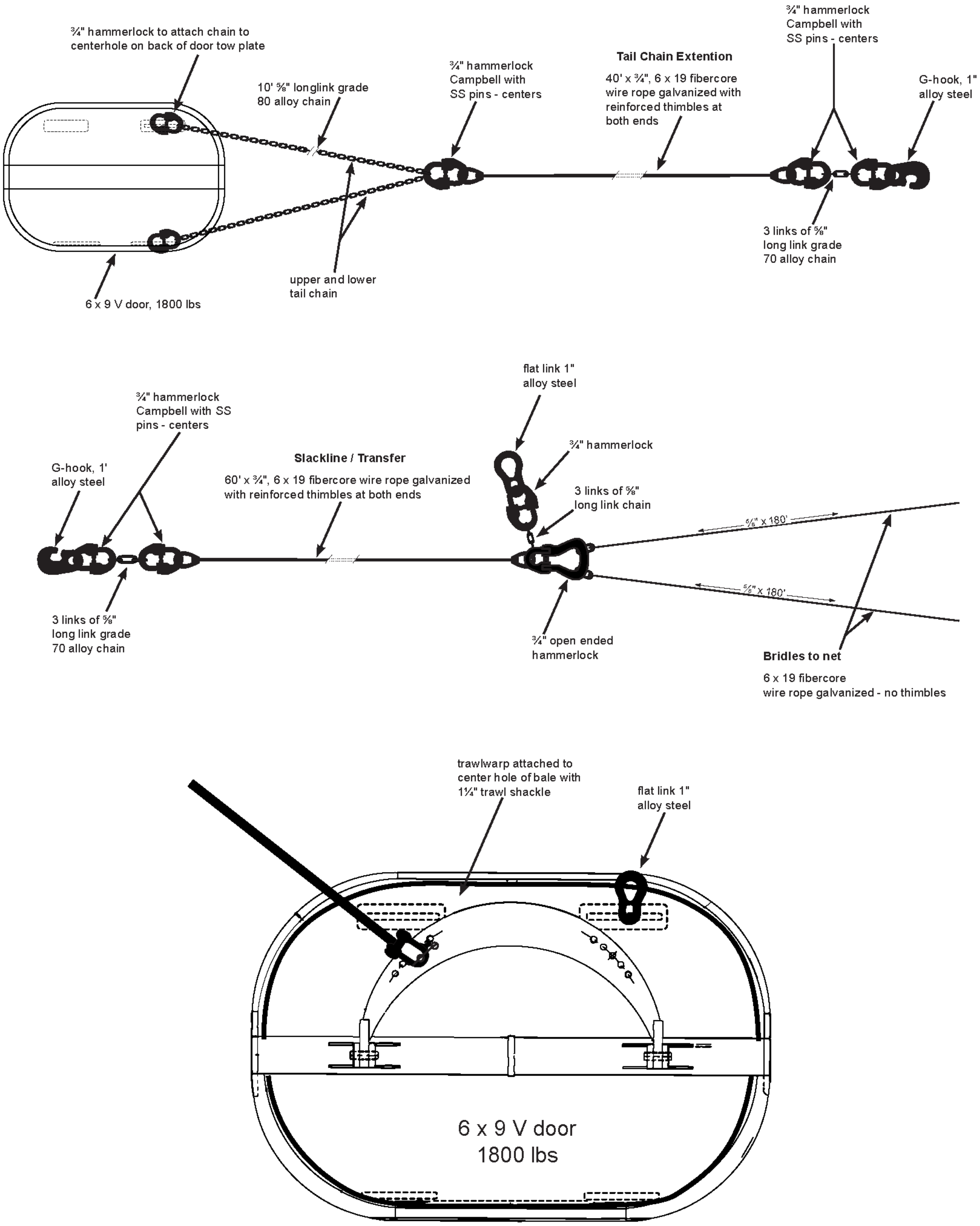


Figure 2b.--Detailed diagram of door rigging, slackline, and bridle configuration of the 83-112 Eastern trawl gear used during the 2012 Chukchi Sea bottom trawl survey.

Table 1.--Details of sampling and data recording gear used on the FV *Alaska Knight* during the 2012 Chukchi Sea survey.

Net & mensuration gear	Data type/function	Model/version/serial #
83/112 Eastern bottom trawl	research sampling tool	Net #38 Hauls 1- 38 Net #34 Hauls 40-45 Net #33 Hauls 48-78 Net #40 Hauls 82-120
Doors	spread the net	76, 732
Plumb staff beam trawl	research sampling tool	Supplied by University of Alaska Fairbanks
Vessel skipper and trawl master	conduct trawling operations	Hauls 1-65 Jim Hampton, Hauls 66-121 Vidar Ljung
Marport height sensor	measure net height	Marport serial #'s A1081000
Marport slave spread sensor	measure net spread	Marport serial #1135006
Marport master spread sensor	measure net spread	Marport serial # 1138002, offset 0m, speed of sound 1,500m/s
Marport receiver cabinets	spread and height signal	Marport Mark II acoustic receiver
Marport program	records data input from net mensuration gear	Software Version 3.5.1
Vessel depth sounder	record depth soundings	Simrad ES60 software 1.5.2.77 1998
U.S. GlobalSat Mr-350 GPS	determine latitude and longitude	Serial #001376
SeaBird SBE-39 V1.8	depth and water temperature	Serial # 859, 3766
Bottom contact sensor (HOBO Pendandt G accelorometer)	record footrope bottom contact	Serial #2243739
Olympic wire counter	measure trawl cable	Model # 750-N
Catch processing	**Data type/function**	**Model/version/serial #**
Marel basket scale	weigh baskets of catch	Model # M100
Marel specimen scale	weigh individual specimens	Type M2000 Model 2030, 6643
Measurement Systems International (MSI) load cell	weigh cod end with catch	Model # 9300
Catch data entry program	onboard catch database	Written in Access 2003 AFSC version no. 20090324
Juniper systems LS 600 Polycorder	record fish length data	Models 3333, 3227, P60-5482, P60-5400
Ichthystick	record fish length data	GF-36-003, GF-36-005
Dell computer	data recording	Dell Models 5067,05357
Laser printers	produce hard copy of data	HP 1670, 1671, 1675, VND2509
Digital camera	photograph specimens	Optio W60, Serial #9307182
Federal Scientific Research Permit	allows research sampling	SRP # 2012-15
State of Alaska Research Permit	allows research sampling	CF-12-098
Northwest Arctic Burough Title 9 Permit	allows research sampling	Title 9 Minor Use Permit #: 118-03-12

Species identification guides

Clark, R.N. 2006. *Field Guide to the Benthic Marine Invertebrates of Alaska's Shelf and Upper Slope.* AFSC unpublished manuscript.

Jorgenson, E.M. 2009. *Field Guide to the Squids and Octopods of the Eastern North Pacific and Bering Sea.* Alaska Sea Grant College Program. University of Alaska Fairbanks, 100 p.

Kessler, D. 2006. *A Working Field Guide to Trawl Caught Animals* AFSC unpublished manuscript.

Mecklenburg, C.W., T.A. Mecklenburg, and L.K. Thorsteinson. 2002. *Fishes of Alaska.* American Fisheries Society, 1037 p.

Orr, J.W., M.A. Brown and D. Baker. 2000. *Guide to rockfishes (Scorpaenidae) of the genera Sebastes, Sebastolobus, and Adelosebastes of the Northeast Pacific Ocean.* 2nd Edition NOAA Tech. Memo. NMFS-AFSC-117, 47 p.

Stevenson, D.E., J.W. Orr, G.R. Hoff and J.D. McEachran. 2007. *Field Guide to Sharks, Skates, and Ratfish of Alaska.* Alaska Sea Grant College Program. University of Alaska Fairbanks, 77 p.

Table 2.--Vessel itinerary and scientists participating in the 2012 Chukchi Sea bottom trawl survey.

Name	**Survey Position**	**Affiliation**
Leg 1: August 9- 31		
Bob Lauth	Chief Scientist	AFSC[1]
Lyle Britt	Deck Lead	AFSC
Roger Clark	Invertebrate Taxonomy	AFSC Contractor
Dan Urban	Crab Biologist	AFSC
Ben Gray	Biologist	UAF[2]
Dave Drumm	Food Web Ecology	AFSC
Leg 2: September 1-24		
Lyle Britt	Chief Scientist	AFSC
Jay Orr	Deck Lead	AFSC
Roger Clark	Invertebrate Taxonomy	AFSC Contractor
Jan Haaga	Crab Biologist	AFSC
Lauren Divine	Biologist	UAF
Andy Whitehouse	Food Web Ecology	UW/JISAO[3]

[1] Alaska Fisheries Science Center

[2] University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Fairbanks, AK.

[3] University of Washington, Joint Institute for the Study of the Atmosphere and Ocean

Table 3.--Summary of special project collections from the 2012 Chukchi bottom trawl survey.

Project Title	PI	Agency	Contact Information
Saffron cod genetics	A. J. Gharrett	UAF[1]	a.gharrett@alaska.edu
Age and growth of Arctic cod, saffron cod, and capelin	Tom Helser	AFSC[2]	thomas.helser@noaa.gov
Snow crab life history and diet studies	Katrin Iken	UAF	kbiken@alaska.edu
Diet comparison of six demersal fishes inhabiting the Beaufort and Chukchi Seas	Ben Gray Brenda Norcross	UAF UAF	bpgray@alaska.edu bnorcross@alaska.edu
Fish trophic interactions	Troy Buckley Kerim Aydin	AFSC AFSC	troy.buckley@noaa.gov kerim.aydin@noaa.gov
Spatial and temporal variability in the trophic roles of the Chukchi Sea fishes using N and C stable isotopes	Jen Marsh Franz Mueter	UAF UAF	jmmarsh@alaska.edu fmueter@alaska.edu
Plumb staff beam trawl catch comparison to the 83-112 eastern bottom trawl	Brenda Norcross Bob Lauth	UAF AFSC	bnorcross@alaska.edu bob.lauth@noaa.gov
Stock composition of salmon, Arctic cod, and capelin	Jeff Guyon	AFSC	jeff.guyon@noaa.gov
Fish energetics and nutritional condition	Ron Heintz Johanna Vollenweider	AFSC AFSC	ron.heintz@noaa.gov johanna.vollenweider@noaa.gov
Assessing the role of light on the vertical distribution of fishes	Stan Kotwicki	AFSC	stan.kotwicki@noaa.gov
Taxonomic investigation of northern populations of wattled eelpouts	Duane Stevenson	AFSC	duane.stevenson@noaa.gov
Snailfish taxonomy and systematics	James Orr	AFSC	james.orr@noaa.gov
Bitter crab syndrome in snow crabs	Frank Morado	AFSC	frank.morado@noaa.gov
Gadiformes fish photos for Sea Grant book	Gerald Hoff	AFSC	jerry.hoff@noaa.go
Flathead sole and Bering flounder genetics in the Arctic	James Orr	AFSC	james.orr@noaa.gov
Develop a marine paleoclimate proxy time series from Arctic surfclam	Tom Helser	AFSC	thomas.helser@noaa.gov
Develop a marine paleoclimate proxy time series part B	Tom Helser	AFSC	thomas.helser@noaa.gov
Digital photos of fishes and invertebrates.	Gay Sheffield	UAF/ASG[3]	gay.sheffield@alaska.edu
Conductivity, temperature, depth (CTD) profile data	Ned Cokelet	PMEL[4]	cokelet@pmel.noaa.gov
Prey library for marine mammals.	Robert Suydam Heather Smith	NSB[5] NSB	robert.suydam@north-slope.org heathersmith.r@gmail.com

[1] University of Alaska, Fairbanks (UAF),

[2] NOAA-Alaska Fisheries Science Center (AFSC),

[3] Alaska Sea Grant, Nome, AK (ASG)

[4] NOAA-Pacific Marine Environmental Laboratory (PMEL)

[5] North Slope Borough-Department of Wildlife Management (NSB)

4. RESULTS

Seventy-one of the 73 stations were successfully completed during the 2012 Chukchi Sea survey (Fig. 1). Two stations were determined to be untrawlable. Station Ch30-O01 was covered in ice, therefore no attempt was made to sample the station. Two attempts were made to sample station Ch30-N06, but due to excessive mud in the catch sample, the station was abandoned. Summarized haul and catch data at each station can be found in Appendix A. Mean bottom depths by station ranged from 12 m at Station Ch30-G04 in Ledyard Bay to 90 m at Station Ch30-I08 along the northern boundary of the survey area at the edge of Barrow Canyon. Mean bottom depth for all stations was 42 m. Mean bottom temperatures by station ranged from -1.7 to 10.7°C with a combined mean of 2.7°C (Figs. 3 and 4). The coldest bottom temperatures were in the north with the exception of station Ch30-B06, in Kotzebue Sound, where the bottom temperature was -0.4°C, the coldest temperature recorded south of Wainwright. Warmer bottom temperatures were generally in the shallowest waters along the coast. Surface temperature ranged from -0.5 to 11.2°C with a mean of 5.2°C (Figs. 3 and 5). The warmest surface temperatures were observed close to the coastline while the coldest temperatures were observed at the northernmost stations. A total of 56 fish and 277 invertebrate taxa were identified during the 2012 Chukchi Sea survey. See Appendix B for a descending rank of all organisms caught. lists of all fishes and invertebrates caught on the survey can be found in tables 7 and 8 and Appendices C and D. Fishes accounted for 4.6% of the total survey CPUE (kg/ha) (Fig. 6; tables 4 and 7) compared to 95.4% for invertebrates (Fig. 7; tables 5 and 8). The 15 most abundant fish species accounted for 96% of the total fish CPUE (kg/ha). Fish lengths were collected from 48 species (table 6). Maps of CPUE by station and plots of estimated abundance-at-length for the top 15 fish species and *Gadus chalcogrammus* (walleye pollock) are presented in Figs. 8-38. *Boreogadus saida* (Arctic cod) was the most abundant fish species by weight and number, and was the only fish or invertebrate taxon observed at 70 of 71 stations. *Eleginus gracilis* (saffron cod) was the second most abundant fish species with the largest abundance occurring south of Point hope in Kotzebue Sound. Invertebrates dominated the catches and accounted for 95.4% of the total survey CPUE (kg/ha). Maps with CPUE by station for the top 15 species are presented in Figures 39-54. *Strongylocentrotus droebachiensis* (green sea urchin) was the dominant species by weight and number (table 8). Although *S. droebachiensis* was the most abundant invertebrate species, it only occurred at 38 of 71 stations. *Pagurus trigonocheirus* (fuzzy hermit) and *Hyas coarctatus* (circumboreal toad crab) were the most frequently observed invertebrates, occurring at 65 stations each. *Labidochirus splendescens* (splendid hermit crab) and *Argis lar* (kuro argid shrimp) occurred at 64 and 63 stations, respectively. 11 Three commercially important crab species were identified, *Chionoecetes opilio* (snow crab), *Paralithodes camtschaticus* (red king crab), and *Paralithodes platypus* (blue king crab; Figs. 55-60; table 9). Over 28,000 *C. opilio* were caught at 63 stations. Of the 28,000 caught, only 29 were legal males (carapace width >78 mm). A total of 34 *P. platypus* occurred in eight hauls (Fig. 59; Appendix D), while only two *P. camtschaticus* (red king crab) occurred in two hauls (Fig. 60; Appendix D).

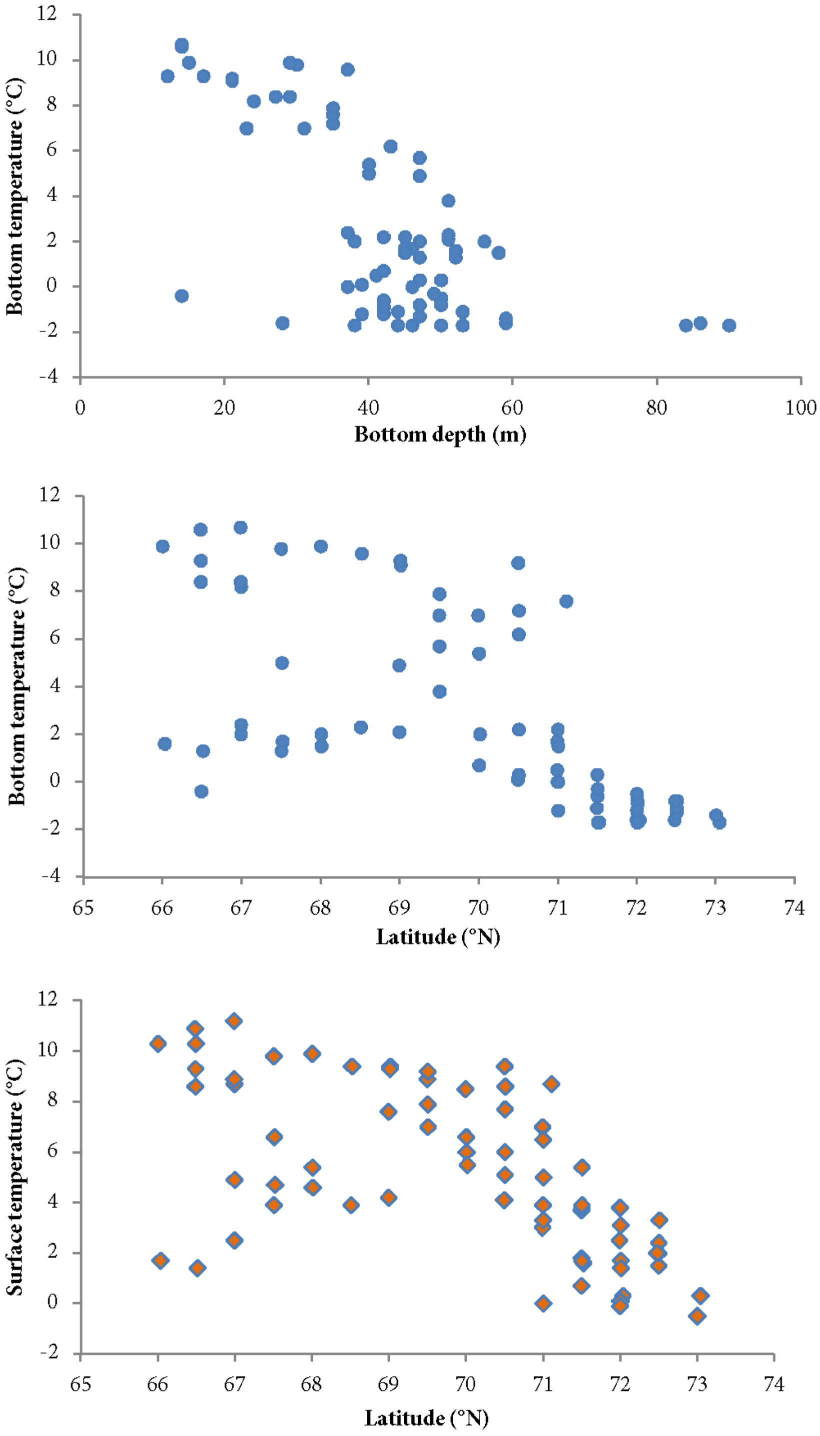


Figure 3.--Relationship between bottom temperature (°C), bottom depth (m), and latitude (°N) collected during the 2012 Chukchi Sea bottom trawl survey.

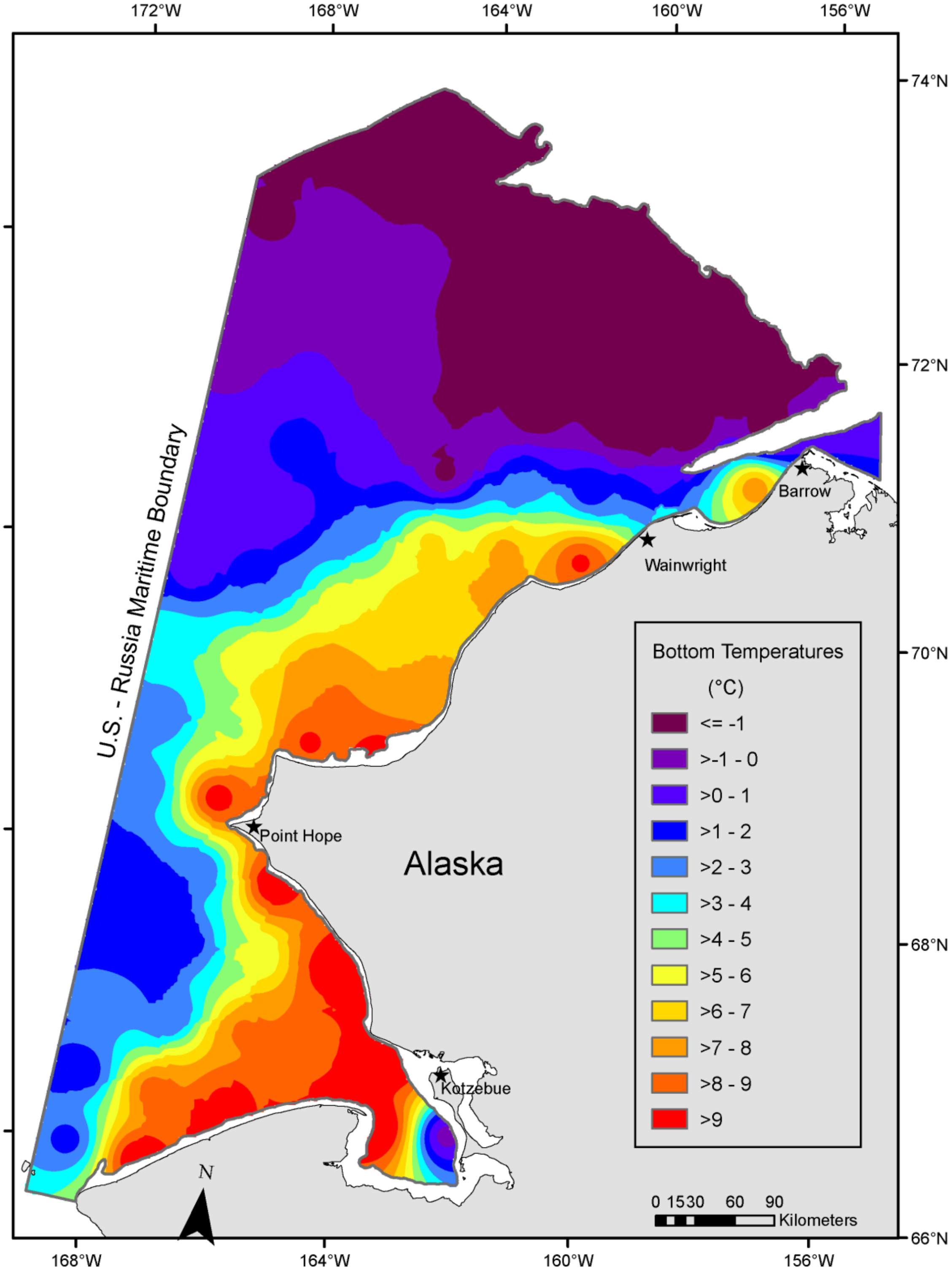


Figure 4.--Map of bottom temperatures (°C) collected during the 2012 Chukchi Sea bottom trawl survey.

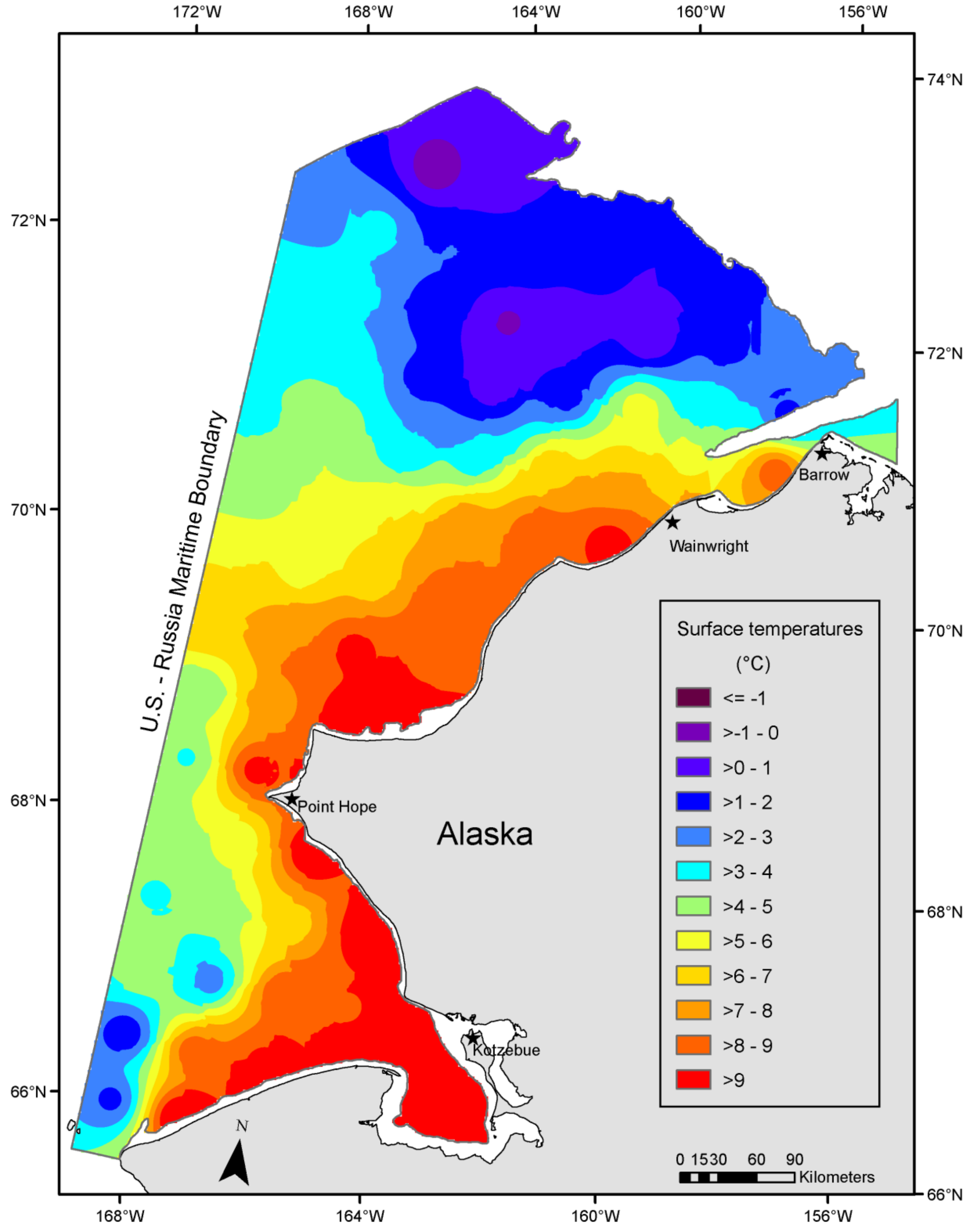
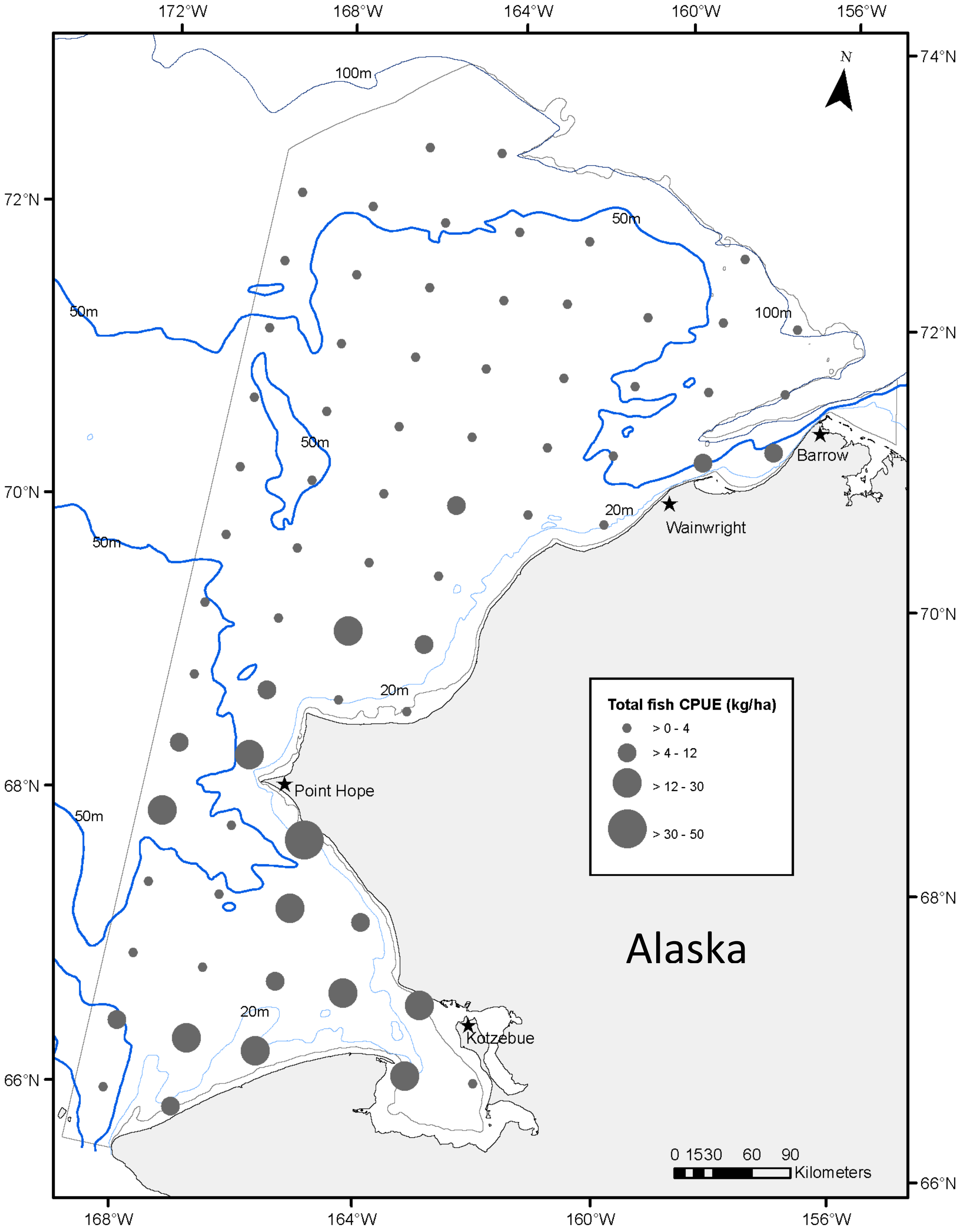


Figure 5.--Map of surface temperatures (°C) collected during the 2012 Chukchi Sea bottom trawl survey.


172°W
168°W
164°W
160°W
156°W
74°N
72°N
70°N
68°N
66°N
N
100m
50m
20m
Barrow
Wainwright
Point Hope
Kotzebue
Alaska
Total fish CPUE (kg/ha)
> 0 - 4
> 4 - 12
> 12 - 30
> 30 - 50
0 15 30 60 90
Kilometers
168°W
164°W
160°W
156°W

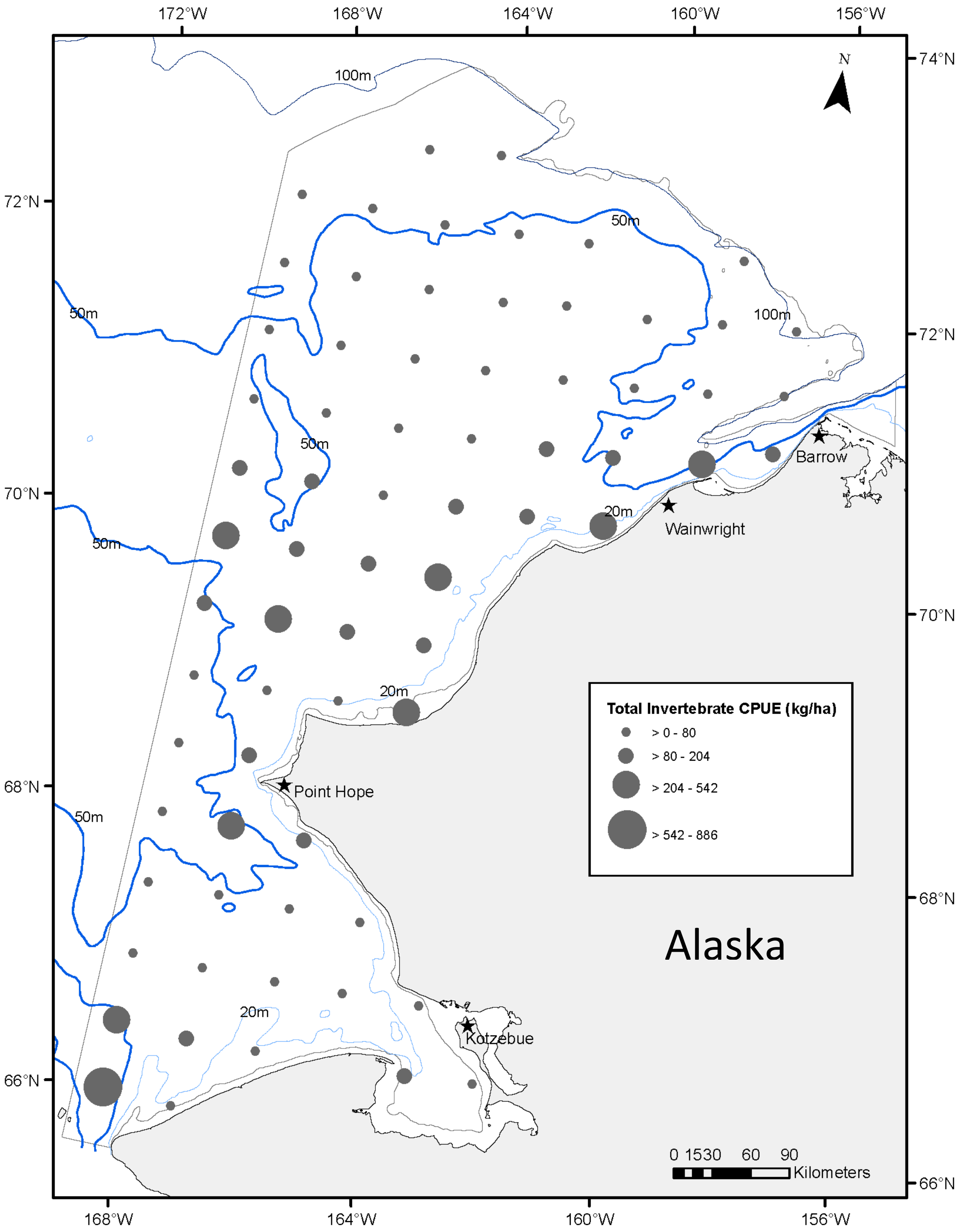

172°W
168°W
164°W
160°W
156°W
74°N
72°N
70°N
68°N
66°N
N
100m
50m
20m
Point Hope
Wainwright
Barrow
Kotzebue
Alaska
Total Invertebrate CPUE (kg/ha)
> 0 - 80
> 80 - 204
> 204 - 542
> 542 - 886
0 15 30 60 90
Kilometers

Table 4.--Mean catch per unit effort (CPUE), estimated biomass (t), estimated population, and standard error for the 25 most abundant fish species, ranked by weight (kg/ha), caught during the 2012 Chukchi Sea bottom trawl survey.

Common name	Mean CPUE (kg/ha)	St. error mean CPUE (kg/ha)	Mean CPUE (no./ha)	St. error of mean CPUE (no./ha)	Biomass (t)	Standard Error Biomass (t)	Population	Standard Error Population
Arctic cod	1.46	0.31	119.73	24.17	31,537	210,914	2,586,433,070	522,118,492
saffron cod	1.08	0.58	12.05	5.04	23,333	397,569	260,274,268	108,916,425
Pacific herring	0.83	0.30	7.45	2.79	17,940	208,043	160,995,341	60,270,866
yellowfin sole	0.33	0.11	7.97	3.32	7,164	78,231	172,066,672	71,678,375
starry flounder	0.25	0.10	0.40	0.15	5,481	66,095	8,553,103	3,340,924
warty sculpin	0.14	0.05	4.56	1.67	3,091	32,667	98,397,326	36,008,960
rainbow smelt	0.13	0.05	2.53	0.97	2,842	37,323	54,715,205	21,003,265
polar eelpout	0.10	0.06	0.65	0.49	2,201	44,359	14,128,022	10,516,616
Bering flounder	0.10	0.03	2.54	0.57	2,058	17,557	54,969,124	12,213,997
Arctic staghorn sculpin	0.08	0.02	7.22	2.65	1,795	12,541	155,874,337	57,234,160
Alaska plaice	0.08	0.03	0.77	0.31	1,675	17,966	16,531,168	6,796,991
variegated snailfish	0.07	0.03	0.86	0.28	1,566	17,119	18,613,728	6,104,642
Alaska skate	0.05	0.05	0.01	0.01	1,159	36,646	167,465	167,465
wattled eelpout	0.03	0.01	0.66	0.24	621	7,980	14,263,997	5,168,052
slender eelblenny	0.03	0.01	3.80	1.06	596	7,190	82,146,461	22,984,398
marbled eelpout	0.02	0.01	0.31	0.11	509	8,476	6,674,000	2,442,822
longhead dab	0.02	0.02	0.48	0.35	484	10,984	10,382,734	7,572,021
kelp snailfish	0.02	0.01	1.33	0.39	449	4,694	28,731,221	8,322,915
antlered sculpin	0.02	0.01	0.31	0.13	420	5,883	6,748,470	2,782,499
plain sculpin	0.02	0.01	0.63	0.34	357	5,741	13,594,925	7,337,139
capelin	0.01	0.01	1.82	0.59	300	3,798	39,207,490	12,681,879
Canadian eelpout	0.01	0.01	0.30	0.13	281	4,082	6,374,722	2,705,565
fourhorn sculpin	0.01	0.01	0.05	0.03	145	3,461	1,025,804	562,408
threaded sculpin	0.01	0.01	0.26	0.25	132	4,013	5,634,930	5,358,111
walleye pollock	0.01	0.00	0.79	0.29	117	1,369	17,035,608	6,332,279

Table 5.--Mean catch per unit effort (CPUE), estimated biomass (t), estimated population, and standard error for the 25 most abundant invertebrate species, ranked by weight (kg/ha), caught during the 2012 Chukchi Sea bottom trawl survey.

Scientific name	Common name	Mean CPUE (kg/ha)	Standard error of mean CPUE kg/ha	Mean CPUE (no./ha)	Standard error Mean CPUE (no./ha)	Estimated biomass (t)	Standard error estimated biomass (t)	Estimated Population	Standard error estimated population
Strongylocentrotus droebachiensis	green sea urchin	15.89	6.93	387.17	213.89	343,265	4,733,303	8,363,427,230	4,620,317,923
Asterias amurensis	purple-orange sea star	8.80	3.39	236.35	127.27	190,113	2,318,260	5,105,542,392	2,749,230,382
Pagurus trigonocheirus	fuzzy hermit crab	7.87	1.67	162.34	27.54	170,039	1,141,284	3,506,792,235	594,813,754
Chionoecetes opilio	snow crab	7.45	2.58	212.50	76.12	160,948	1,759,426	4,590,286,550	1,644,327,579
Psolus fabricii	brownscaled sea cucumber	5.54	2.45	156.93	72.28	119,752	1,676,834	3,389,893,515	1,561,295,023
Neptunea heros		4.48	1.18	45.42	11.27	96,776	807,653	981,091,430	243,536,410
Boltenia ovifera		4.17	3.32	1.71	0.85	89,984	2,268,205	37,001,397	18,375,188
Leptasterias polaris		3.99	0.94	40.30	8.76	86,216	642,624	870,489,225	189,236,796
Gorgonocephalus sp. cf. *arcticus*		3.59	1.51	37.42	13.69	77,583	1,031,208	808,280,790	295,779,859
	empty gastropod shells	3.55	1.14	0.00	0.00	76,774	779,824	-	-
Halichondria sp.		3.30	3.17	0.00	0.00	71,372	2,163,711	-	-
Styela rustica	sea potato	2.42	1.16	1.10	0.60	52,329	794,959	23,858,086	13,020,864
Chrysaora melanaster		2.27	0.42	2.46	0.54	48,965	287,109	53,136,528	11,725,802
Urticina crassicornis	mottled anemone	1.93	0.60	43.76	14.55	41,724	412,168	945,383,652	314,279,895
Halichondria sitiens	black papillate sponge	1.77	1.24	0.00	0.00	38,168	846,784	-	-
Halocynthia aurantium	sea peach	1.65	0.96	5.40	4.77	35,685	657,765	116,610,358	103,051,984
Gorgonocephalus eucnemis	basketstar	1.58	1.23	9.81	6.48	34,110	841,310	211,917,234	140,045,115
Cyanea capillata	lion's mane	1.45	0.43	12.35	4.24	31,351	294,511	266,826,663	91,615,179
Hyas coarctatus	circumboreal toad crab	1.34	0.49	43.91	14.21	28,886	331,865	948,592,151	306,878,461
Neptunea ventricosa	fat whelk	1.33	0.73	15.30	7.91	28,818	495,693	330,555,670	170,793,503
	empty bivalve shells	1.16	0.74	0.01	0.01	25,162	507,151	216,766	216,766
Urasterias lincki		1.15	0.47	8.31	3.81	24,948	320,169	179,609,454	82,245,717
Ascidiacea	tunicate unident.	1.12	0.65	3.25	2.63	24,150	444,385	70,218,674	56,909,782
Solaster arcticus		0.98	0.86	1.24	0.64	21,242	585,942	26,820,402	13,835,244
Telmessus cheiragonus	helmet crab	0.89	0.36	12.22	5.57	19,160	244,774	263,889,573	120,357,593

Table 6.--Fish species with length data from the 2012 Chukchi Sea bottom trawl survey.

Scientific name	Common name	Number of lengths	Minimum length (cm)	Maximum length (cm)	Mean length (cm)
Boreogadus saida	Arctic cod	3,839	4	25	12
Gymnocanthus tricuspis	Arctic staghorn sculpin	698	3	41	10
Limanda aspera	yellowfin sole	591	4	29	15
Eleginus gracilis	saffron cod	565	4	36	19
Lumpenus fabricii	slender eelblenny	480	5	29	14
Clupea pallasi	Pacific herring	458	11	29	21
Myoxocephalus verrucosus	warty sculpin	413	5	29	13
Hippoglossoides robustus	Bering flounder	358	4	29	14
Osmerus mordax	rainbow smelt	281	10	30	19
Mallotus villosus	capelin	186	6	16	11
Liparis tunicatus	kelp snailfish	155	3	16	9
Liparis gibbus	variegated snailfish	116	8	31	17
Pleuronectes quadrituberculatus	Alaska plaice	112	11	31	19
Theragra chalcogramma	walleye pollock	106	6	16	10
Myoxocephalus jaok	plain sculpin	94	6	23	13
Lycodes palearis	wattled eelpout	90	9	32	21
Artediellus scaber	hamecon	78	2	9	7
Limanda proboscidea	longhead dab	70	10	23	15
Triglops pingeli	ribbed sculpin	68	4	15	10
Lycodes turneri	polar eelpout	63	11	78	26
Platichthys stellatus	starry flounder	58	19	59	33
Ulcina olrikii	Arctic alligatorfish	47	4	6	5
Podothecus veternus	veteran poacher	46	6	17	12
Enophrys diceraus	antlered sculpin	42	8	19	13
Lycodes polaris	Canadian eelpout	40	11	45	18
Lycodes raridens	marbled eelpout	38	7	38	21
Ammodytes hexapterus	Pacific sand lance	26	5	13	9
Liopsetta glacialis	Arctic flounder	25	10	21	13
Limanda sakhalinensis	Sakhalin sole	21	7	17	14
Acantholumpenus mackayi	pighead prickleback	15	21	39	31
Liparis marmoratus	festive snailfish	15	3	12	9
Hexagrammos stelleri	whitespotted greenling	13	12	19	14
Lumpenus medius	stout eelblenny	10	6	14	11
Nautichthys pribilovius	eyeshade sculpin	10	5	8	7
Hemilepidotus papilio	butterfly sculpin	9	6	17	10
Icelus spatula	spatulate sculpin	9	5	11	8
Stichaeus punctatus	Arctic shanny	6	8	15	11

Table 6.--Continued.

Scientific name	Common name	Number of lengths	Minimum length (cm)	Maximum length (cm)	Mean length (cm)
Myoxocephalus polyacanthocephalus	great sculpin	5	9	10	10
Lycodes mucosus	saddled eelpout	4	13	26	18
Myoxocephalus quadricornis	fourhorn sculpin	4	11	21	16
Gadus macrocephalus	Pacific cod	4	10	13	11
Pallasina barbata	tubenose poacher	4	9	12	11
Lumpenus maculatus	daubed shanny	2	8	9	9
Bathyraja parmifera	Alaska skate	1	95	95	95
Myoxocephalus scorpioides	Arctic sculpin	1	15	15	15
Blepsias bilobus	crested sculpin	1	14	14	14
Reinhardtius hippoglossoides	Greenland turbot	1	10	10	10
Liparis fabricii	gelatinous seasnail	1	10	10	10

Table 7.--Mean and standard error of catch per unit effort (kg/ha and no./ha) for fish species caught during the 2012 Chukchi Sea bottom trawl survey.

Scientific name	Common name	Mean CPUE (kg/ha)	Standard error CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error CPUE (no./ha)
Boreogadus saida	Arctic cod	1.46	0.31	119.73	24.17
Eleginus gracilis	saffron cod	1.08	0.58	12.05	5.04
Clupea pallasi	Pacific herring	0.83	0.30	7.45	2.79
Limanda aspera	yellowfin sole	0.33	0.11	7.97	3.32
Platichthys stellatus	starry flounder	0.25	0.10	0.40	0.15
Myoxocephalus verrucosus	warty sculpin	0.14	0.05	4.56	1.67
Osmerus mordax	rainbow smelt	0.13	0.05	2.53	0.97
Lycodes turneri	polar eelpout	0.10	0.06	0.65	0.49
Hippoglossoides robustus	Bering flounder	0.10	0.03	2.54	0.57
Gymnocanthus tricuspis	Arctic staghorn sculpin	0.08	0.02	7.22	2.65
Pleuronectes quadrituberculatus	Alaska plaice	0.08	0.03	0.77	0.31
Liparis gibbus	variegated snailfish	0.07	0.03	0.86	0.28
Bathyraja parmifera	Alaska skate	0.05	0.05	0.01	0.01
Lycodes palearis	wattled eelpout	0.03	0.01	0.66	0.24
Lumpenus fabricii	slender eelblenny	0.03	0.01	3.80	1.06
Lycodes raridens	marbled eelpout	0.02	0.01	0.31	0.11
Limanda proboscidea	longhead dab	0.02	0.02	0.48	0.35
Liparis tunicatus	kelp snailfish	0.02	0.01	1.33	0.39
Enophrys diceraus	antlered sculpin	0.02	0.01	0.31	0.13
Myoxocephalus jaok	plain sculpin	0.02	0.01	0.63	0.34
Mallotus villosus	capelin	0.01	0.01	1.82	0.59
Lycodes polaris	Canadian eelpout	0.01	0.01	0.30	0.13
Myoxocephalus quadricornis	fourhorn sculpin	0.01	0.01	0.05	0.03
Gymnocanthus pistilliger	threaded sculpin	0.01	0.01	0.26	0.25
Gadus chalcogramma	walleye pollock	0.01	<0.01	0.79	0.29
Acantholumpenus mackayi	pighead prickleback	0.01	0.01	0.10	0.10
Liopsetta glacialis	Arctic flounder	<0.01	<0.01	0.17	0.16
Triglops pingeli	ribbed sculpin	<0.01	<0.01	0.63	0.30
Podothecus veternus	veteran poacher	<0.01	<0.01	0.43	0.14
Limanda sakhalinensis	Sakhalin sole	<0.01	<0.01	0.15	0.09
Artediellus scaber	hamecon	<0.01	<0.01	0.71	0.26
Enophrys lucasi	leister sculpin	<0.01	<0.01	0.05	0.03
Hexagrammos stelleri	whitespotted greenling	<0.01	<0.01	0.08	0.06
Chirolophis snyderi	bearded warbonnet	<0.01	<0.01	0.05	0.05

Table 7.—Continued.

Scientific name	Common name	Mean CPUE (kg/ha)	Standard error CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error CPUE (no./ha)
Liparis marmoratus	festive snailfish	<0.01	<0.01	0.11	0.03
Lycodes mucosus	saddled eelpout	<0.01	<0.01	0.03	0.02
Blepsias bilobus	crested sculpin	<0.01	<0.01	0.01	0.01
Hemilepidotus papilio	butterfly sculpin	<0.01	<0.01	0.07	0.03
Megalocottus platycephalus	belligerent sculpin	<0.01	<0.01	0.01	0.01
Myoxocephalus scorpioides	Arctic sculpin	<0.01	<0.01	0.01	0.01
Icelus spatula	spatulate sculpin	<0.01	<0.01	0.07	0.05
Nautichthys pribilovius	eyeshade sculpin	<0.01	<0.01	0.12	0.05
Ulcina olrikii	Arctic alligatorfish	<0.01	<0.01	0.39	0.14
Pleuronectiformes	flatfish unident.	<0.01	<0.01	0.01	0.01
Myoxocephalus polyacanthocephalus	great sculpin	<0.01	<0.01	0.04	0.03
Lumpenus medius	stout eelblenny	<0.01	<0.01	0.10	0.08
Ammodytes hexapterus	Pacific sand lance	<0.01	<0.01	0.19	0.14
Gadus macrocephalus	Pacific cod	<0.01	<0.01	0.03	0.02
Stichaeus punctatus	Arctic shanny	<0.01	<0.01	0.04	0.03
Liparis sp.		<0.01	<0.01	0.02	0.01
Bathyraja parmifera egg case	Alaska skate egg case	<0.01	<0.01	0.01	0.01
Liparis fabricii	gelatinous seasnail	<0.01	<0.01	0.01	0.01
Pallasina barbata	tubenose poacher	<0.01	<0.01	0.05	0.03
Lumpenus maculatus	daubed shanny	<0.01	<0.01	0.02	0.02
Reinhardtius hippoglossoides	Greenland turbot	<0.01	<0.01	0.01	0.01

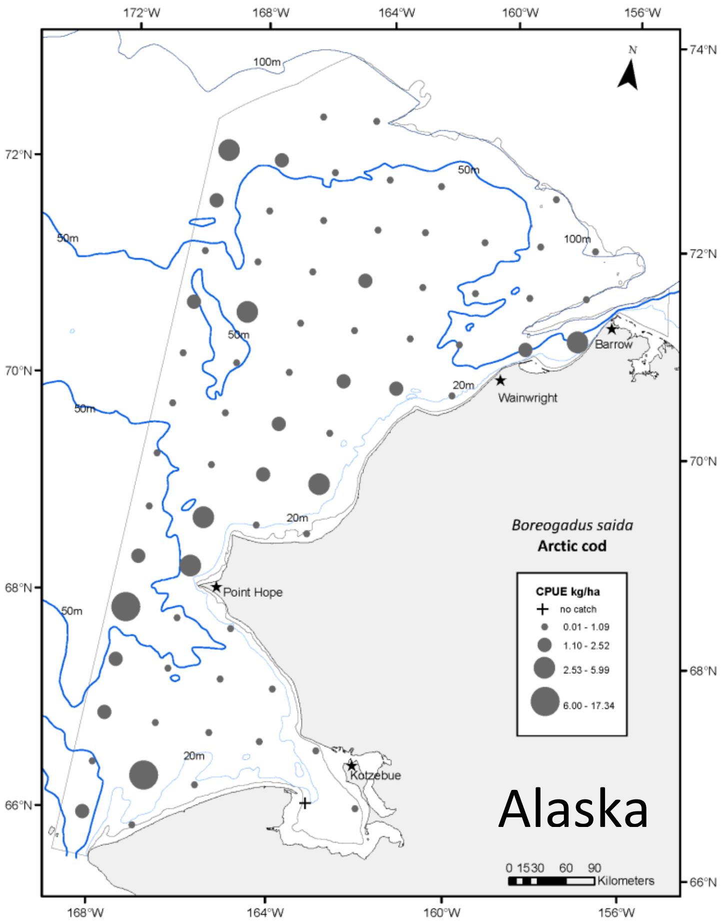


Figure 8.--Distribution and relative abundance (CPUE kg/ha) of *Boreogadus saida* (Arctic cod) for the 2012 Chukchi Sea bottom trawl survey.

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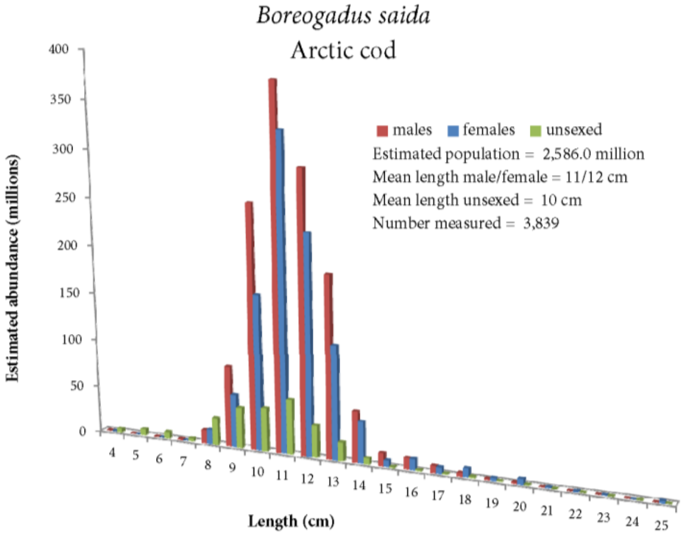


Figure 9.--Estimated abundance at length by sex of *Boreogadus saida* (Arctic cod) for the 2012 Chukchi Sea bottom trawl survey

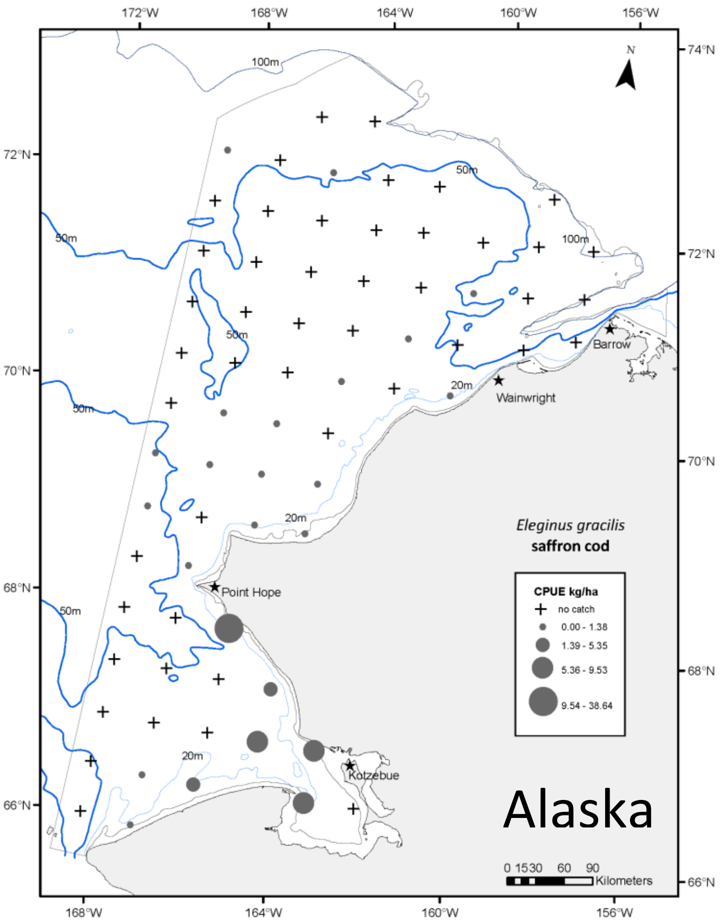


Figure 10.--Distribution and relative abundance (CPUE kg/ha) of *Eleginus gracilis* (saffron cod) for the 2012 Chukchi Sea bottom trawl survey.

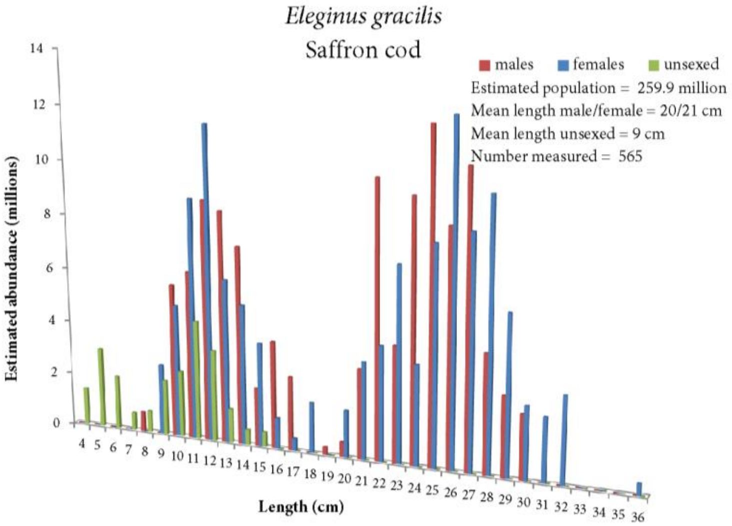


Figure 11.--Estimated abundance at length by sex of *Eleginus gracilis* (saffron cod) for the 2012 Chukchi Sea bottom trawl survey.

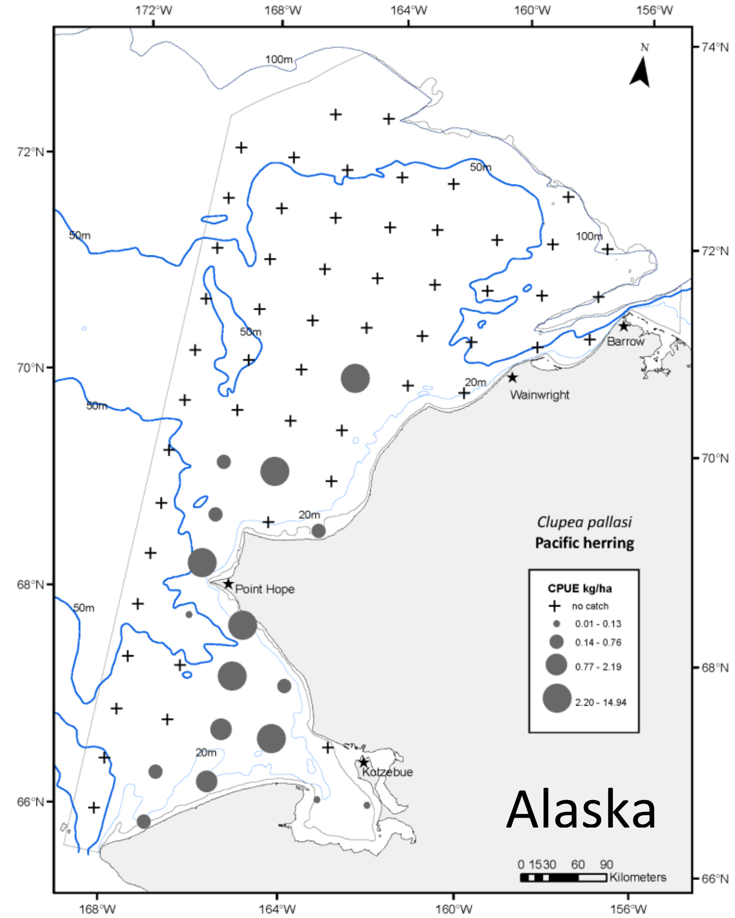


Figure 12.--Distribution and relative abundance (CPUE kg/ha) of *Clupea pallasi* (Pacific herring) for the 2012 Chukchi Sea bottom trawl survey.

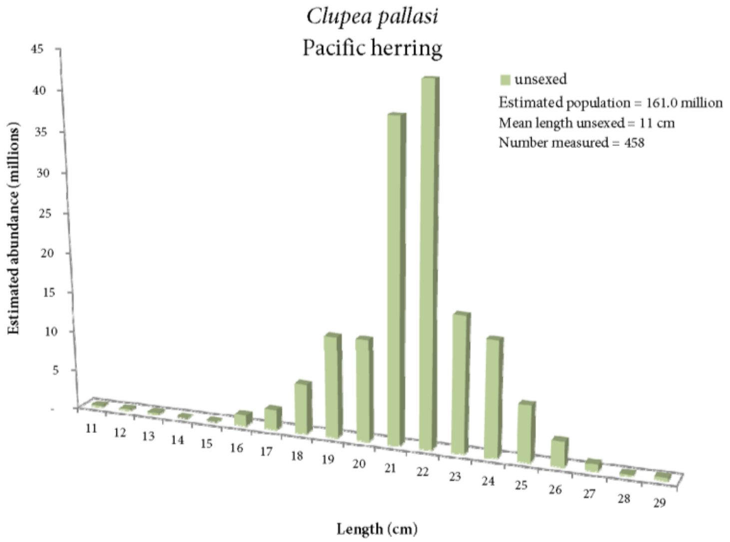


Figure 13.--Estimated abundance at length by sex of *Clupea pallasi* (Pacific herring) for the 2012 Chukchi Sea bottom trawl survey.

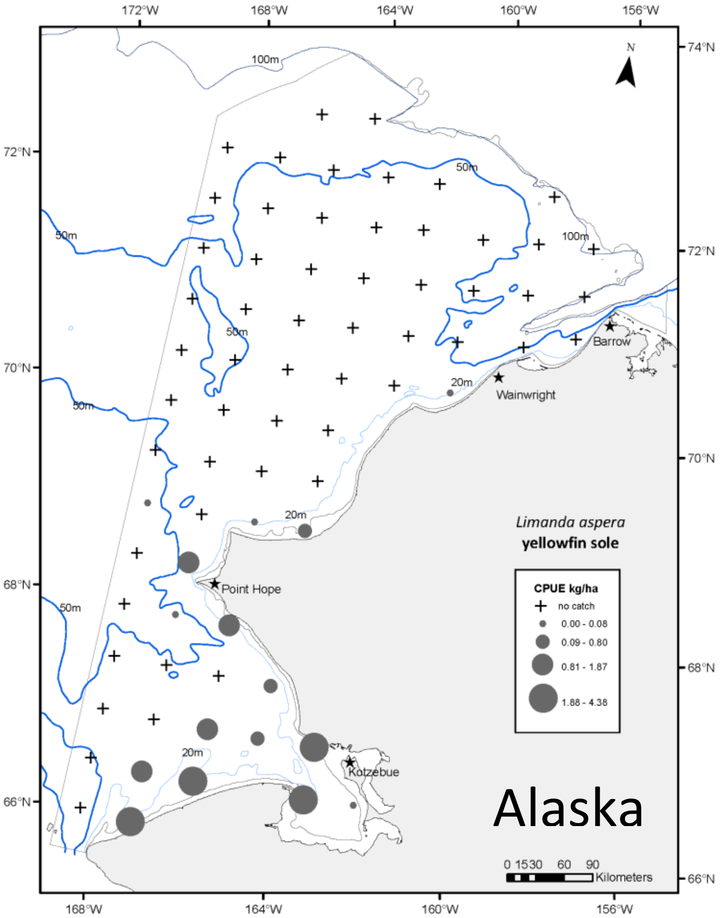


Figure 14.--Distribution and relative abundance (CPUE kg/ha) of *Limanda aspera* (yellowfin sole) for the 2012 Chukchi Sea bottom trawl survey.

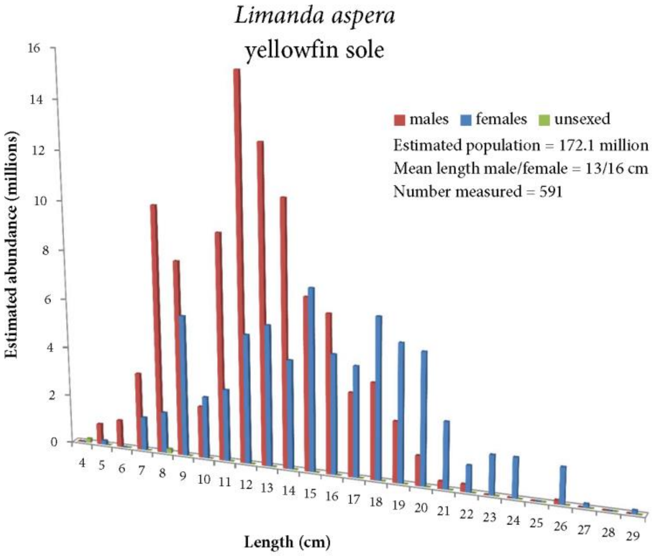


Figure 15.--Estimated abundance at length by sex of *Limanda aspera* (yellowfin sole) for the 2012 Chukchi Sea bottom trawl survey.

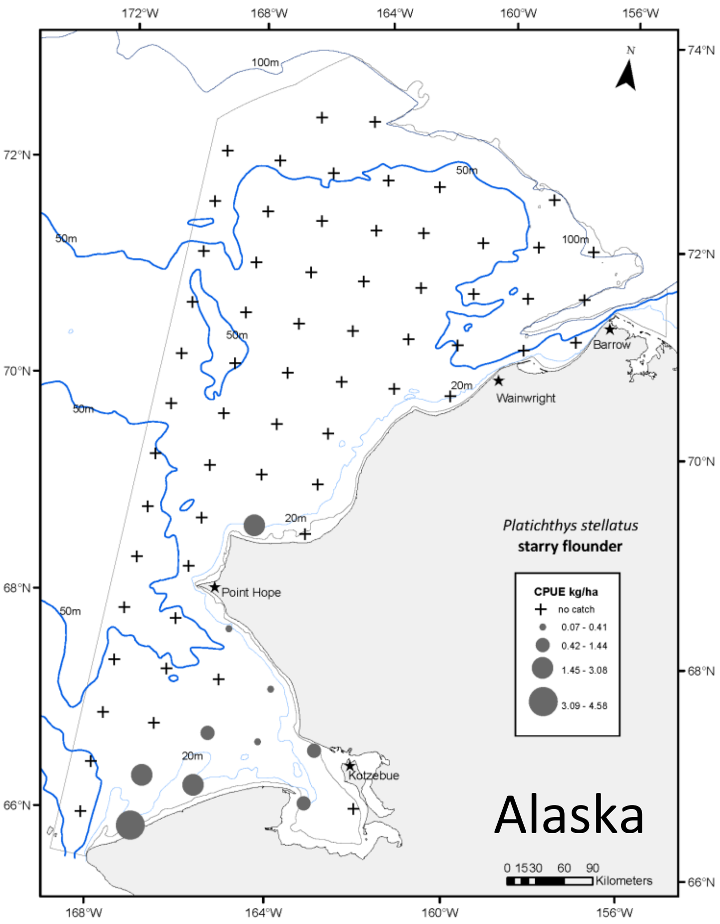


Figure 16.--Distribution and relative abundance (CPUE kg/ha) of *Platichthys stellatus* (starry flounder) for the 2012 Chukchi Sea bottom trawl survey.

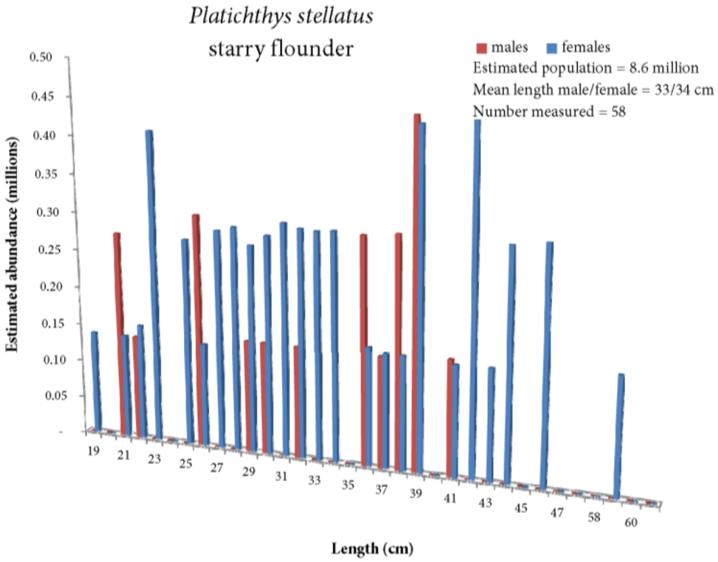


Figure 17.--Estimated abundance at length by sex of *Platichthys stellatus* (starry flounder) for the 2012 Chukchi Sea bottom trawl survey.

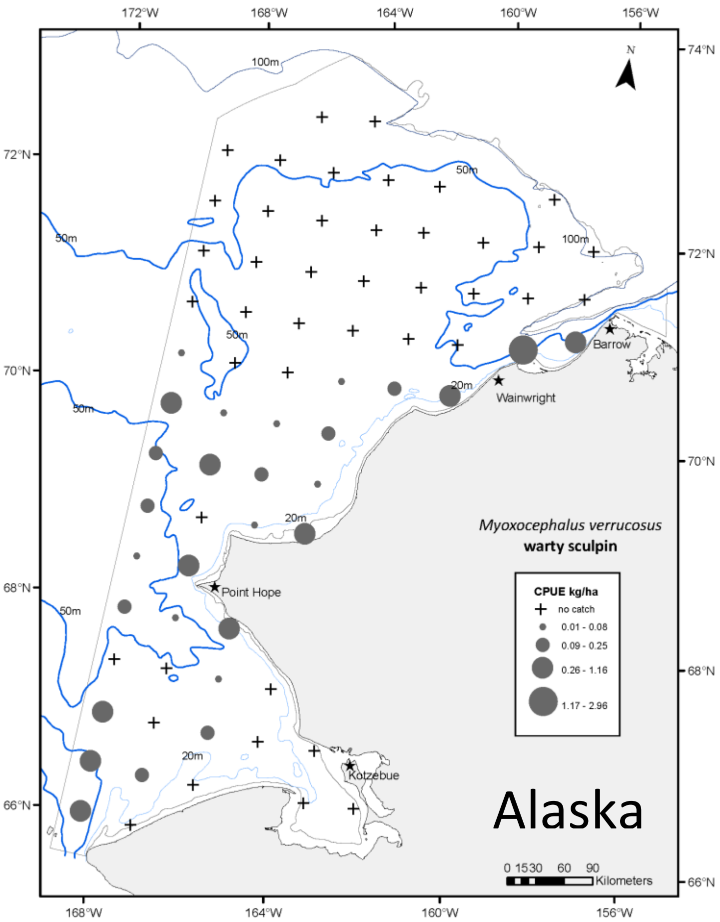


Figure 18.--Distribution and relative abundance (CPUE kg/ha) of *Myoxocephalus verrucosus* (warty sculpin) for the 2012 Chukchi Sea bottom trawl survey.

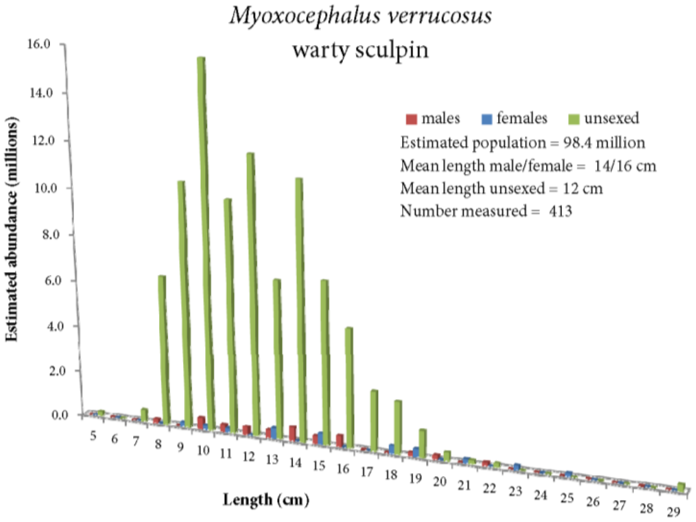


Figure 19.--Estimated abundance at length by sex of *Myoxocephalus verrucosus* (warty sculpin) for the 2012 Chukchi Sea bottom trawl survey.

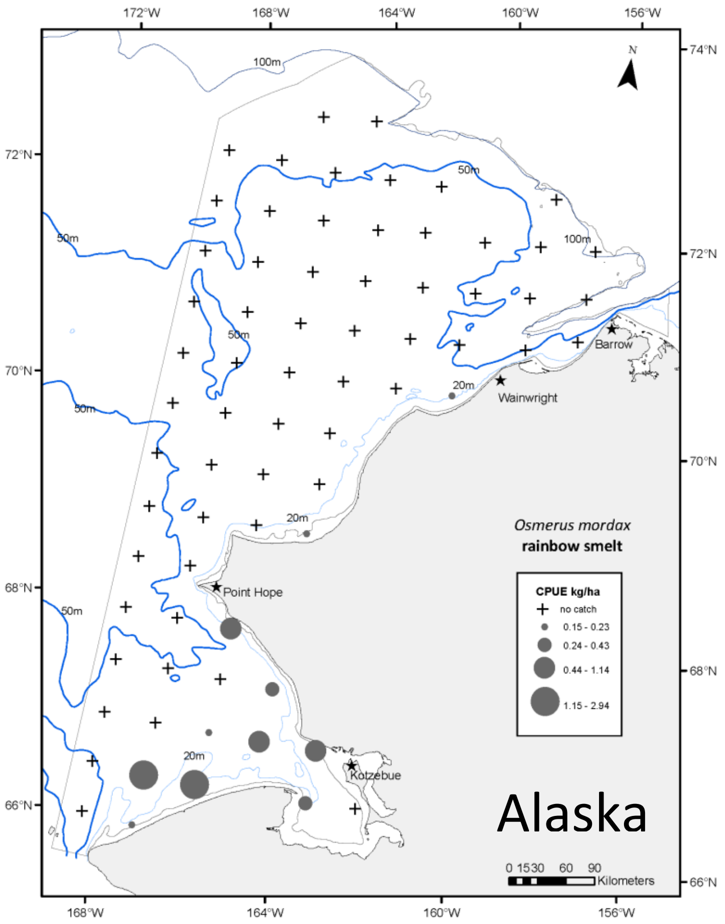


Figure 20.--Distribution and relative abundance (CPUE kg/ha) of *Osmerus mordax* (rainbow smelt) for the 2012 Chukchi Sea bottom trawl survey.

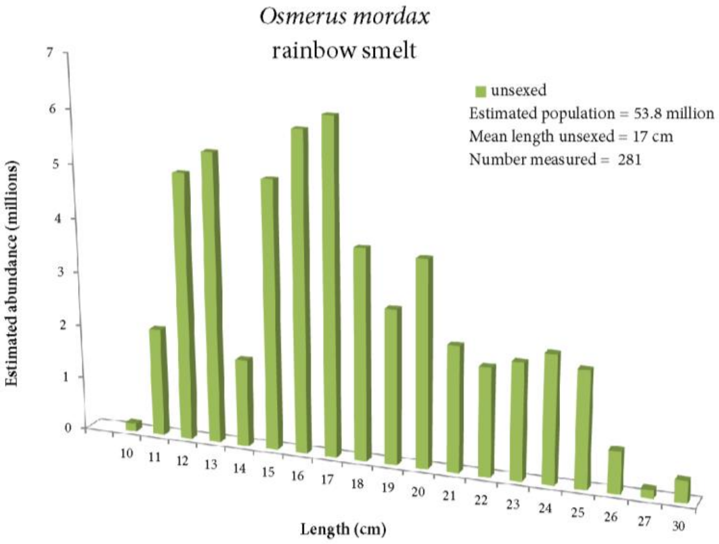


Figure 21.--Estimated abundance at length by sex of *Osmerus mordax* (rainbow smelt) for the 2012 Chukchi Sea bottom trawl survey.

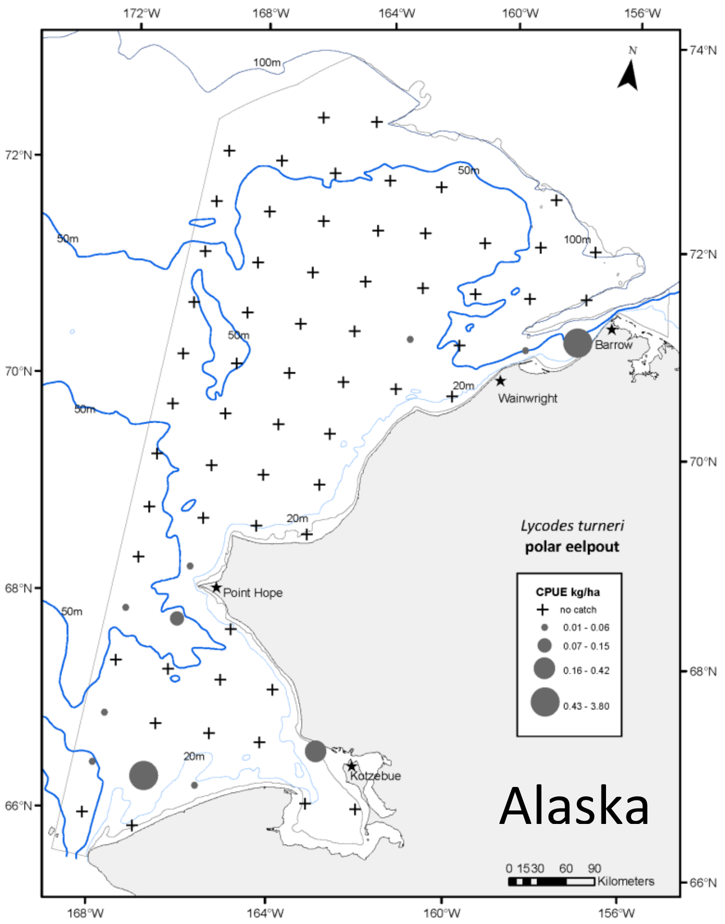


Figure 22.--Distribution and relative abundance (CPUE kg/ha) of *Lycodes turneri* (polar eelpout) for the 2012 Chukchi Sea bottom trawl survey.

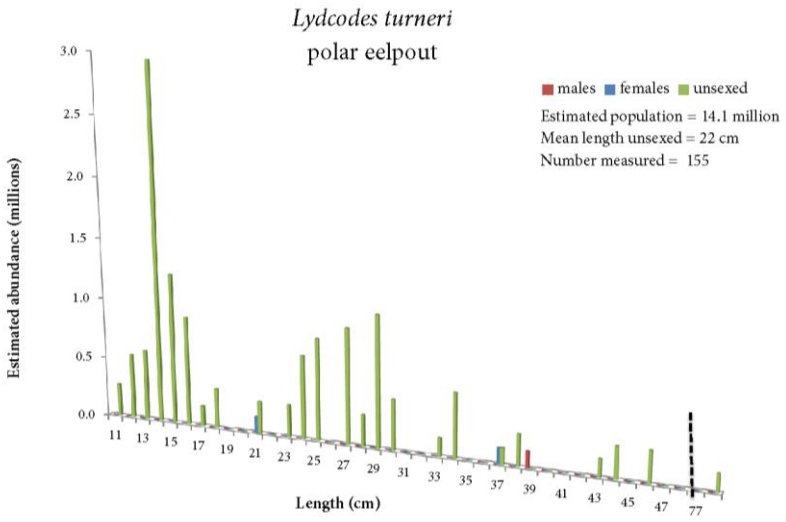


Figure 23.--Estimated abundance at length by sex of *Lycodes turneri* (polar eelpout) for the 2012 Chukchi Sea bottom trawl survey.

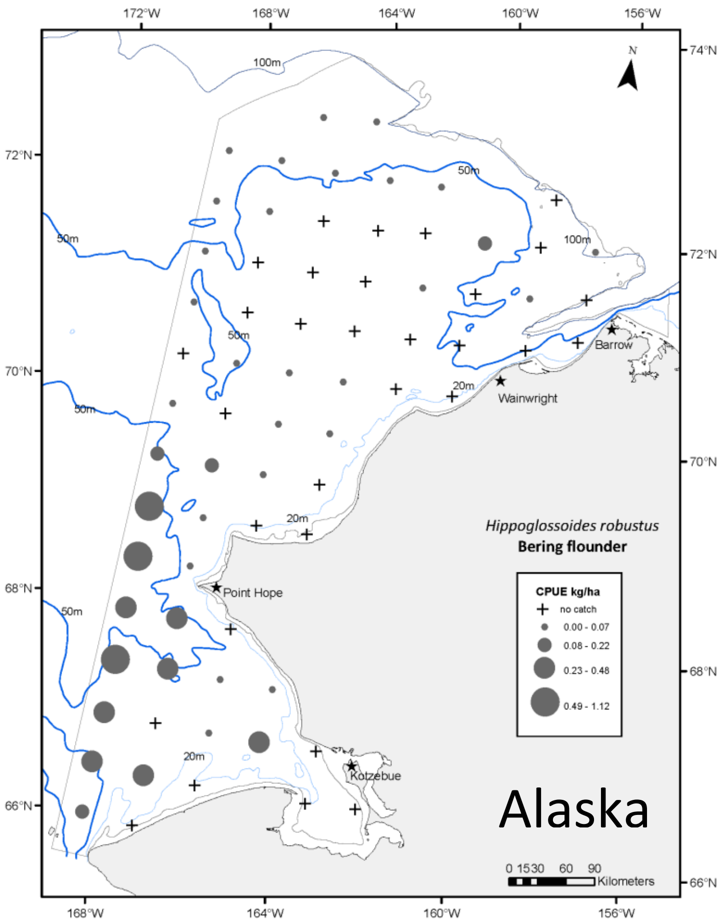


Figure 24.--Distribution and relative abundance (CPUE kg/ha) of *Hippoglossoides robustus* (Bering flounder) for the 2012 Chukchi Sea bottom trawl survey.

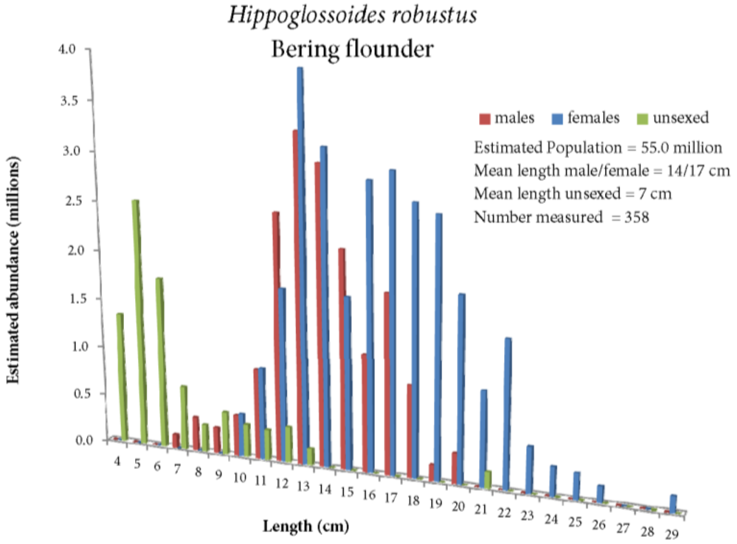


Figure 25.--Estimated abundance at length by sex of *Hippoglossoides robustus* (Bering flounder) for the 2012 Chukchi Sea bottom trawl survey.

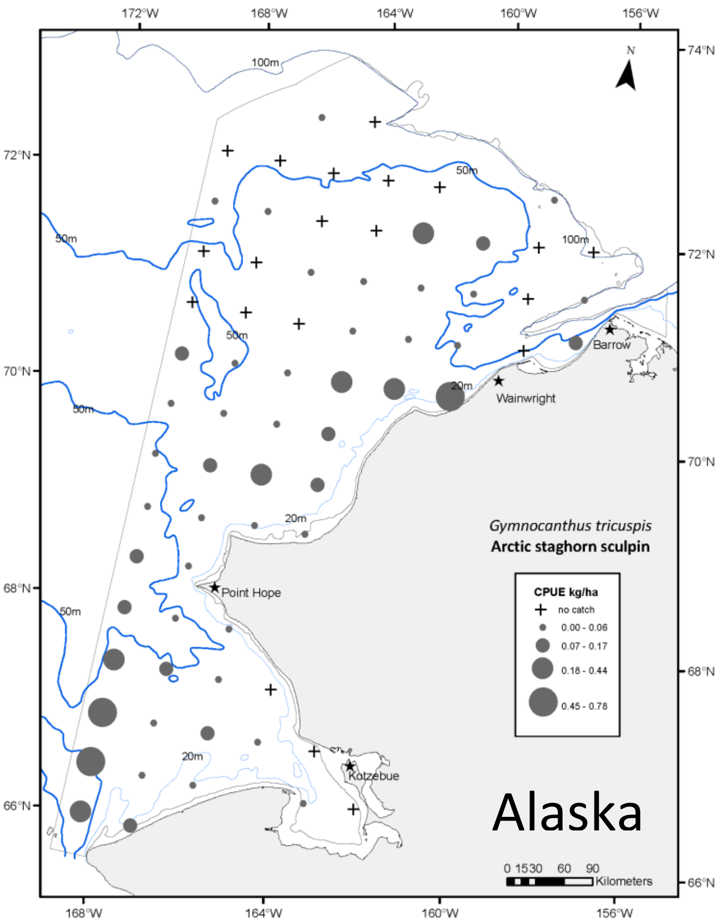


Figure 26.--Distribution and relative abundance (CPUE kg/ha) of *Gymnocanthus tricuspis* (Arctic staghorn sculpin) for the 2012 Chukchi Sea bottom trawl survey.

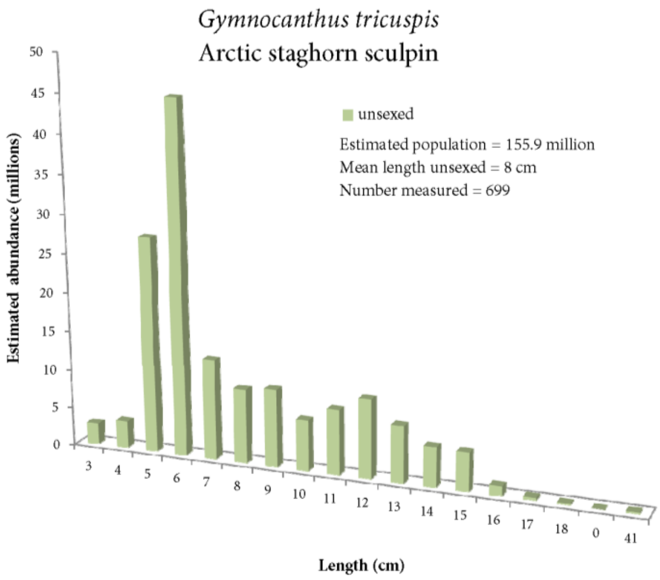


Figure 27.--Estimated abundance at length by sex of *Gymnocanthus tricuspis* (Arctic staghorn sculpin) for the 2012 Chukchi Sea bottom trawl survey.

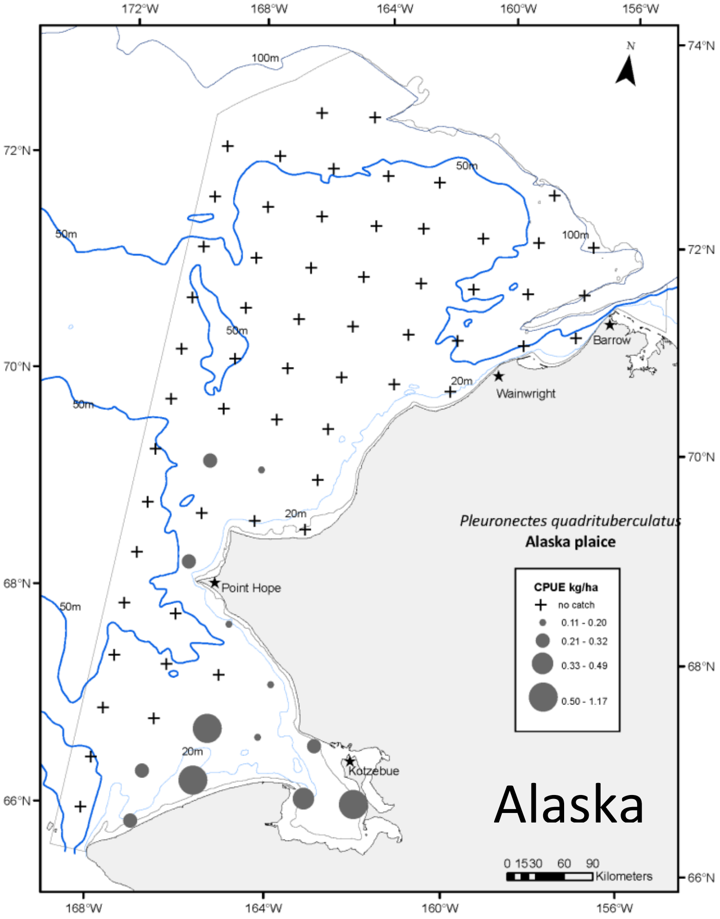


Figure 28.--Distribution and relative abundance (CPUE kg/ha) of *Pleuronectes quadrituberculatus* (Alaska plaice) for the 2012 Chukchi Sea bottom trawl survey.

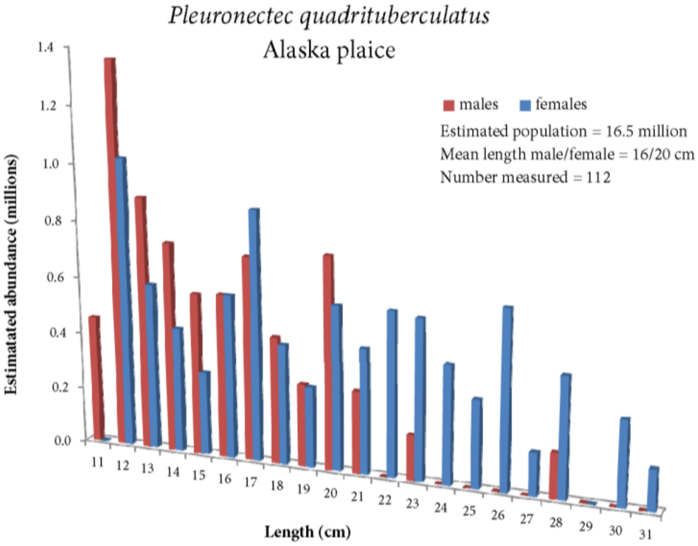


Figure 29.--Estimated abundance at length by sex of *Pleuronectes quadrituberculatus* (Alaska plaice) for the 2012 Chukchi Sea bottom trawl survey.

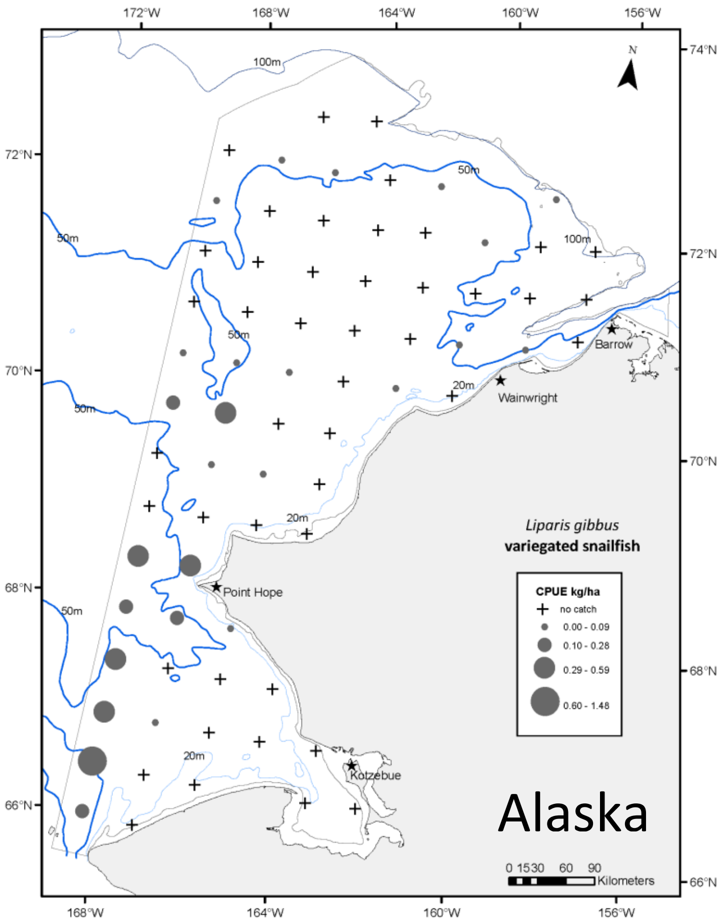


Figure 30.--Distribution and relative abundance (CPUE kg/ha) of *Liparis gibbus* (variegated snailfish) for the 2012 Chukchi Sea bottom trawl survey.

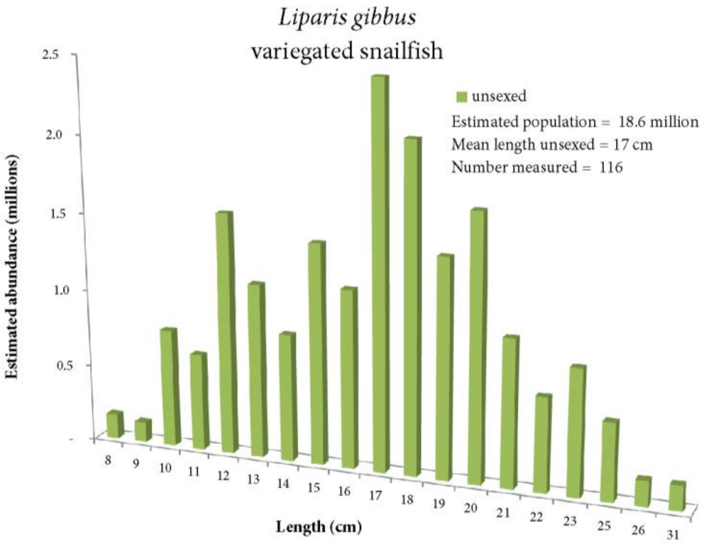


Figure 31.--Estimated abundance at length by sex of *Liparis gibbus* (variegated snailfish) for the 2012 Chukchi Sea bottom trawl survey.

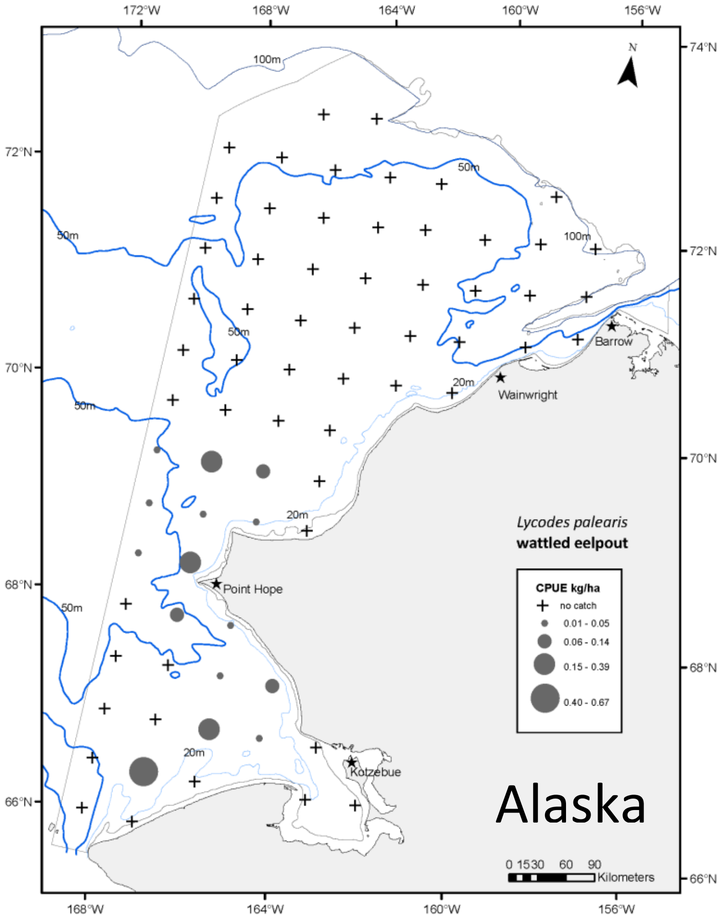


Figure 32.--Distribution and relative abundance (CPUE kg/ha) of *Bathyraja parmifera* (Alaska skate) for the 2012 Chukchi Sea bottom trawl survey.

Only one large skate was encountered during the survey therefore an estimated abundance at length plot was not created.

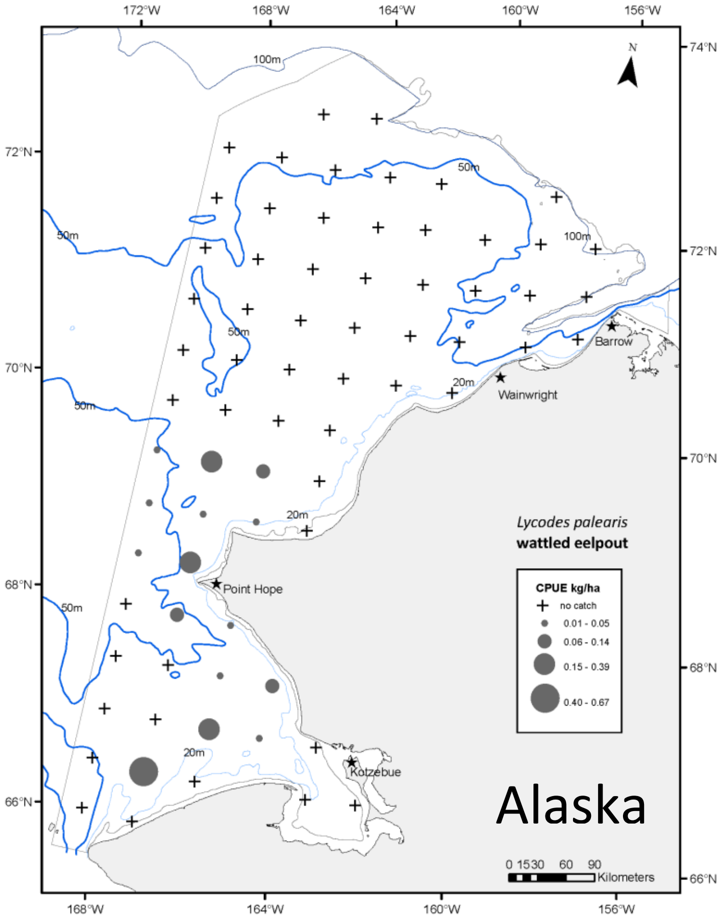


Figure 33.--Distribution and relative abundance (CPUE kg/ha) of *Lycodes palearis* (wattled eelpout) for the 2012 Chukchi Sea bottom trawl survey.

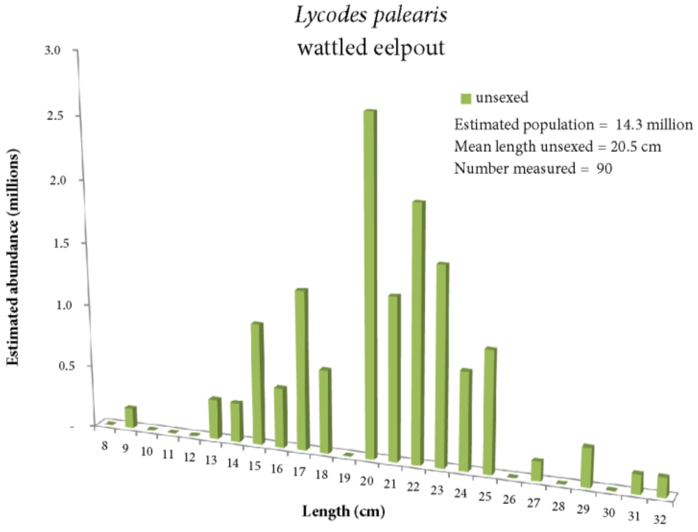


Figure 34.--Estimated abundance at length by sex of *Lycodes palearis* (wattled eelpout) for the 2012 Chukchi Sea bottom trawl survey.

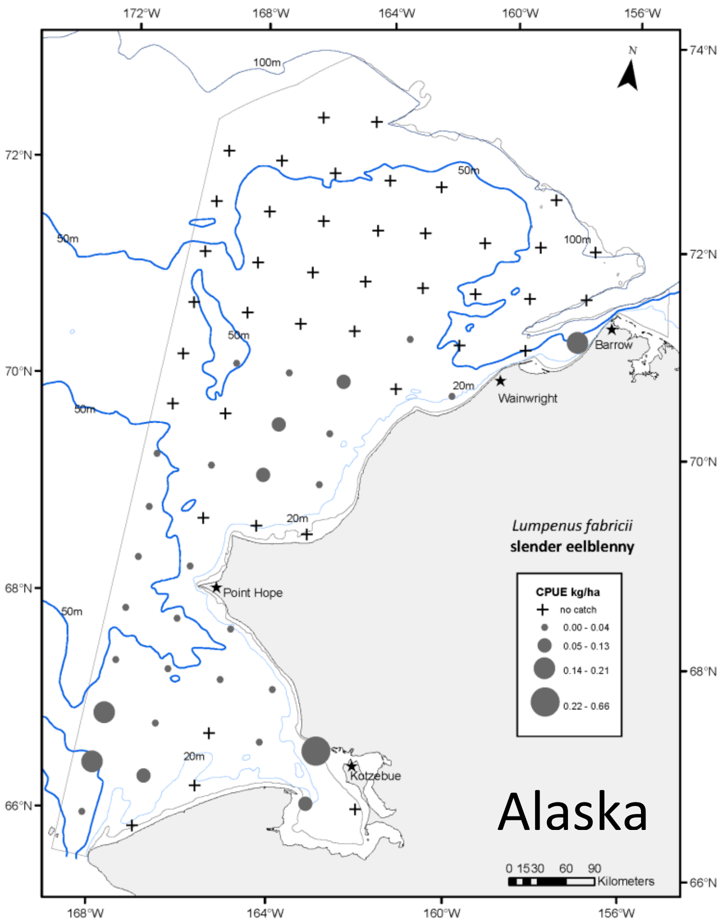


Figure 35.--Distribution and relative abundance (CPUE kg/ha) of *Lumpenus fabricii* (slender eelblenny) for the 2012 Chukchi Sea bottom trawl survey.

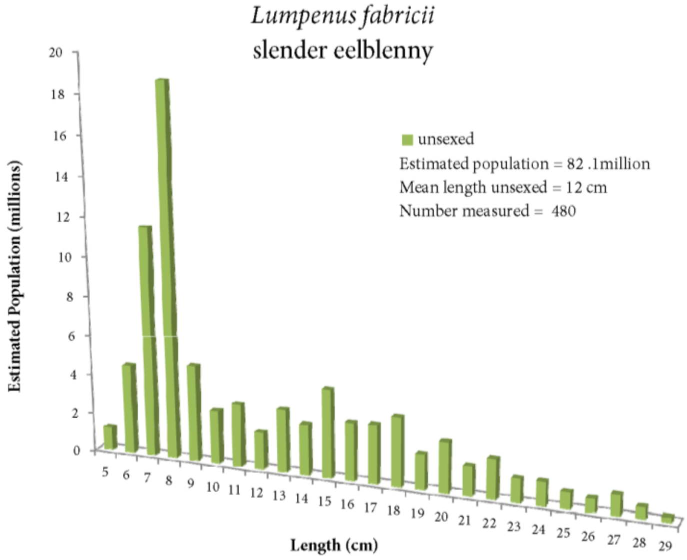


Figure 36.--Estimated abundance at length by sex of *Lumpenus fabricii* (slender eelblenny) for the 2012 Chukchi Sea bottom trawl survey.

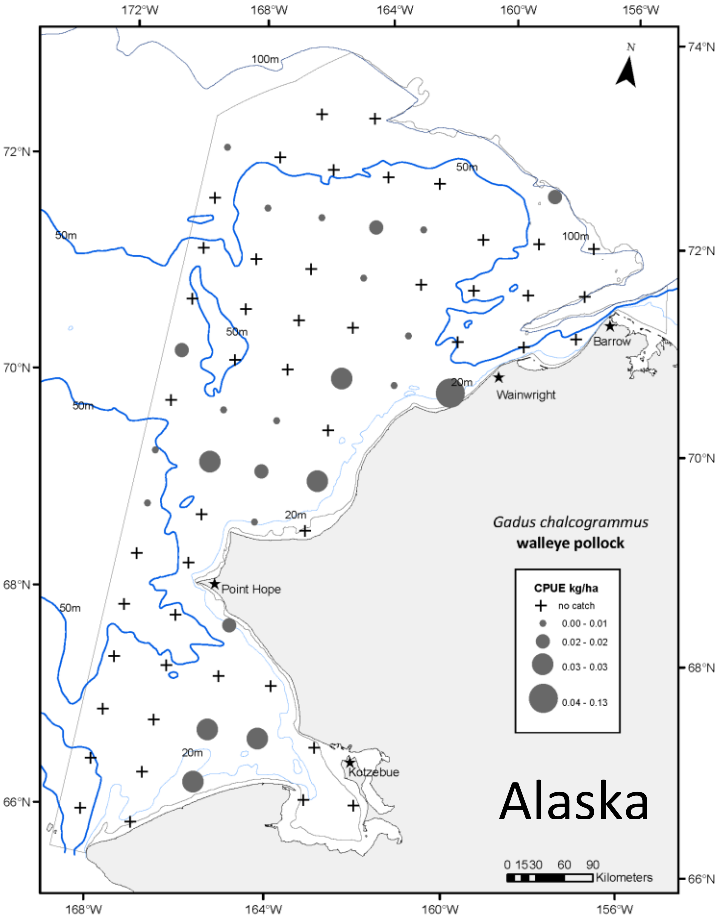


Figure 37.--Distribution and relative abundance (CPUE kg/ha) of *Gadus chalcogrammus* (walleye pollock) for the 2012 Chukchi Sea bottom trawl survey.

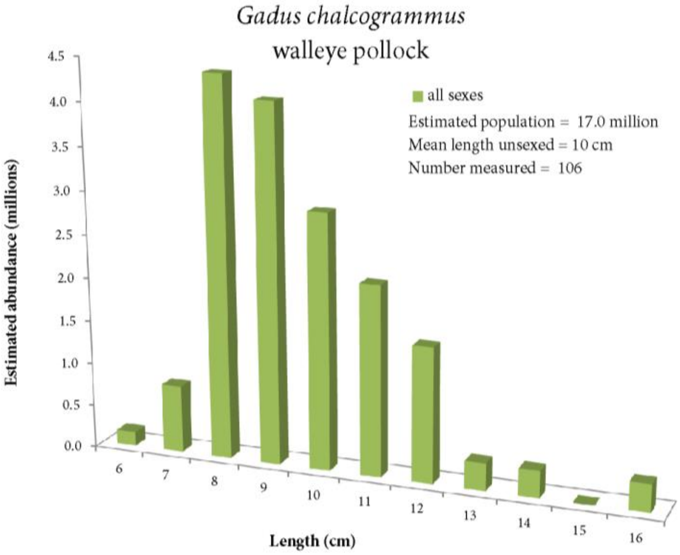


Figure 38.--Estimated abundance at length by sex of *Gadus chalcogrammus* (walleye pollock) for the 2012 Chukchi Sea bottom trawl survey.

Table 8.--Mean and standard error of catch per unit effort (CPUE kg/ha and no./ha) for invertebrate taxa caught during the 2012 Chukchi Sea bottom trawl survey.

Scientific name	Common name	Mean CPUE (kg/ha)	Standard error mean CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error mean CPUE (no./ha)
Strongylocentrotus droebachiensis	green sea urchin	15.89	6.93	387.17	213.89
Asterias amurensis	purple-orange sea star	8.80	3.39	236.35	127.27
Pagurus trigonocheirus	fuzzy hermit crab	7.87	1.67	162.34	27.54
Chionoecetes opilio	snow crab	7.45	2.58	212.50	76.12
Psolus fabricii	brownscaled sea cucumber	5.54	2.45	156.93	72.28
Neptunea heros		4.48	1.18	45.42	11.27
Boltenia ovifera		4.17	3.32	1.71	0.85
Leptasterias polaris		3.99	0.94	40.30	8.76
Gorgonocephalus sp. cf. *arcticus*		3.59	1.51	37.42	13.69
	empty gastropod shells	3.55	1.14	-	-
Halichondria sp.		3.30	3.17	-	-
Styela rustica	sea potato	2.42	1.16	1.10	0.60
Chrysaora melanaster		2.27	0.42	2.46	0.54
Urticina crassicornis	mottled anemone	1.93	0.60	43.76	14.55
Halichondria sitiens	black papilliate sponge	1.77	1.24	-	-
Halocynthia aurantium	sea peach	1.65	0.96	5.40	4.77
Gorgonocephalus eucnemis	basketstar	1.58	1.23	9.81	6.48
Cyanea capillata	lion's mane	1.45	0.43	12.35	4.24
Hyas coarctatus	circumboreal toad crab	1.34	0.49	43.91	14.21
Neptunea ventricosa	fat whelk	1.33	0.73	15.30	7.91
	empty bivalve shells	1.16	0.74	0.01	0.01
Urasterias lincki		1.15	0.47	8.31	3.81
Ascidiacea	tunicate unident.	1.12	0.65	3.25	2.63
Solaster arcticus		0.98	0.86	1.24	0.64
Telmessus cheiragonus	helmet crab	0.89	0.36	12.22	5.57
Lethasterias nanimensis	blackspined sea star	0.84	0.30	3.42	1.12
Thoracica	barnacle unident.	0.75	0.41	2.60	1.28
Ctenodiscus crispatus	common mud star	0.66	0.46	87.75	59.49
Ophiura sarsi	notched brittlestar	0.62	0.19	190.80	73.66
Pagurus capillatus	hairy hermit crab	0.62	0.26	23.24	10.55
Echinarachnius parma	parma sand dollar	0.58	0.58	0.44	0.32
Porifera	sponge unident.	0.46	0.26	-	-
Suberites sp.		0.43	0.43	-	-
Boltenia ecinata		0.40	0.22	0.14	0.12
Bryozoa	bryozoan unident.	0.39	0.20	0.03	0.02

Table 8.—Continued.

Scientific name	Common name	Mean CPUE (kg/ha)	Standard error mean CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error mean CPUE (no./ha)
Gersemia sp.	sea raspberry	0.36	0.17	1.78	1.03
Evasterias echinosoma	giant sea star	0.35	0.12	1.96	1.00
Actiniaria	sea anemone unident.	0.33	0.14	17.44	10.94
Leptasterias arctica		0.33	0.14	13.90	3.96
Pagurus rathbuni	longfinger hermit	0.32	0.06	17.16	3.14
Neptunea borealis		0.31	0.05	20.51	4.49
Beringius beringii		0.30	0.15	3.15	1.33
Stomphia sp.		0.26	0.25	4.91	4.69
Labidochirus splendescens	splendid hermit	0.25	0.07	21.93	5.84
Chlamys behringiana	Iceland scallop	0.21	0.12	3.49	2.02
Serripes laperousii	broad cockle	0.18	0.18	0.44	0.39
Chelyosoma productum		0.18	0.12	24.51	19.42
Stomphia coccinea	swimming anemone	0.17	0.12	4.46	3.00
Plicifusus kroyeri		0.17	0.06	6.50	2.29
Leptasterias groenlandica		0.16	0.04	27.51	14.45
Buccinum glaciale	glacial whelk	0.16	0.15	3.10	2.73
Polychaete tubes		0.14	0.13	-	-
Buccinum sp. eggs		0.13	0.04	-	-
Sclerocrangon boreas	sculptured shrimp	0.12	0.08	9.33	5.56
Argis lar	kuro argid	0.12	0.02	22.80	4.81
Crossaster papposus	rose sea star	0.12	0.03	6.52	1.74
Paralithodes platypus	blue king crab	0.11	0.05	0.25	0.13
	hydroid unident.	0.11	0.04	-	-
	compound ascidian unid.	0.11	0.10	0.03	0.03
Tritonia diomedea	rosy tritonia	0.10	0.10	1.54	1.53
Pyrulofusus deformis	warped whelk	0.10	0.03	1.52	0.41
Myriotrochus rinkii		0.10	0.04	273.76	130.60
Pteraster obscurus	obscure sea star	0.09	0.03	1.29	0.41
Naticidae eggs	moonsnail eggs unident.	0.09	0.02	-	-
Alcyonidium enteromorpha	noodle bryozoan	0.09	0.05	1.45	1.45
Molgula sp.		0.09	0.09	5.92	5.92
Alcyonidium disforme		0.09	0.05	22.95	18.78
Buccinum angulosum	angular whelk	0.08	0.02	3.73	1.19
gastropod eggs	snail eggs	0.08	0.03	-	-
Volutopsius fragilis	fragile whelk	0.08	0.04	1.85	0.70

Table 8.—Continued.

Scientific name	Common name	Mean CPUE (kg/ha)	Standard error mean CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error mean CPUE (no./ha)
Gersemia fruticosa		0.08	0.03	0.11	0.05
Amicula vestita		0.07	0.04	7.58	3.86
Beringius stimpsoni		0.07	0.05	0.92	0.46
Buccinum scalariforme	ladder whelk	0.07	0.02	4.00	1.10
Stylissa sp.	drumstick sponge	0.06	0.05	0.63	0.38
Musculus discors	discordant mussel	0.06	0.03	8.68	6.29
Neptunea sp. eggs		0.05	0.03	-	-
Ocnus glacialis		0.05	0.03	7.28	4.76
Buccinum polare	polar whelk	0.05	0.01	2.16	0.45
Volutopsius stefanssoni	shouldered whelk	0.04	0.03	0.63	0.40
Clinocardium ciliatum	hairy cockle	0.04	0.03	1.68	1.08
Actinostola sp.		0.04	0.03	0.52	0.39
Metridium sp.		0.04	0.02	0.72	0.41
Nuculana pernula	northern nutclam	0.04	0.02	26.32	13.51
Tritonia sp.		0.03	0.02	0.73	0.42
Alcyonidium pedunculatum		0.03	0.01	0.42	0.29
Cribrinopsis fernaldi	chevron-tentacled anemon	0.03	0.03	0.49	0.35
Aplidium sp. A (Clark 2006)	sea glob	0.03	0.01	0.11	0.08
Urticina sp.		0.03	0.02	1.36	0.90
	tube worm unident.	0.03	0.02	-	-
Actinostola groenlandica		0.03	0.02	0.46	0.29
Polychaeta	polychaete worm unident.	0.03	0.02	3.83	2.79
Serripes groenlandicus	Greenland cockle	0.03	0.01	0.85	0.22
Polymastia sp.		0.03	0.02	0.01	0.01
Cryptonatica (=*Natica*) *russa*	rusty moonsnail	0.02	0.01	2.18	0.57
Ocnus sp.		0.02	0.02	17.41	17.26
Euspira pallida	pale moonsnail	0.02	0.01	1.42	0.30
Pandalus goniurus	humpy shrimp	0.02	0.01	13.95	6.86
Distaplia sp. A (Clark 2006)		0.02	0.02	-	-
Astarte arctica		0.02	0.01	0.81	0.37
Hiatella arctica	Arctic hiatella	0.02	0.02	5.51	5.33
Halocynthia sp.	sea peach unident.	0.02	0.02	0.00	0.00
Mytilus sp.		0.02	0.02	0.89	0.89
Paralithodes camtschaticus	red king crab	0.02	0.01	0.02	0.01
Ophiacantha bidentata		0.02	0.02	15.26	15.26
Alcyonidium sp.		0.02	0.02	0.01	0.01
Henricia tumida	tumid sea star	0.02	0.01	2.28	1.09

Table 8.—Continued.

Scientific name	Common name	Mean CPUE (kg/ha)	Standard error mean CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error mean CPUE (no./ha)
Holothuroidea	sea cucumber unident.	0.02	0.01	0.18	0.17
Actinostolidae		0.01	0.01	0.67	0.44
Colus halli	shrew whelk	0.01	0.00	1.09	0.31
Colus sp.		0.01	0.01	0.41	0.39
Musculus niger	black mussel	0.01	0.01	1.40	1.39
Trichotropis bicarinata	two-keel hairysnail	0.01	0.01	0.96	0.69
Molgula griffithsii	sea grape	0.01	0.01	0.52	0.44
Amphiophiura nodosa		0.01	0.01	6.99	4.29
Cucumaria sp.		0.01	0.01	0.02	0.02
Eualus sp.		0.01	<0.01	12.57	4.54
Eunoe nodosa	giant scale worm	0.01	<0.01	1.54	0.50
Pagurus ochotensis	Alaskan hermit	0.01	0.01	0.16	0.12
Saduria entomon		0.01	0.01	0.25	0.18
Eunoe depressa	depressed scale worm	0.01	0.01	1.67	0.68
Balanus sp.		0.01	0.01	0.31	0.29
Clinopegma magnum	helmet whelk	0.01	<0.01	0.27	0.10
Colus sabini		0.01	0.01	0.54	0.48
Eualus gaimardii		0.01	<0.01	7.23	3.22
Henricia beringiania	Bering Henricia	0.01	<0.01	0.10	0.04
Eunoe sp.		0.01	<0.01	0.98	0.53
Echiura	echiuroid worm unident.	0.01	<0.01	0.19	0.10
Golfingia margaritacea		0.01	<0.01	0.34	0.17
Benthoctopus sibiricus		0.01	<0.01	0.06	0.02
Colus spitzbergensis	thick-ribbed whelk	0.01	<0.01	0.60	0.28
Dendrobeania sp.		0.01	0.01	-	-
Nemertea	nemertean worm unident.	0.01	<0.01	1.50	0.88
Margarites costalis	boreal rosy margarite	0.01	<0.01	0.97	0.35
Onchidiopsis sp.		0.01	<0.01	0.63	0.33
Onchidiopsis carnea		0.01	<0.01	0.14	0.06
Volutopsius sp. eggs		0.00	<0.01	-	-
Calycidoris guentheri		<0.01	<0.01	0.53	0.42
Pteraster tesselatus		<0.01	<0.01	0.01	0.01
Astarte sp.		<0.01	<0.01	2.09	2.08
Argis sp.		<0.01	<0.01	0.46	0.45
Astarte esquimalti		<0.01	<0.01	1.53	0.92
Eualus suckleyi	shortscale eualid	<0.01	<0.01	3.85	2.11
Ptychodactis patula		<0.01	<0.01	0.10	0.06

Table 8.—Continued.

Scientific name	Common name	Mean CPUE (kg/ha)	Standard error mean CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error mean CPUE (no./ha)
Buccinum tenellum		<0.01	<0.01	0.17	0.16
Neptunea middendorffii		<0.01	<0.01	0.09	0.09
Buccinum ectomycina		<0.01	<0.01	0.07	0.05
Plicifusus johanseni		<0.01	<0.01	0.18	0.06
Rhamphostomella costata	ribbed bryozoan	<0.01	<0.01	0.01	0.01
Buccinum plectrum	sinuous whelk	<0.01	<0.01	0.11	0.05
Onchidiopsis glacialis	icy lamellaria	<0.01	<0.01	0.10	0.06
Cryptonatica (=*Natica*) *aleutica*	Aleutian moonsnail	<0.01	<0.01	0.29	0.28
Colus hypolispus		<0.01	<0.01	0.17	0.07
Buccinum obsoletum		<0.01	<0.01	0.14	0.04
Ophiopholis aculeata	ubiquitous brittle star	<0.01	<0.01	1.74	0.98
Dendronotus frondosus	frond-aeolis	<0.01	<0.01	0.13	0.12
Stegocephalus inflatus		<0.01	<0.01	0.32	0.21
Eualus macilentus	Greenland shrimp	<0.01	<0.01	1.34	0.96
Distaplia sp.		<0.01	<0.01	0.01	0.01
Asteroidea	sea star unident.	<0.01	<0.01	0.01	0.01
Flustra serrulata	leafy bryozoan	<0.01	<0.01	-	-
Onchidiopsis sp. *B* (Clark & McLean)		<0.01	<0.01	0.03	0.03
Pteraster octaster		<0.01	<0.01	0.02	0.02
Beroe sp.		<0.01	<0.01	0.02	0.02
Sipuncula	peanut worm unident.	<0.01	<0.01	1.03	0.76
Scyphozoa	jellyfish unident.	<0.01	<0.01	0.03	0.02
Lebbeus groenlandicus	spiny lebbeid	<0.01	<0.01	0.28	0.19
Crangon sp.		<0.01	<0.01	0.44	0.34
Amphipoda	amphipod unident.	<0.01	<0.01	2.22	1.45
Cyclocardia crassidens	thick carditid	<0.01	<0.01	0.21	0.17
Macoma calcarea	chalky macoma	<0.01	<0.01	0.12	0.09
Lamellaria sp.		<0.01	<0.01	0.03	0.03
Argis dentata	Arctic argid	<0.01	<0.01	0.21	0.21
Heliometra glacialis		<0.01	<0.01	0.10	0.10
Nudibranchia	nudibranch unident.	<0.01	<0.01	0.12	0.09
Sabinea septemcarinata		<0.01	<0.01	0.35	0.19
Ophiura sp.		<0.01	<0.01	3.35	3.21
Cyclocardia sp. cf. *borealis* (Clark 2006)	northern carditid	<0.01	<0.01	0.33	0.29
Tochuina tetraquetra	giant orange tochui	<0.01	<0.01	0.01	0.01

Table 8.—Continued.

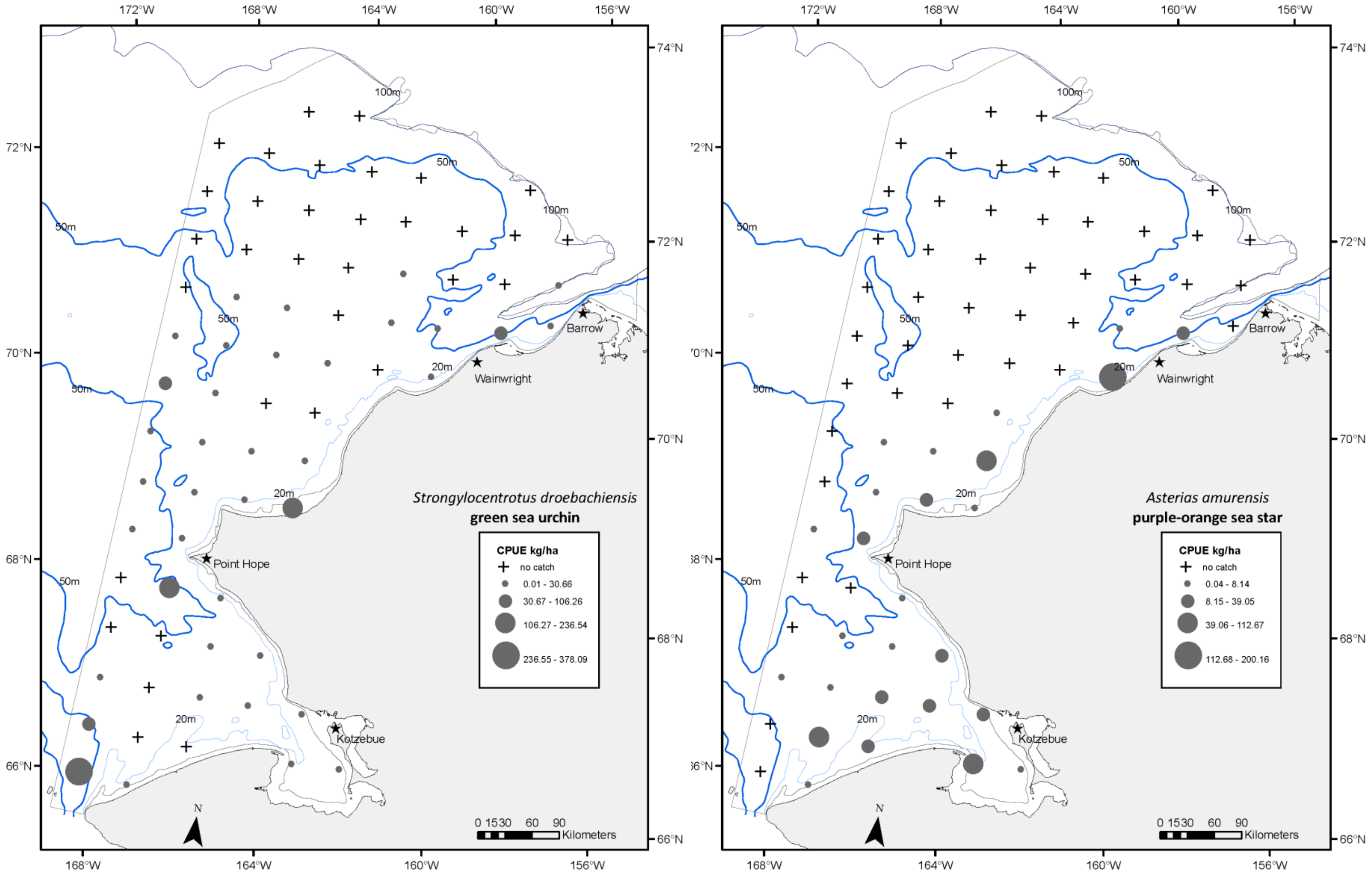
Scientific name	Common name	Mean CPUE (kg/ha)	Standard error mean CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error mean CPUE (no./ha)
Dendronotus sp.		<0.01	0.00	0.09	0.04
Distaplia occidentalis		<0.01	0.00	0.02	0.02
Serripes notabilis	oblique smoothcockle	<0.01	0.00	0.03	0.03
Crangon communis	twospine crangon	<0.01	0.00	0.52	0.52
Crangon sp. cf. *communis* (*CAS*)		<0.01	0.00	0.26	0.26
Mya truncata	truncate softshell	<0.01	0.00	0.01	0.01
Cribrinopsis sp.		<0.01	0.00	0.01	0.01
Colus martensi		<0.01	0.00	0.09	0.04
Tachyrhynchus erosus	eroded turretsnail	<0.01	0.00	0.85	0.72
Crangon dalli	ridged crangon	<0.01	<0.01	0.29	0.13
Nucula tenuis	smooth nutclam	<0.01	<0.01	0.04	0.04
Rachotropis sp.		<0.01	<0.01	0.87	0.57
Hemithiris psittacea	black brachiopod	<0.01	<0.01	0.28	0.19
Macoma sp.		<0.01	<0.01	0.15	0.09
Colus ombronius	shady whelk	<0.01	<0.01	0.07	0.03
Polynoidae	scale worm unident.	<0.01	<0.01	0.34	0.16
Mactromeris polynyma	Arctic surfclam	<0.01	<0.01	0.01	0.01
Boreotrophon pacificus		<0.01	<0.01	0.26	0.15
Clinocardium californiense	California cockle	<0.01	<0.01	0.02	0.02
Rhachotropis aculeata		<0.01	<0.01	0.66	0.32
	worm unident.	<0.01	<0.01	0.17	0.06
Boreotrophon coronatus		<0.01	<0.01	0.09	0.03
Henricia sanguinolenta	sanguine sea star	<0.01	<0.01	0.01	0.01
Pelonaia corrugata		<0.01	<0.01	0.77	0.75
Volutopsius attenuatus	attenuate melon whelk	<0.01	<0.01	0.04	0.03
Buccinum normale		<0.01	<0.01	0.07	0.05
Beringius sp. eggs		<0.01	<0.01	-	-
Maldanidae unident.	bamboo worm unident.	<0.01	<0.01	0.10	0.07
Pandalus eous (=*borealis*)	Alaskan pink shrimp	<0.01	<0.01	0.23	0.19
Nototropis sp.		<0.01	<0.01	0.23	0.19
Oractis diomedeae	grape anemone	<0.01	<0.01	0.01	0.01
Hapalogaster grebnitzkii		<0.01	<0.01	0.03	0.02
Psolus phantapus		<0.01	<0.01	0.04	0.04
Priapulus caudatus		<0.01	<0.01	0.01	0.01
Admete regina	noble admete	<0.01	<0.01	0.05	0.02

Table 8.—Continued.

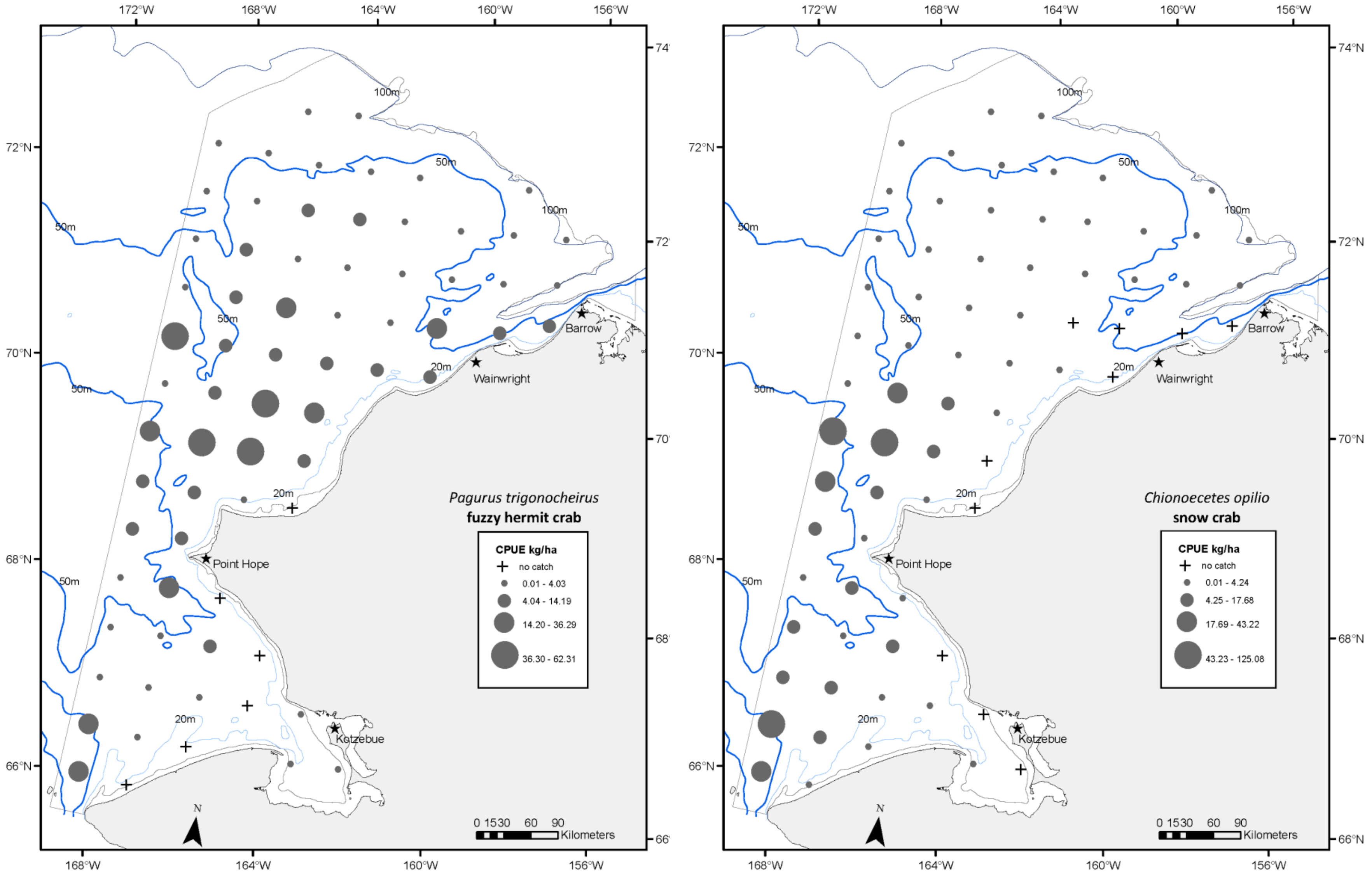
Scientific name	Common name	Mean CPUE (kg/ha)	Standard error mean CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error mean CPUE (no./ha)
Arctolembos arcticus		<0.01	<0.01	0.17	0.15
Nephtyidae	cat worm unident.	<0.01	<0.01	0.03	0.02
Yoldia hyperborea	northern yoldia	<0.01	<0.01	0.26	0.23
Crangonidae	crangonid unident.	<0.01	<0.01	0.04	0.03
Sertulariidae unident.	Sertulariid hydroid	<0.01	<0.01	0.00	0.00
Ophiuroidea	brittlestar unident.	<0.01	<0.01	1.25	1.25
Trididemnum sp.		<0.01	<0.01	-	-
Anonyx nugax	riddick amphipod	<0.01	<0.01	0.38	0.34
Tachyrhynchus reticulatus	reticulated turretsnail	<0.01	<0.01	0.11	0.09
Spirontocaris arcuata	Rathbun blade shrimp	<0.01	<0.01	0.19	0.18
Liomesus ooides	egg whelk	<0.01	<0.01	0.01	0.01
Colus bristolensis		<0.01	<0.01	0.01	0.01
Astarte montagui		<0.01	<0.01	0.03	0.03
Heteropora sp.		<0.01	<0.01	-	-
Yoldia sp.		<0.01	<0.01	0.25	0.25
Thaliacea	salp unident.	<0.01	<0.01	0.01	0.01
Travisia sp.		<0.01	<0.01	0.04	0.04
Buccinum solenum		<0.01	<0.01	0.01	0.01
Cryptonatica sp.		<0.01	<0.01	0.01	0.01
Colus capponius		<0.01	<0.01	0.02	0.02
Eunice valens		<0.01	<0.01	0.01	0.01
Stenosemus albus	northern white chiton	<0.01	<0.01	0.10	0.05
Boreotrophon clathratus	clathrate trophon	<0.01	<0.01	0.02	0.01
Dorididae	dorid nudibranch unid.	<0.01	<0.01	0.02	0.02
Crangon septemspinosa	sevenspine bay shrimp	<0.01	<0.01	0.03	0.03
Costazia ventricosa	rusty bryozoan	<0.01	<0.01	0.00	0.00
Trichotropis borealis		<0.01	<0.01	0.09	0.08
Argis levior	Nelson's argid	<0.01	<0.01	0.09	0.09
Buccinum sp.		<0.01	<0.01	0.01	0.01
Musculus sp.		<0.01	<0.01	0.03	0.03
Velutina undata	wavy lamellaria	<0.01	<0.01	0.02	0.02
Ctenophora	comb jelly unident.	<0.01	<0.01	-	-
Pentamera sp.		<0.01	<0.01	0.01	0.01
Dendronotus dalli	Dall's dendronotid	<0.01	<0.01	0.01	0.01
Spirontocaris sp.		<0.01	<0.01	0.02	0.02
Colus roseus	rosy whelk	<0.01	<0.01	0.03	0.02

Table 8.—Continued.

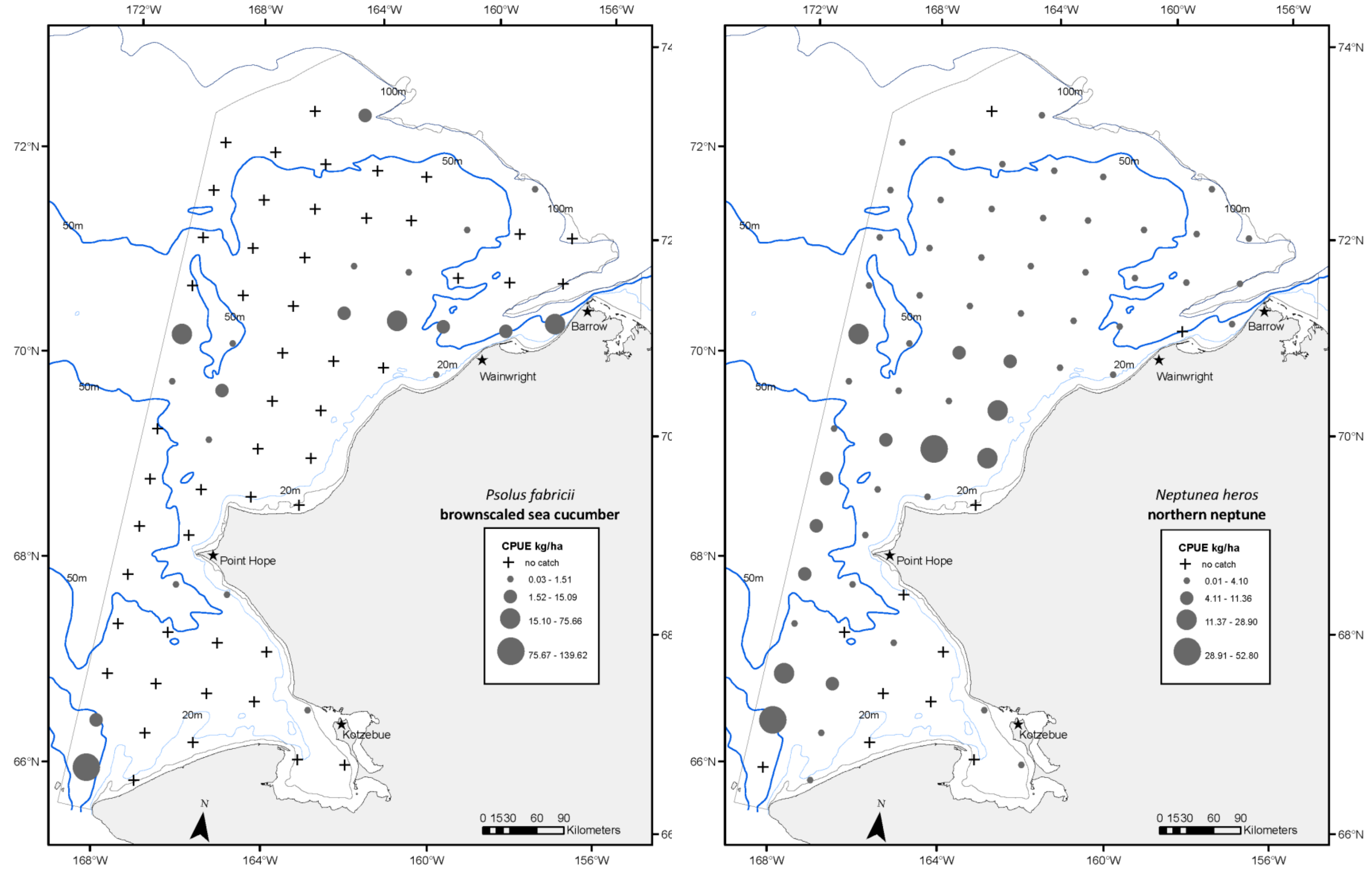
Scientific name	Common name	Mean CPUE (kg/ha)	Standard error mean CPUE (kg/ha)	Mean CPUE (no./ha)	Standard error mean CPUE (no./ha)
Emplectonema sp.		<0.01	<0.01	0.01	0.01
Bivalvia	bivalve unident.	<0.01	<0.01	0.05	0.05
Hemithyridae	hemithyrid brachiopods	<0.01	<0.01	0.02	0.02
Buccinum ciliatum		<0.01	<0.01	0.01	0.01
Sabellidae	sabellid unident.	<0.01	<0.01	0.01	0.01
Anonyx sp.		<0.01	<0.01	0.03	0.03
Pandora glacialis	glacial pandora	<0.01	<0.01	0.01	0.01
Eusirus cuspidatus		<0.01	<0.01	0.04	0.04
	limpet unident.	<0.01	<0.01	0.04	0.04
Cyclocardia sp.		<0.01	<0.01	0.01	0.01
Velutina prolongata	elongate lamellaria	<0.01	<0.01	0.01	0.01
Velutina sp.		<0.01	<0.01	0.02	0.02
Musculus glacialis	corrugate mussel	<0.01	<0.01	0.01	0.01
Cerebratulus californienesis		<0.01	<0.01	0.01	0.01
Eualus fabricii	Arctic eualid	<0.01	<0.01	0.02	0.02
Margarites giganteus	giant margarite	<0.01	<0.01	0.02	0.01
Mysida	opossum shrimps	<0.01	<0.01	0.05	0.05
Phyllodocidae unident.		<0.01	<0.01	0.03	0.02
Oenopota sp.		<0.01	<0.01	0.01	0.01
Eunoe senta		<0.01	<0.01	0.01	0.01
Melita dentata		<0.01	<0.01	0.03	0.03
Margarites sp.		<0.01	<0.01	0.01	0.01
Neoiphinoe echinata		<0.01	<0.01	0.01	0.01
Bugula sp.		<0.01	<0.01	0.01	0.01
Tubulanus sp.		<0.01	<0.01	0.01	0.01
Solariella obscura	obscure solarelle	<0.01	<0.01	0.01	0.01
Quasimelita formosa		<0.01	<0.01	0.01	0.01



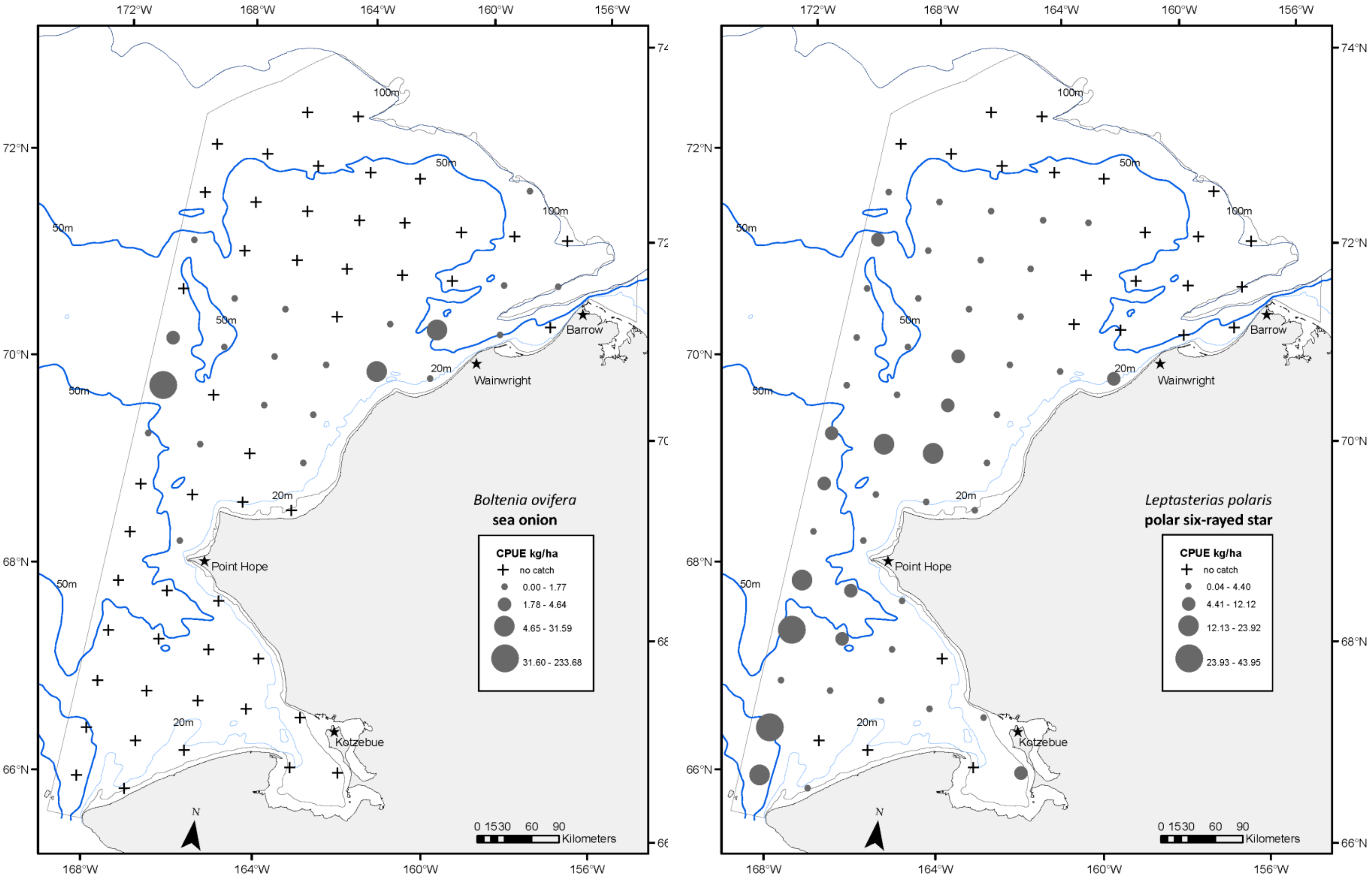
Figures 39-40.--Distribution and relative abundance (CPUE kg/ha) of *Stongylocentrotus droebachiensis* (green sea urchin) and *Asterias amurensis* (purple-orange sea star) for the 2012 Chukchi Sea bottom trawl survey.



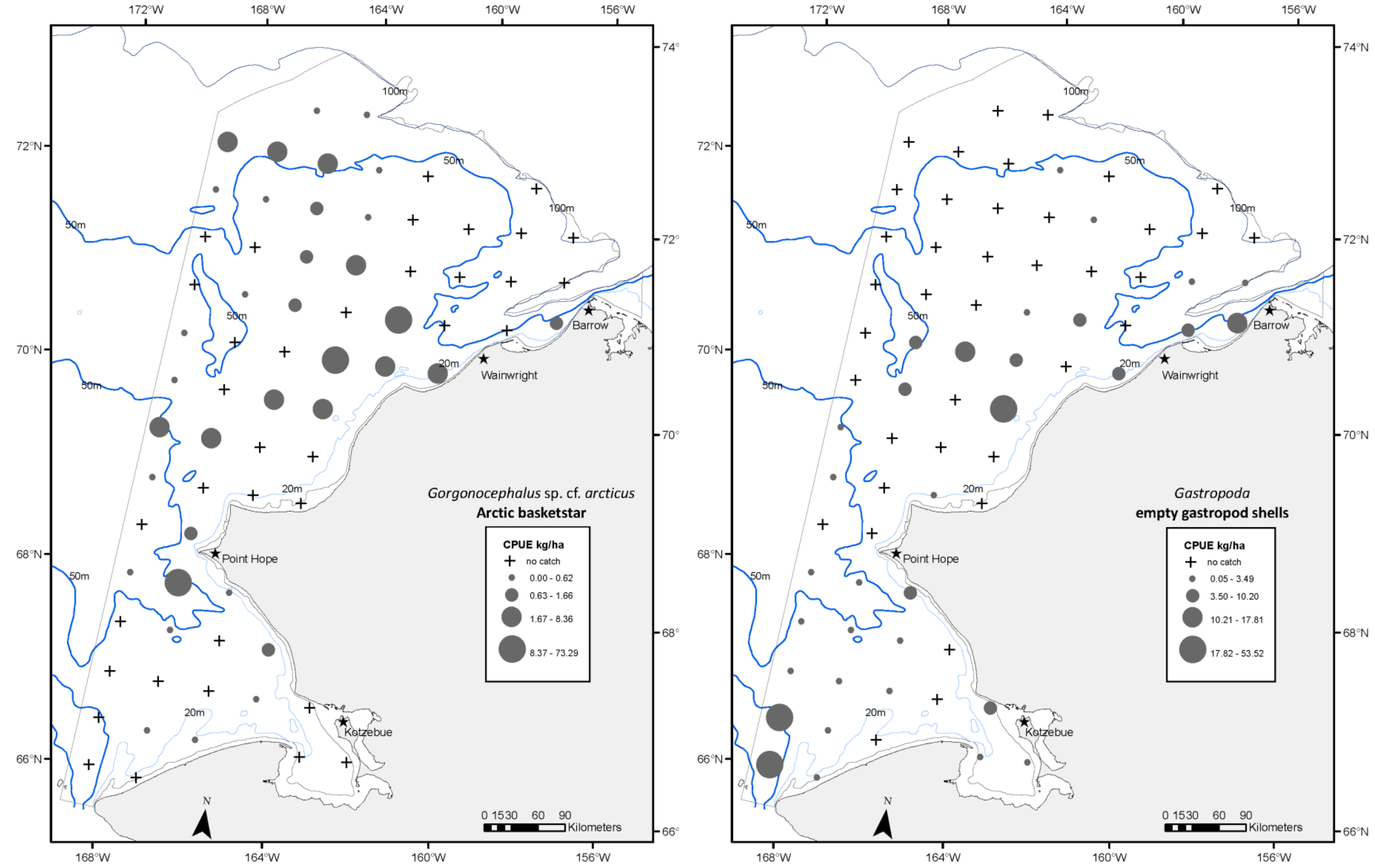
Figures 41-42.--Distribution and relative abundance (CPUE kg/ha) of *Pagurus trigonocheirus* (fuzzy hermit crab) and *Chionoecetes opilio* (snow crab) for the 2012 Chukchi Sea bottom trawl survey.



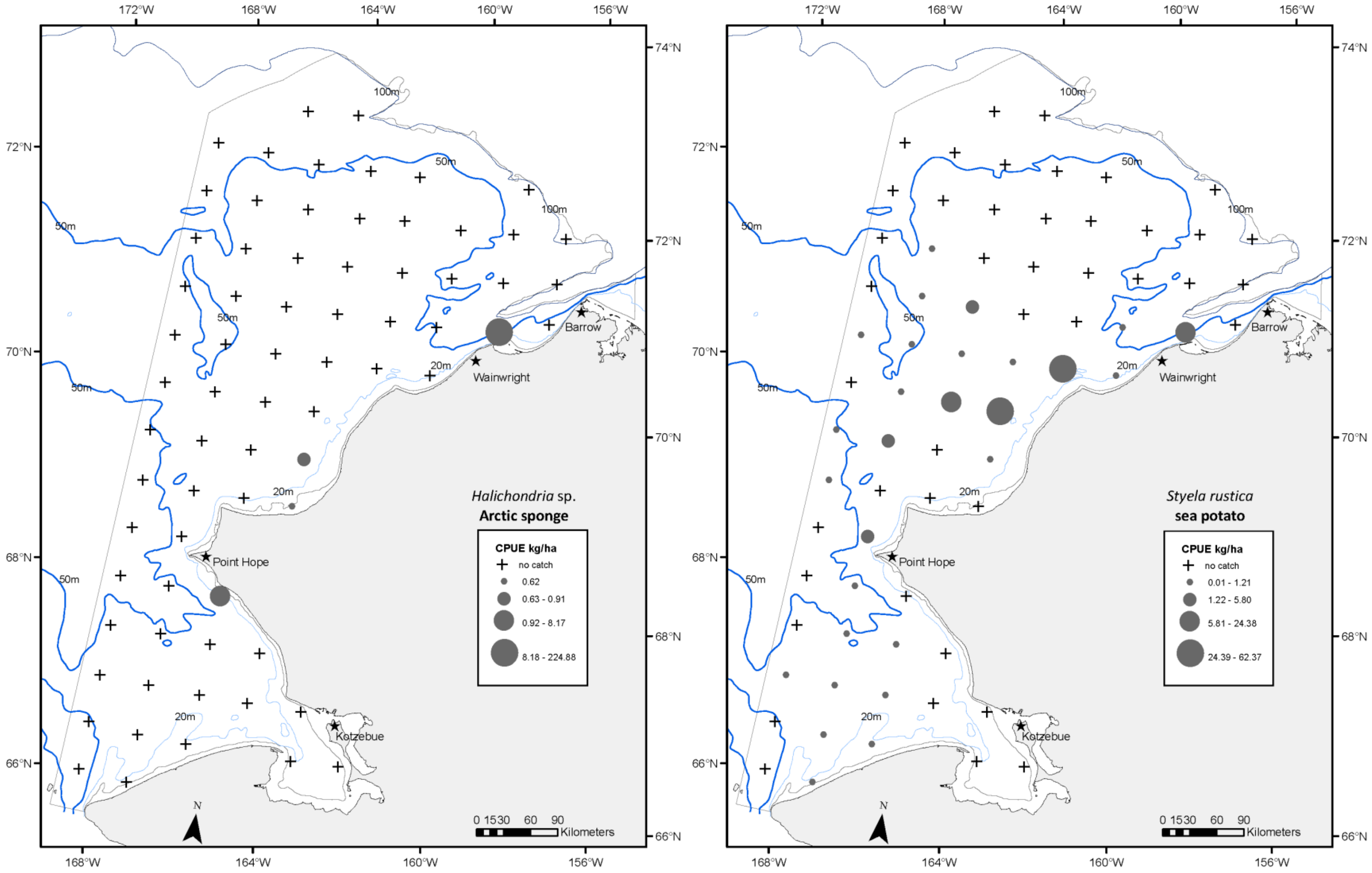
Figures 43-44.--Distribution and relative abundance (CPUE kg/ha) of *Psolus fabricii* (brownscaled sea cucumber) and *Neptunea heros* (northern neptune) for the 2012 Chukchi Sea bottom trawl survey.



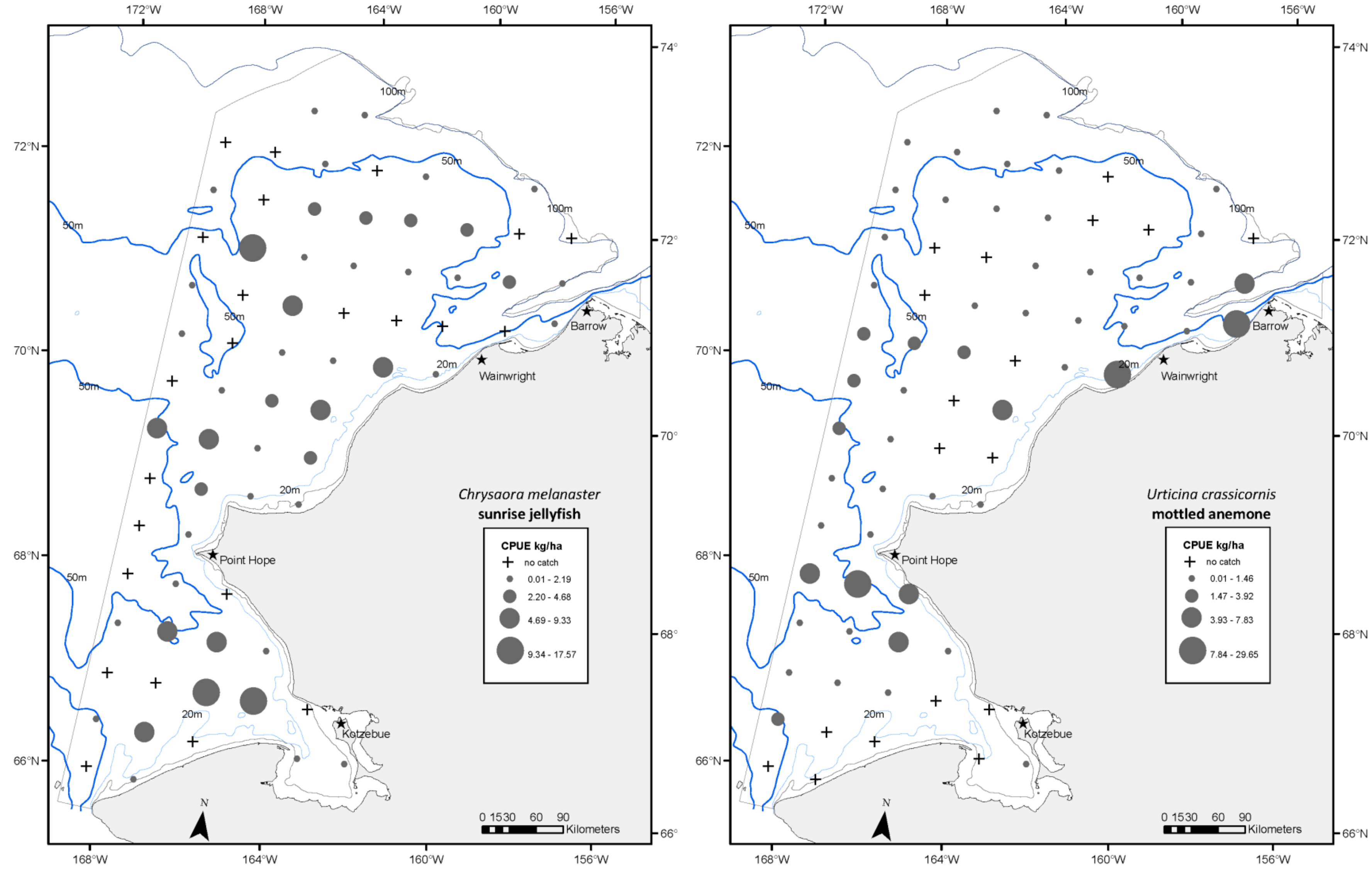
Figures 45-46.--Distribution and relative abundance (CPUE kg/ha) of *Boltenia ovifera* (sea onion) and *Leptasterias polaris* (polar six-rayed star) for the 2012 Chukchi Sea bottom trawl survey.



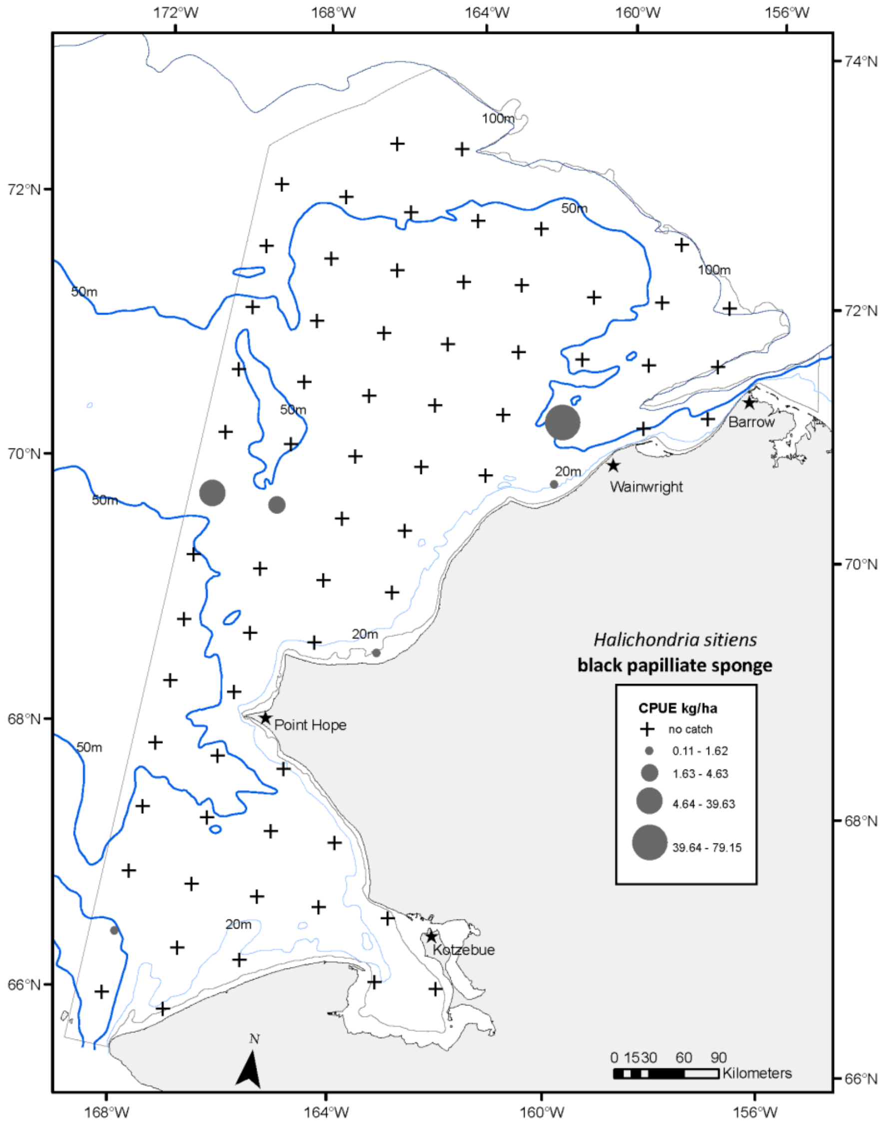
Figures 47-48.--Distribution and relative abundance (CPUE kg/ha) of *Gorgonocephalus* sp. cf. *arcticus* (Arctic basketstar) and Gastropoda (empty gastropod shells) for the 2012 Chukchi Sea bottom trawl survey.



Figures 49-50.--Distribution and relative abundance (CPUE kg/ha) of *Halichondria* sp. and *Styela rustica* (sea potato) for the 2012 Chukchi Sea bottom trawl survey.



Figures 51-52.--Distribution and relative abundance (CPUE kg/ha) of *Chrysaora melanaster* (sunrise jellyfish) and *Urticina crassicornis* (mottled anemone) for the 2012 Chukchi Sea bottom trawl survey.



Figures 53.--Distribution and relative abundance (CPUE kg/ha) of *Halichondria sitiens* (black papillate sponge) for the 2012 Chukchi Sea bottom trawl survey.

Table 9.--Summary of data collected for *Chionoecetes opilio* on the 2012 Chukchi Sea bottom trawl survey.

	Number of stations	Stations with crab	Number measured	Number caught	Estimate abundance	Estimated abundance CI	Estimated biomass (t)	Estimated biomass (t) CI
Immature male (< 75 mm CW)	71	58	2,952	14,640	2,382,547,304	1,981,901,110	86,917	67,469
Mature male (≥ 75 mm CW)	71	11	34	61	9,679,638	7,974,330	1,981	1,582
Legal (≥ 78 mm CW)	71	10	18	29	4,434,317	2,993,756	1,057	702
Immature female (< 50 mm CW)	71	52	1,816	9,005	1,491,533,174	1,119,118,560	52,882	36,159
Mature female (≥ 50 mm CW)	71	43	468	3,856	653,503,181	626,440,030	56,156	56,099
Immature unsexed (< 16 mm)	71	9	304	799	120,235,857	112,385,343	*	*

* no size-weight regression factors available for unsexed crab

CW = carapace width

CI = confidence interval

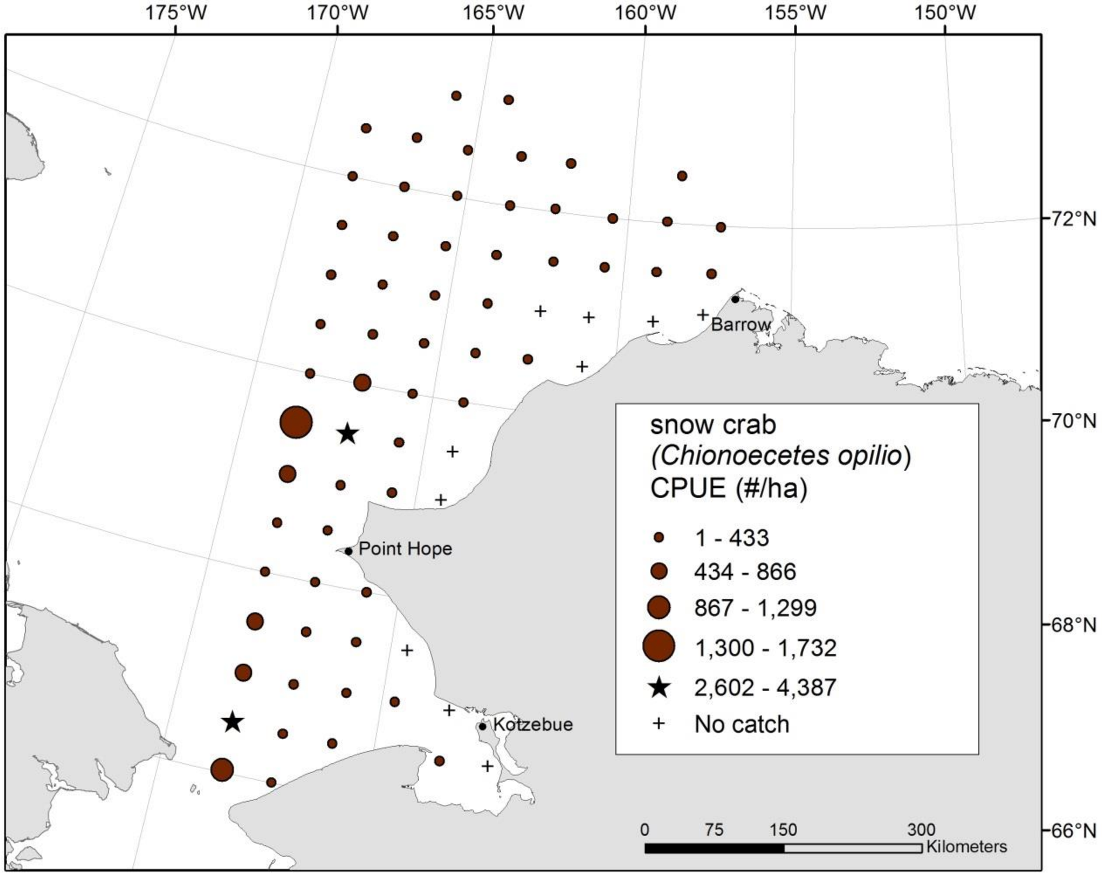


Figure 54.--Total density (CPUE no./ha) of *Chionoecetes opilio* (snow crab) at each station sampled in the 2012 Chukchi Sea bottom trawl survey. Data depicted by circles are crab densities at equal intervals.

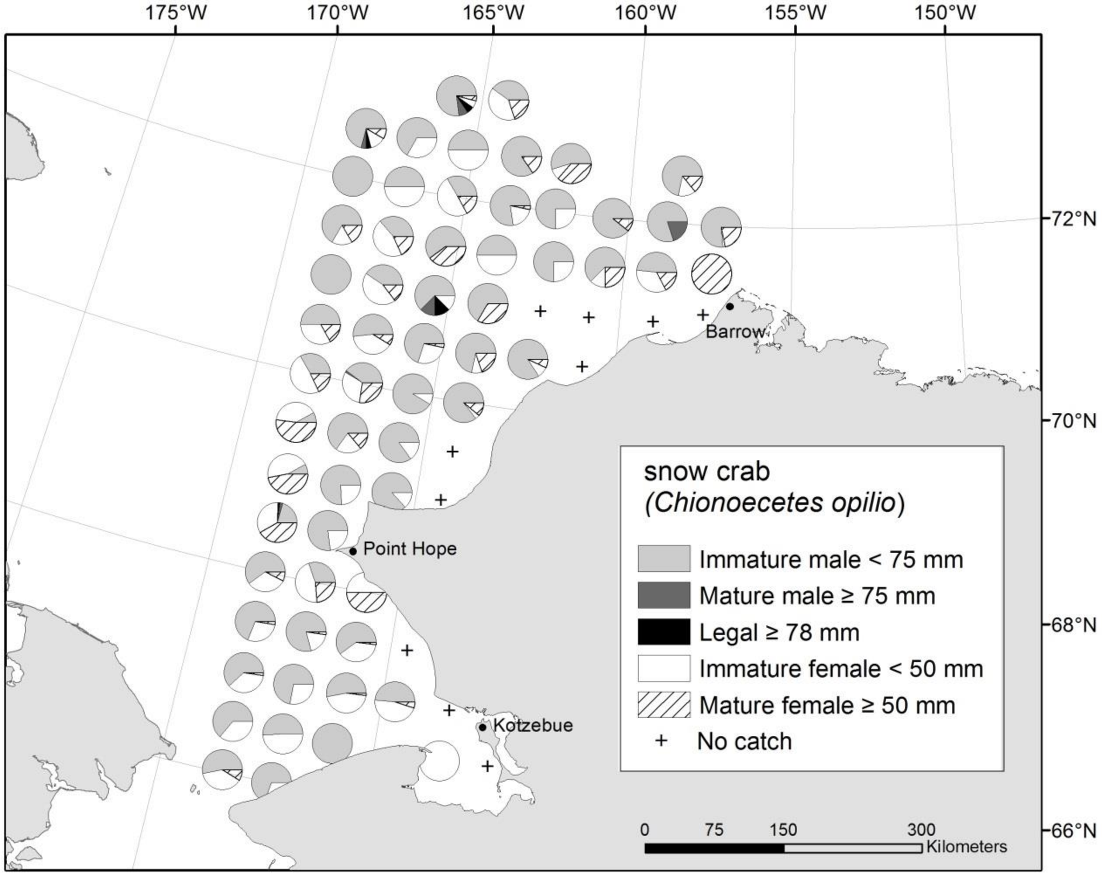


Figure 55.--Percentage of male and female *Chionoecetes opilio* (snow crab) size categories caught at each station sampled in the 2012 Chukchi Sea bottom trawl survey.

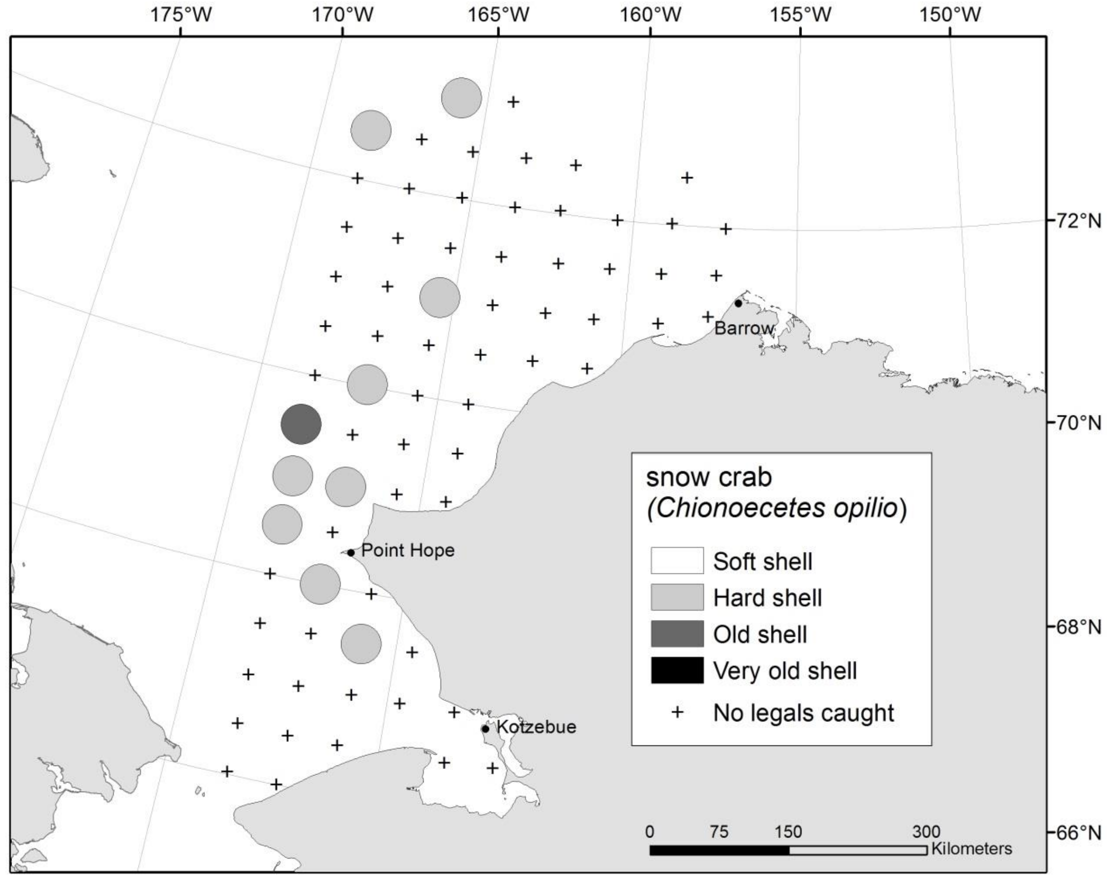


Figure 56.--Distribution of legal-sized male *Chionoecetes opilio* (snow crab), distinguished by shell condition, caught at each station sampled in the 2012 Chukchi Sea bottom trawl survey.

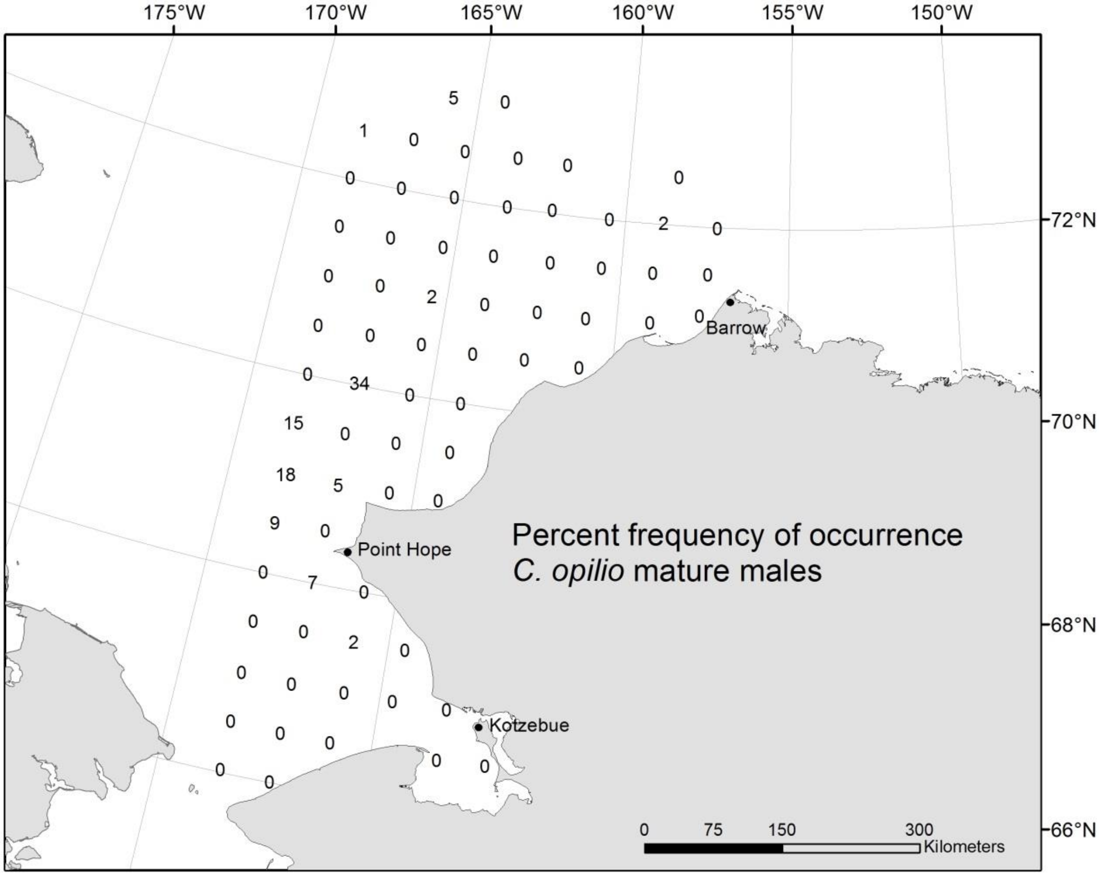


Figure 57.--Percent occurrence of mature male *Chionoecetes opilio* (snow crab) sampled in the 2012 Chukchi Sea bottom trawl survey (e.g., 34 means that 34% of all the mature male *C. opilio* observed during the survey were sampled at that station).

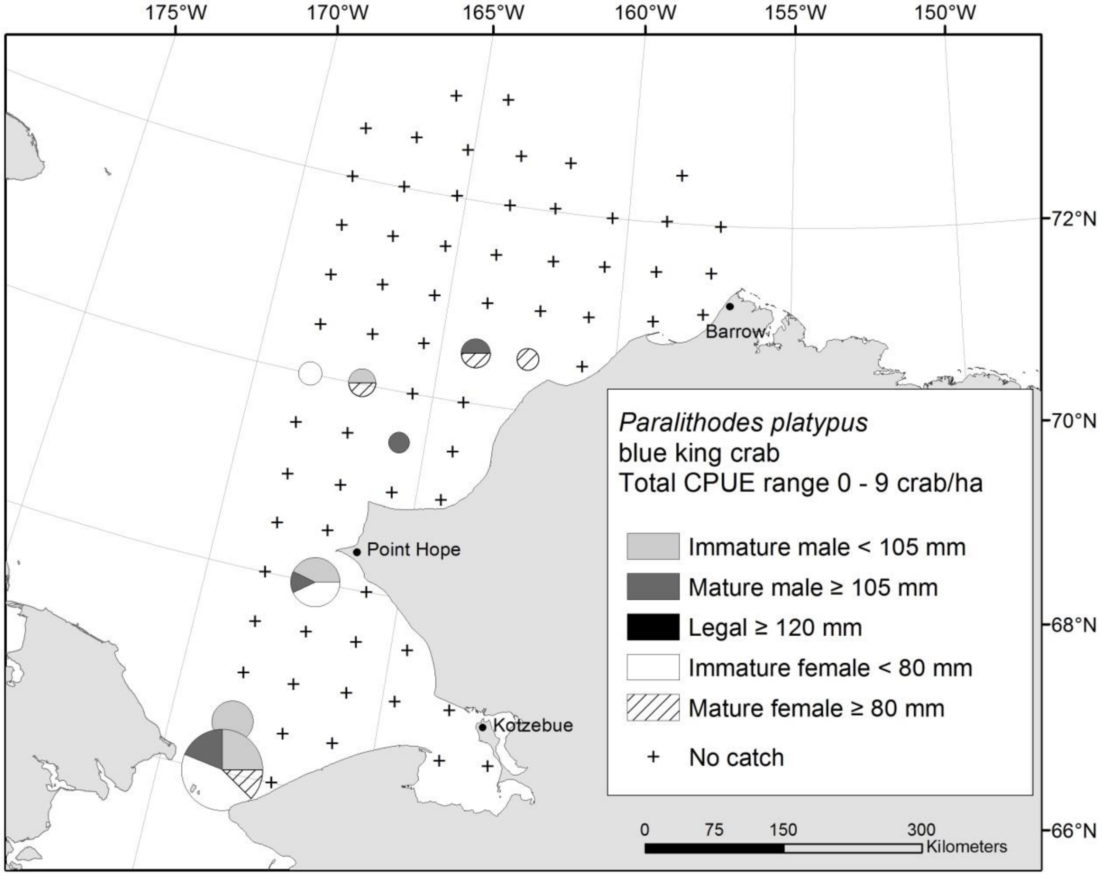


Figure 58.--Total density (CPUE no./ha) and percentage of male and female *Paralithodes platypus* (blue king crab) size categories at each station sampled in the 2012 Chukchi Sea bottom trawl survey.

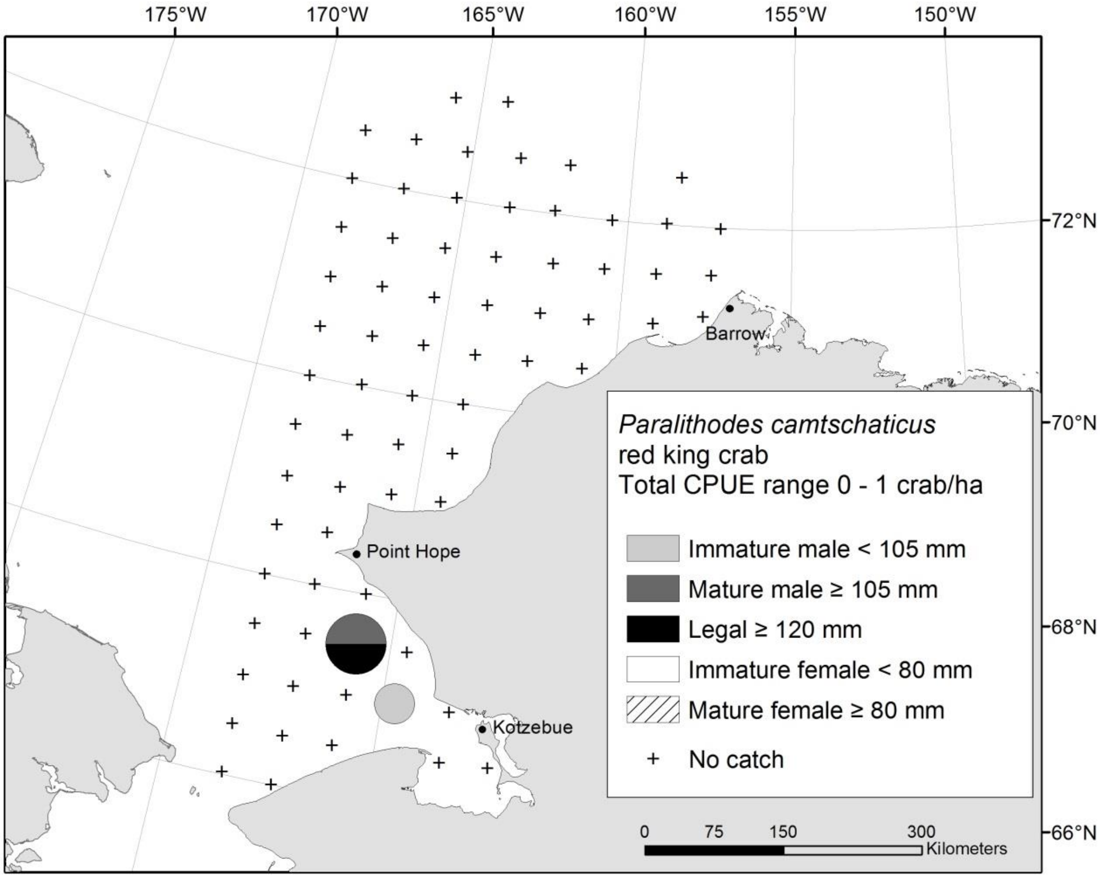


Figure 59.--Total density (CPUE no./ha) and percentage of male and female *Paralithodes camtschaticus* (red king crab) size categories at each station sampled in the 2012 Chukchi Sea bottom trawl survey.

5. ACKNOWLEDGEMENTS

Recognition and appreciation is extended to the captains, crew, vessel managers, and parent corporations of the FV Alaska Knight. Their cooperation, expertise, and goodwill made this survey possible. Appreciation is also extended to the scientists, researchers, and contractors who worked tirelessly aboard the vessel to complete the survey in a safe and successful manner. We also thank the survey support team who provided us with technical and scientific equipment. Finally, appreciation is extended to the reviewers of this document whose comments and suggestions improved it.

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APPENDICES

Appendix A.--Haul and catch (kg) data for successfully completed tows during the 2012 Chukchi Sea bottom trawl survey.

Appendix B. --Rank of fish and invertebrate taxa by the mean catch per unit effort (CPUE kg/ha) from the 2012 Chukchi Sea bottom trawl survey.

Appendix C.--Fish species encountered, in alphabetical order by family, during the 2012 Chukchi Sea bottom trawl survey.

Appendix D.--Invertebrate species, in alphabetical order by phylum or subphylum, encountered during the 2012 Chukchi Sea bottom trawl survey.

Appendix A.--Haul and catch (kg) data for successfully completed tows during the 2012 Chukchi Sea bottom trawl survey.

Haul No.	1	2	3	5	6	8
Station	CH30-B01	CH30-A01	CH30-A02	CH30-B02	CH30-B03	CH30-C03
Date	14-AUG-12	14-AUG-12	14-AUG-12	15-AUG-12	15-AUG-12	15-AUG-12
Start Latitude	66.51	66.03	66.00	66.48	66.48	66.99
Start Longitude	-168.50	-168.49	-167.29	-167.25	-166.03	-165.92
Net width (m)	14.99	15.2	13.61	14.43	13.67	14.37
Distance fished (km)	1.21	1.23	1.47	1.37	1.51	1.44
Duration	0.23	0.23	0.26	0.25	0.27	0.26
Depth (m)	52	52	15	29	17	24
Bottom temperature (°C)	1.3	1.6	9.9	8.4	9.3	8.2
Surface temperature (°C)	1.4	1.7	10.3	8.6	9.3	8.7
Bathyraja parmifera	6.92					
Hippoglossoides robustus	0.55	0.33		0.70		0.12
Limanda aspera			8.78	2.80	8.14	3.88
Platichthys stellatus			9.18	5.34	6.36	2.62
Pleuronectes quadrituberculatus			0.56	0.56	2.07	1.84
Other flatfish	3.19	1.70	1.76	3.63	11.29	3.93
Clupea pallasi			1.08	1.01	4.52	3.26
Sculpins	1.81	2.27	1.16	0.53	1.13	0.55
Boreogadus saida	1.64	4.26	0.04	34.31	0.04	1.57
Eleginus gracilis			1.12	0.12	11.03	0.44
Snailfish	2.70	0.40		0.01		
Eelpouts	0.75			6.59	0.05	
Other roundfish	3.22	0.69	2.38	48.72		4.06
Chionoecetes opilio	170.58	44.04	0.94	15.64	0.12	1.67
Paralithodes camtschaticus						
Paralithodes platypus	1.43	5.05			36.97	
Other crab	249.02	472.01	9.44	26.98	0.00	12.89
Shrimp	1.15	0.10	0.03	0.73	0.23	0.18
Snails	181.26	99.28	0.51	4.85		0.02
Sea stars	70.39	152.65	14.35	223.01	28.66	64.68
Sea urchins	193.06	705.73	0.02	0.00	7.43	0.36
Other inverts	587.89	2000.12	11.35	132.50		114.14

Appendix A.--Continued.

Haul No.	9	10	13	14	15	17
Station	CH30-B05	CH30-B06	CH30-C05	CH30-C04	CH30-D04	CH30-D03
Date	16-AUG-12	16-AUG-12	16-AUG-12	17-AUG-12	17-AUG-12	17-AUG-12
Start Latitude	66.48	66.49	66.98	66.99	67.50	67.51
Start Longitude	-163.40	-162.21	-163.32	-164.69	-164.58	-165.88
Net width (m)	14.07	15.2	15.79	14.62	14.79	13.81
Distance fished (km)	1.46	1.43	1.40	1.32	1.34	1.22
Duration	0.27	0.27	0.26	0.25	0.24	0.23
Depth (m)	14	14	14	27	30	40
Bottom temperature (°C)	10.6	-0.4	10.7	8.4	9.8	5
Surface temperature (°C)	10.9	10.3	11.2	8.9	9.8	6.6
Bathyraja parmifera						
Hippoglossoides robustus				0.61	0.14	0.04
Limanda aspera	6.00	0.18	9.68	0.83	0.90	
Platichthys stellatus	2.96		3.15	0.80	0.14	
Pleuronectes quadrituberculatus	1.00	2.54	0.72	0.34	0.39	
Other flatfish	3.02		0.56	3.06	0.68	0.22
Clupea pallasi	0.27	0.01		17.74	1.51	25.21
Sculpins	0.75	0.04	1.94	0.01	0.19	0.07
Boreogadus saida	18.03	0.03	0.01	2.02	0.09	0.05
Eleginus gracilis			16.47	18.42	8.67	
Snailfish						
Eelpouts			0.94	0.05	0.19	0.09
Other roundfish	8.19		37.79	13.01	5.70	3.15
Chionoecetes opilio	0.02	44.63		1.48		13.68
Paralithodes camtschaticus				0.63		1.66
Paralithodes platypus						
Other crab	65.96		73.92	2.73	11.64	107.73
Shrimp	0.12	0.16	0.49	0.40	0.27	0.14
Snails		10.72	1.77		0.10	4.17
Sea stars	140.06	42.03	63.88	58.63	37.34	25.23
Sea urchins	0.48	0.32	1.43	1.11	1.80	0.14
Other inverts	36.53	21.97	97.41	214.22	62.45	140.08

Appendix A.--Continued.

Haul No.	18	19	21	23	25	27
Station	CH30-D02	CH30-C02	CH30-C01	CH30-D01	CH30-E01	CH30-E02
Date	18-AUG-12	18-AUG-12	18-AUG-12	19-AUG-12	19-AUG-12	20-AUG-12
Start Latitude	67.52	66.99	66.99	67.50	68.01	68.00
Start Longitude	-167.19	-167.22	-168.48	-168.49	-168.51	-167.21
Net width (m)	16.49	17.03	14.3	16.32	16.72	15.92
Distance fished (km)	1.25	1.29	1.26	1.39	1.38	1.40
Duration	0.23	0.24	0.23	0.26	0.25	0.26
Depth (m)	46	38	37	47	58	56
Bottom temperature (°C)	1.7	2	2.4	1.3	1.5	2
Surface temperature (°C)	4.7	2.5	4.9	3.9	4.6	5.4
Bathyraja parmifera						
Hippoglossoides robustus	0.59		0.74	1.72	1.11	0.84
Limanda aspera						
Platichthys stellatus						
Pleuronectes quadrituberculatus						
Other flatfish	2.96		3.83	8.59	5.57	5.99
Clupea pallasi						0.11
Sculpins	0.28	0.04	1.74	0.63	0.63	0.63
Boreogadus saida	0.55	0.41	3.05	4.89	26.34	0.52
Eleginus gracilis						
Snailfish		0.21	1.06	0.94	0.55	0.62
Eelpouts			0.02		0.14	0.48
Other roundfish	0.18	0.37	2.38	1.60	2.30	1.44
Chionoecetes opilio	3.43	14.53	16.07	19.23	4.57	39.30
Paralithodes camtschaticus						
Paralithodes platypus						2.91
Other crab	10.88	42.50	33.12	8.03	45.30	161.97
Shrimp	0.04	0.01	0.09	0.21	0.11	1.33
Snails	1.56	20.56	40.78	2.55	28.28	14.07
Sea stars	35.33	10.90	13.83	101.52	39.08	16.03
Sea urchins			0.08		142.61	525.70
Other inverts	70.39	36.67	22.28	64.37		852.82

Appendix A.--Continued.

Haul No.	28	30	31	33	34	35
Station	CH30-E03	CH30-F02	CH30-G02	CH30-G03	CH30-G04	CH30-H04
Date	20-AUG-12	21-AUG-12	21-AUG-12	21-AUG-12	22-AUG-12	22-AUG-12
Start Latitude	68.00	68.52	68.99	69.01	69.01	69.50
Start Longitude	-165.84	-167.14	-167.06	-165.67	-164.34	-164.22
Net width (m)	13.51	13.85	15.58	14.01	13.71	13.46
Distance fished (km)	1.33	1.33	1.27	1.38	1.53	1.40
Duration	0.25	0.24	0.25	0.24	0.27	0.25
Depth (m)	29	37	47	21	12	23
Bottom temperature (°C)	9.9	9.6	4.9	9.1	9.3	7
Surface temperature (°C)	9.9	9.4	7.6	9.4	9.3	8.9
Bathyraja parmifera						
Hippoglossoides robustus		0.08	0.07			
Limanda aspera	2.40	2.78		0.05	1.67	
Platichthys stellatus	0.60			5.25		
Pleuronectes quadrituberculatus	0.22	0.41				
Other flatfish		0.61	0.34	0.13		
Clupea pallasi	11.95	10.85	1.20		0.77	
Sculpins	1.37	1.61	0.45	0.42	1.76	0.33
Boreogadus saida	0.08	9.26	8.83	0.13	0.06	11.26
Eleginus gracilis	69.33	2.56		0.26	0.75	0.01
Snailfish	0.07	0.92	0.01			0.01
Eelpouts	0.04	0.77	0.08	0.05		
Other roundfish	17.78	1.20	0.16	0.94	4.27	0.77
Chionoecetes opilio	0.09	0.50	17.41	1.19	95.06	81.75
Paralithodes camtschaticus						
Paralithodes platypus						
Other crab	136.78	160.90	61.96	94.61		
Shrimp	1.49	0.33	0.90	0.50	0.51	0.30
Snails		10.19	6.65	1.04		56.96
Sea stars	10.47	33.22	7.46	35.00	22.53	102.72
Sea urchins	18.68	3.00	0.25	0.13	374.25	0.49
Other inverts	346.47	551.32	96.69	44.53	32.30	61.04

Appendix A.--Continued.

Haul No.	37	38	40	42	43	45
Station	CH30-I04	CH30-J05	CH30-J06	CH30-K06	CH30-K07	CH30-K08
Date	22-AUG-12	23-AUG-12	23-AUG-12	23-AUG-12	24-AUG-12	24-AUG-12
Start Latitude	69.99	70.51	70.50	70.99	71.00	71.11
Start Longitude	-164.14	-162.52	-160.96	-160.91	-159.04	-157.57
Net width (m)	13.47	13.03	12.46	14.09	13.25	12.17
Distance fished (km)	1.32	1.26	1.50	1.28	1.39	0.93
Duration	0.24	0.23	0.28	0.24	0.25	0.17
Depth (m)	31	35	21	45	37	35
Bottom temperature (°C)	7	7.2	9.2	1.7		7.6
Surface temperature (°C)	8.5	8.6	9.4	7		8.7
Bathyraja parmifera						
Hippoglossoides robustus	0.04					
Limanda aspera						
Platichthys stellatus						
Pleuronectes quadrituberculatus						
Other flatfish	0.22					
Clupea pallasi			3.81	0.06	5.54	0.87
Sculpins	0.56	0.85	1.83	0.43	4.15	4.50
Boreogadus saida	1.06	2.40	0.06			
Eleginus gracilis			0.01	0.10	0.03	
Snailfish	0.03	0.06			0.07	0.47
Eelpouts						4.46
Other roundfish	0.42	0.67	2.34			8.78
Chionoecetes opilio	6.95	4.50				
Paralithodes camtschaticus		0.56				
Paralithodes platypus						
Other crab	202.94	95.08	52.04	149.77	72.08	37.42
Shrimp			3.42	0.18	9.61	1.80
Snails	58.77	9.86	17.24	9.95	11.01	7.22
Sea stars	25.98	2.51	425.60	2.20	81.16	1.02
Sea urchins			0.91	55.25	184.99	0.39
Other inverts	1452.50	993.84	396.60	800.06	2627.54	555.07

Appendix A.--Continued.

Haul No.	48	50	52	54	57	59
Station	CH30-L08	CH30-K05	CH30-J04	CH30-I03	CH30-H03	CH30-H02
Date	24-AUG-12	25-AUG-12	25-AUG-12	26-AUG-12	26-AUG-12	27-AUG-12
Start Latitude	71.52	71.00	70.50	70.00	69.50	69.50
Start Longitude	-157.39	-162.30	-163.99	-165.55	-165.73	-167.12
Net width (m)	17.12	14.28	13.68	15.38	13.17	14.20
Distance fished (km)	1.01	1.41	1.35	1.46	1.35	1.33
Duration	0.19	0.26	0.25	0.27	0.25	0.25
Depth (m)	90	45	43	40	35	47
Bottom temperature (°C)	-1.7	2.2	6.2	5.4	7.9	5.7
Surface temperature (°C)	1.6	6.5	7.7	6.6	9.2	7.9
Bathyraja parmifera						
Hippoglossoides robustus			0.01	0.08	0.04	0.41
Limanda aspera						
Platichthys stellatus						
Pleuronectes quadrituberculatus					0.19	0.46
Other flatfish			0.30	0.39	0.18	2.06
Clupea pallasi			11.90		15.16	1.13
Sculpins	0.16	0.01	0.74	0.11	0.77	1.39
Boreogadus saida	0.69	1.25	4.23	4.85	3.76	1.00
Eleginus gracilis					0.03	0.04
Snailfish		0.02	0.07	0.21	0.19	0.09
Eelpouts		0.02	0.09	0.40	1.73	0.51
Other roundfish	0.02	0.32	2.78	3.65	4.67	1.07
Chionoecetes opilio	0.04		1.66	0.54	1.26	1.28
Paralithodes camtschaticus			3.41	14.51	13.52	236.76
Paralithodes platypus			1.69	571.74	1.33	438.24
Other crab	30.09	24.41	132.62		526.98	
Shrimp	0.05	0.55				
Snails	7.33	9.52	12.77	12.07	98.73	28.95
Sea stars	5.86	3.21	7.70	17.67	51.86	41.78
Sea urchins	0.31	0.20	0.09	243.24	0.64	0.11
Other inverts	171.77	1039.69	652.94		33.61	323.86

Appendix A.Table 1.--Continued.

Haul No.	61	63	65	67	68	69
Station	CH30-H01	CH30-G01	CH30-F01	CH30-I02	CH30-J02	CH30-J03
Date	27-AUG-12	28-AUG-12	28-AUG-12	02-SEP-12	03-SEP-12	03-SEP-12
Start Latitude	69.50	68.99	68.50	70.01	70.50	70.50
Start Longitude	-168.59	-168.49	-168.49	-167.02	-166.99	-165.51
Net width (m)	13.34	14.08	14.62	15.04	14.99	15.14
Distance fished (km)	1.28	1.26	1.26	1.38	1.35	1.43
Duration	0.23	0.23	0.23	0.25	0.24	0.26
Depth (m)	51	51	51	47	50	42
Bottom temperature (°C)	3.8	2.1	2.3	2	0.3	2.2
Surface temperature (°C)	7	4.2	3.9	5.5	5.1	6
Bathyraja parmifera						
Hippoglossoides robustus	0.24	1.78	2.06		0.02	0.02
Limanda aspera						
Platichthys stellatus						
Pleuronectes quadrituberculatus						
Other flatfish	1.19	8.91	10.31		0.16	0.09
Clupea pallasi						
Sculpins	0.49	0.27	0.20	0.30		0.09
Boreogadus saida	1.73	1.79	3.76	2.02	1.08	0.50
Eleginus gracilis	0.01	0.01	1.17	0.01		
Snailfish	0.04	0.22	0.27	0.79	0.19	0.26
Eelpouts	0.02	0.44		0.07		
Other roundfish	0.46	2.05	3.28	0.16	0.19	1.66
Chionoecetes opilio	150.41	76.50	14.00	74.39	8.59	1.50
Paralithodes camtschaticus						
Paralithodes platypus				1.64		
Other crab	122.13	75.05	83.09	137.90	62.08	114.17
Shrimp	2.05	1.12	0.44	0.60	0.14	0.32
Snails	11.59	14.29	14.51	14.81	2.63	19.60
Sea stars	11.56	11.74	10.65	5.64	18.81	21.91
Sea urchins	0.21	0.09	0.11	60.39	0.09	0.08
Other inverts	196.02	29.12	9.17	845.59	802.17	248.06

Appendix A.--Continued.

Haul No.	70	72	73	74	76	77
Station	CH30-K04	CH30-L05	CH30-L06	CH30-L07	CH30-M08	CH30-M07
Date	04-SEP-12	05-SEP-12	05-SEP-12	05-SEP-12	06-SEP-12	06-SEP-12
Start Latitude	71.00	71.50	71.50	71.50	71.99	72.01
Start Longitude	-163.89	-162.13	-160.60	-159.02	-157.19	-158.82
Net width (m)	15.27	16.29	16.24	16.18	16.79	15.63
Distance fished (km)	1.38	1.08	1.33	1.31	1.29	0.90
Duration	0.25	0.19	0.25	0.23	0.23	0.16
Depth (m)	42	44	46	50	86	53
Bottom temperature (°C)	-1.2	-1.7	-1.7	-1.7	-1.6	-1.7
Surface temperature (°C)	3.3	1.7	5.4	3.9	2.5	1.7
Bathyraja parmifera						
Hippoglossoides robustus		0.10		0.04	0.15	
Limanda aspera						
Platichthys stellatus						
Pleuronectes quadrituberculatus						
Other flatfish		0.52		0.22	0.77	
Clupea pallasi						
Sculpins	0.02	0.12	0.04		0.01	
Boreogadus saida	0.51	0.74	1.17	0.28	0.33	0.27
Eleginus gracilis			0.01			
Snailfish	0.07	0.03			0.01	
Eelpouts	0.00	0.13	0.02		0.06	
Other roundfish	0.54	0.13			0.06	
Chionoecetes opilio	0.17	0.15	0.32	1.17	2.34	0.33
Paralithodes camtschaticus						
Paralithodes platypus						
Other crab	3.54	7.40	3.41	4.25	6.77	10.57
Shrimp	0.27	0.15	0.05	0.07	0.02	0.03
Snails	6.11	3.25	1.32	4.65	2.56	2.95
Sea stars	7.93	3.08	2.04	4.52	72.77	1.63
Sea urchins		0.01				
Other inverts	349.46	51.55	28.47	67.45	18.08	14.22

Appendix A.--Continued.

Haul No.	78	82	84	85	86	88
Station	CH30-N07	CH30-M06	CH30-N05	CH30-N04	CH30-O03	CH30-O02
Date	07-SEP-12	07-SEP-12	08-SEP-12	08-SEP-12	08-SEP-12	09-SEP-12
Start Latitude	72.48	72.00	72.50	72.50	73.04	73.00
Start Longitude	-158.44	-160.47	-161.93	-163.51	-164.17	-165.82
Net width (m)	16.62	14.53	17.43	16.76	17.78	18.04
Distance fished (km)	1.40	1.31	0.94	1.38	0.50	1.42
Duration	0.26	0.23	0.17	0.24	0.09	0.25
Depth (m)	59	38	42	47	84	59
Bottom temperature (°C)	-1.6	-1.7	-1.2	-1.3	-1.7	-1.4
Surface temperature (°C)	2	0.1	1.5	2	0.3	-0.5
Bathyraja parmifera						
Hippoglossoides robustus		0.19	0.09	0.12		0.12
Limanda aspera						
Platichthys stellatus						
Pleuronectes quadrituberculatus						
Other flatfish		0.97	0.44	0.60	0.01	0.58
Clupea pallasi						
Sculpins	0.13	0.21	0.01		0.01	0.03
Boreogadus saida	0.66	1.21	0.45	1.91	0.26	1.64
Eleginus gracilis						
Snailfish	0.03	0.05	0.03	0.02	0.03	
Eelpouts	0.30	0.50	0.08	0.11		0.07
Other roundfish	0.03	0.35		0.13	0.29	
Chionoecetes opilio	0.92	2.13	0.66	1.03	0.20	3.40
Paralithodes camtschaticus						
Paralithodes platypus						
Other crab	22.62	13.30	5.78	11.77	9.66	4.61
Shrimp	0.23	0.06	0.05	0.08		0.02
Snails	3.82	1.70	0.89	2.16	2.91	1.28
Sea stars	19.85	0.02	0.04	0.07	4.25	54.46
Sea urchins						
Other inverts	46.17	33.86	15.70	17.86	66.29	14.22

Appendix A.--Continued.

Haul No.	89	92	93	94	96	97
Station	CH30-N01	CH30-N02	CH30-N03	CH30-M03	CH30-M04	CH30-M05
Date	09-SEP-12	10-SEP-12	10-SEP-12	10-SEP-12	11-SEP-12	11-SEP-12
Start Latitude	72.50	72.51	72.48	72.01	72.00	72.04
Start Longitude	-168.46	-166.84	-165.18	-165.28	-163.65	-162.25
Net width (m)	16.14	16.14	16.11	16.37	13.07	12.43
Distance fished (km)	1.34	1.29	0.88	1.04	1.27	1.40
Duration	0.23	0.23	0.15	0.18	0.23	0.25
Depth (m)	53	50	50	42	39	28
Bottom temperature (°C)	-1.1	-0.8	-0.8	-0.9	-1.2	-1.6
Surface temperature (°C)	2.4	3.3	2	1.4	-0.1	0.3
Bathyraja parmifera						
Hippoglossoides robustus	0.01	0.01	0.01			
Limanda aspera						
Platichthys stellatus						
Pleuronectes quadrituberculatus						
Other flatfish	0.04	0.03	0.04			
Clupea pallasi						0.76
Sculpins			0.77	1.86	0.68	0.69
Boreogadus saida	7.55	4.48	0.01			
Eleginus gracilis	0.01					
Snailfish	0.01	0.12	0.03	0.03	0.01	0.02
Eelpouts	0.01					
Other roundfish	0.14	0.05		0.21	0.13	0.16
Chionoecetes opilio	1.08	0.13	0.05	0.41	0.98	0.09
Paralithodes camtschaticus						
Paralithodes platypus						
Other crab	5.64	7.41	5.01	46.78	48.06	4.56
Shrimp	0.05	0.03	0.06	0.02	0.04	0.03
Snails	3.92	3.96	3.46	8.02	9.17	1.02
Sea stars	20.21	1.05				
Sea urchins			0.36	1.92	2.53	0.34
Other inverts	110.29	87.87	54.63	36.14	36.36	23.11

Appendix A.--Continued.

Haul No.	100	102	107	108	109	111
Station	CH30-L04	CH30-L03	CH30-K03	CH30-K02	CH30-L02	CH30-M02
Date	12-SEP-12	12-SEP-12	13-SEP-12	13-SEP-12	13-SEP-12	14-SEP-12
Start Latitude	71.49	71.50	70.99	71.01	71.50	72.01
Start Longitude	-163.80	-165.34	-165.43	-166.97	-166.95	-166.90
Net width (m)	15.55	16.24	13.01	15.86	16.25	17.14
Distance fished (km)	1.44	1.43	1.30	1.43	1.01	1.44
Duration	0.25	0.25	0.23	0.25	0.19	0.25
Depth (m)	44	42	41	45	47	47
Bottom temperature (°C)	-1.1	-0.6	0.5	1.5	0.3	-0.8
Surface temperature (°C)	0.7	1.8	3	5	3.7	3.1
Bathyraja parmifera						
Hippoglossoides robustus						0.07
Limanda aspera						
Platichthys stellatus						
Pleuronectes quadrituberculatus						
Other flatfish						0.34
Clupea pallasi	0.76					
Sculpins	0.69	0.02				
Boreogadus saida		1.53	0.60	9.02	1.64	1.98
Eleginus gracilis						
Snailfish	0.02		0.14	0.04	0.02	
Eelpouts						0.04
Other roundfish	0.16		0.86	0.32	0.18	
Chionoecetes opilio	0.09	0.25	0.43	1.11	0.58	0.16
Paralithodes camtschaticus						
Paralithodes platypus						
Other crab	4.56	9.39	119.05	53.19	42.77	11.78
Shrimp	0.03	0.02	0.06	0.06	0.02	0.02
Snails	1.02	3.48	3.12	7.20	9.53	2.18
Sea stars			6.61	17.02	9.57	4.99
Sea urchins	0.34	1.80	0.08	0.12		
Other inverts	23.11	19.81	126.74	107.38	85.54	3.38

Appendix A.--Continued.

Haul No.	112	113	116	118	120
Station	CH30-M01	CH30-L01	CH30-K01	CH30-J01	CH30-I01
Date	14-SEP-12	14-SEP-12	15-SEP-12	15-SEP-12	16-SEP-12
Start Latitude	72.00	71.50	71.00	70.49	70.00
Start Longitude	-168.50	-168.51	-168.51	-168.49	-168.47
Net width (m)	15.94	16.17	16.12	13.48	15.49
Distance fished (km)	1.38	1.42	1.43	1.32	0.92
Duration	0.24	0.25	0.25	0.24	0.17
Depth (m)	50	49	46	39	42
Bottom temperature (°C)	-0.5	-0.3		0.1	0.7
Surface temperature (°C)	3.8	3.8	3.9	4.1	6
Bathyraja parmifera					
Hippoglossoides robustus	0.02	0.01			0.02
Limanda aspera					
Platichthys stellatus					
Pleuronectes quadrituberculatus					
Other flatfish	0.08	0.06	0.01		0.09
Clupea pallasi					
Sculpins				0.19	0.59
Boreogadus saida	5.56	1.89	3.21	0.46	0.42
Eleginus gracilis					
Snailfish	0.04	0.06	0.01	0.09	0.23
Eelpouts				0.06	
Other roundfish	0.05		0.10	0.74	0.37
Chionoecetes opilio	0.04	1.05	0.04	0.53	1.38
Paralithodes camtschaticus					
Paralithodes platypus					0.32
Other crab	10.53	16.54	36.62	383.72	134.59
Shrimp	0.22	0.10	0.15	0.23	0.94
Snails	9.24	6.97	8.55	81.69	4.79
Sea stars	32.85	69.28	9.77	12.04	0.60
Sea urchins			8.09	0.51	73.23
Other inverts	21.34	11.58		622.60	1728.02

Appendix B. --Rank of fish and invertebrate taxa by the mean catch per unit effort (CPUE kg/ha) from the 2012 Chukchi Sea bottom trawl survey.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
1	82510	15.8907	6.9291	2.0325	29.7490	0.1470	0.1470	*Strongylocentrotus droebachiensis*
2	81742	8.8009	3.3937	2.0134	15.5883	0.0814	0.2285	*Asterias amurensis*
3	69086	7.8716	1.6707	4.5301	11.2131	0.0728	0.3013	*Pagurus trigonocheirus*
4	68580	7.4508	2.5756	2.2995	12.6020	0.0689	0.3702	*Chionoecetes opilio*
5	85219	5.5437	2.4547	0.6342	10.4531	0.0513	0.4215	*Psolus fabricii*
6	71884	4.4800	1.1823	2.1154	6.8447	0.0415	0.4630	*Neptunea heros*
7	98105	4.1656	3.3204	0.0000	10.8065	0.0385	0.5015	*Boltenia ovifera*
8	80590	3.9912	0.9407	2.1097	5.8727	0.0369	0.5384	*Leptasterias polaris*
9	83021	3.5915	1.5096	0.5723	6.6107	0.0332	0.5717	*Gorgonocephalus* sp.
10	99994	3.5541	1.1416	1.2709	5.8373	0.0329	0.6045	empty gastropod shells
11	91049	3.3040	3.1675	0.0000	9.6390	0.0306	0.6351	*Halichondria* sp.
12	98082	2.4225	1.1637	0.0950	4.7500	0.0224	0.6575	*Styela rustica*
13	40504	2.2667	0.4203	1.4261	3.1073	0.0210	0.6785	*Chrysaora melanaster*
14	43042	1.9315	0.6034	0.7248	3.1383	0.0179	0.6964	*Urticina crassicornis*
15	91079	1.7669	1.2396	0.0000	4.2461	0.0163	0.7127	*Halichondria sitiens*
16	98205	1.6520	0.9629	0.0000	3.5778	0.0153	0.7280	*Halocynthia aurantium*
17	83020	1.5791	1.2316	0.0000	4.0423	0.0146	0.7426	*Gorgonocephalus eucnemis*
18	21725	1.4599	0.3088	0.8424	2.0774	0.0135	0.7561	*Boreogadus saida*
19	40561	1.4513	0.4311	0.5891	2.3136	0.0134	0.7695	*Cyanea capillata*
20	68577	1.3372	0.4858	0.3656	2.3089	0.0124	0.7819	*Hyas coarctatus*
21	71882	1.3341	0.7256	0.0000	2.7854	0.0123	0.7943	*Neptunea ventricosa*
22	99993	1.1648	0.7424	0.0000	2.6497	0.0108	0.8050	empty bivalve shells
23	80030	1.1549	0.4687	0.2175	2.0923	0.0107	0.8157	*Urasterias lincki*
24	98000	1.1180	0.6505	0.0000	2.4191	0.0103	0.8261	Ascidiacea
25	21735	1.0801	0.5820	0.0000	2.2442	0.0100	0.8361	*Eleginus gracilis*
26	81073	0.9834	0.8578	0.0000	2.6989	0.0091	0.8452	*Solaster arcticus*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
27	68781	0.8870	0.3583	0.1703	1.6036	0.0082	0.8534	*Telmessus cheiragonus*
28	80200	0.8421	0.3021	0.2379	1.4462	0.0078	0.8612	*Lethasterias nanimensis*
29	21110	0.8305	0.3046	0.2214	1.4396	0.0077	0.8688	*Clupea pallasi*
30	65100	0.7483	0.4071	0.0000	1.5624	0.0069	0.8758	Thoracica
31	81780	0.6552	0.4630	0.0000	1.5811	0.0061	0.8818	*Ctenodiscus crispatus*
32	83320	0.6195	0.1937	0.2322	1.0068	0.0057	0.8876	*Ophiura sarsi*
33	69120	0.6153	0.2614	0.0926	1.1380	0.0057	0.8932	*Pagurus capillatus*
34	82740	0.5829	0.5809	0.0000	1.7446	0.0054	0.8986	*Echinarachnius parma*
35	91000	0.4611	0.2595	0.0000	0.9800	0.0043	0.9029	Porifera
36	91015	0.4326	0.4272	0.0000	1.2870	0.0040	0.9069	*Suberites* sp.
37	98102	0.3963	0.2239	0.0000	0.8441	0.0037	0.9106	*Boltenia ecinata*
38	95000	0.3903	0.1976	0.0000	0.7856	0.0036	0.9142	Bryozoa
39	41201	0.3590	0.1714	0.0162	0.7018	0.0033	0.9175	*Gersemia* sp.
40	80020	0.3549	0.1205	0.1138	0.5959	0.0033	0.9208	*Evasterias echinosoma*
41	43000	0.3347	0.1411	0.0524	0.6169	0.0031	0.9239	Actiniaria
42	10210	0.3316	0.1145	0.1026	0.5607	0.0031	0.9270	*Limanda aspera*
43	80594	0.3299	0.1379	0.0541	0.6057	0.0031	0.9300	*Leptasterias arctica*
44	69095	0.3192	0.0614	0.1964	0.4420	0.0030	0.9330	*Pagurus rathbuni*
45	71835	0.3140	0.0462	0.2217	0.4063	0.0029	0.9359	*Neptunea borealis*
46	71772	0.3028	0.1473	0.0083	0.5974	0.0028	0.9387	*Beringius beringii*
47	43030	0.2573	0.2536	0.0000	0.7645	0.0024	0.9410	*Stomphia* sp.
48	69061	0.2539	0.0702	0.1135	0.3943	0.0023	0.9434	*Labidochirus splendescens*
49	10220	0.2537	0.0968	0.0602	0.4472	0.0023	0.9457	*Platichthys stellatus*
50	74105	0.2107	0.1220	0.0000	0.4548	0.0019	0.9477	*Chlamys behringiana*
51	75286	0.1809	0.1771	0.0000	0.5351	0.0017	0.9494	*Serripes laperousii*
52	98331	0.1793	0.1231	0.0000	0.4255	0.0017	0.9510	*Chelyosoma productum*
53	43032	0.1684	0.1168	0.0000	0.4019	0.0016	0.9526	*Stomphia coccinea*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
54	71891	0.1663	0.0580	0.0504	0.2823	0.0015	0.9541	*Plicifusus kroyeri*
55	80110	0.1570	0.0447	0.0675	0.2464	0.0015	0.9556	*Leptasterias groenlandica*
56	72758	0.1565	0.1474	0.0000	0.4513	0.0014	0.9570	*Buccinum glaciale*
57	21368	0.1431	0.0478	0.0474	0.2387	0.0013	0.9583	*Myoxocephalus verrucosus*
58	99998	0.1383	0.1337	0.0000	0.4057	0.0013	0.9596	Polychaete tubes
59	23055	0.1315	0.0546	0.0223	0.2408	0.0012	0.9608	*Osmerus mordax*
60	71002	0.1292	0.0408	0.0477	0.2107	0.0012	0.9620	*Buccinum* sp.
61	66601	0.1207	0.0752	0.0000	0.2712	0.0011	0.9632	*Sclerocrangon boreas*
62	66611	0.1187	0.0231	0.0724	0.1649	0.0011	0.9643	*Argis lar*
63	81095	0.1184	0.0264	0.0657	0.1712	0.0011	0.9653	*Crossaster papposus*
64	69323	0.1102	0.0470	0.0162	0.2042	0.0010	0.9664	*Paralithodes platypus*
65	40011	0.1094	0.0400	0.0295	0.1893	0.0010	0.9674	hydroid unident.
66	98300	0.1093	0.1028	0.0000	0.3149	0.0010	0.9684	compound ascidian unident.
67	71030	0.1043	0.1015	0.0000	0.3072	0.0010	0.9694	*Tritonia diomedea*
68	24189	0.1019	0.0649	0.0000	0.2318	0.0009	0.9703	*Lycodes turneri*
69	71753	0.1014	0.0286	0.0441	0.1586	0.0009	0.9712	*Pyrulofusus deformis*
70	85085	0.0989	0.0389	0.0211	0.1767	0.0009	0.9721	*Myriotrochus rinkii*
71	10140	0.0953	0.0257	0.0439	0.1467	0.0009	0.9730	*Hippoglossoides robustus*
72	81355	0.0931	0.0292	0.0347	0.1515	0.0009	0.9739	*Pteraster obscurus*
73	71511	0.0910	0.0201	0.0508	0.1311	0.0008	0.9747	Naticidae eggs
74	95041	0.0908	0.0527	0.0000	0.1962	0.0008	0.9756	*Alcyonidium enteromorpha*
75	99900	0.0881	0.0881	0.0000	0.2642	0.0008	0.9764	*Molgula* sp.
76	95039	0.0874	0.0550	0.0000	0.1973	0.0008	0.9772	*Alcyonidium disforme*
77	72743	0.0849	0.0246	0.0356	0.1341	0.0008	0.9780	*Buccinum angulosum*
78	71001	0.0833	0.0322	0.0188	0.1478	0.0008	0.9788	gastropod eggs
79	21315	0.0831	0.0184	0.0464	0.1198	0.0008	0.9795	*Gymnocanthus tricuspis*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
80	71756	0.0817	0.0360	0.0096	0.1538	0.0008	0.9803	*Volutopsius fragilis*
81	10285	0.0775	0.0263	0.0249	0.1301	0.0007	0.9810	*Pleuronectes quadri*tuberculatus
82	41220	0.0770	0.0318	0.0134	0.1405	0.0007	0.9817	*Gersemia fruticosa*
83	70115	0.0741	0.0386	0.0000	0.1513	0.0007	0.9824	*Amicula vestita*
84	22205	0.0725	0.0251	0.0224	0.1226	0.0007	0.9831	*Liparis gibbus*
85	71774	0.0696	0.0476	0.0000	0.1648	0.0006	0.9837	*Beringius stimpsoni*
86	72752	0.0679	0.0201	0.0278	0.1081	0.0006	0.9843	*Buccinum scalariforme*
87	91086	0.0648	0.0450	0.0000	0.1549	0.0006	0.9849	*Stylissa* sp.
88	74562	0.0571	0.0316	0.0000	0.1203	0.0005	0.9855	*Musculus discors*
89	471	0.0536	0.0536	0.0000	0.1609	0.0005	0.9860	*Bathyraja parmifera*
90	71004	0.0483	0.0300	0.0000	0.1083	0.0004	0.9864	*Neptunea* sp.
91	85013	0.0483	0.0320	0.0000	0.1124	0.0004	0.9869	*Ocnus glacialis*
92	72755	0.0467	0.0117	0.0234	0.0700	0.0004	0.9873	*Buccinum polare*
93	71763	0.0423	0.0292	0.0000	0.1008	0.0004	0.9877	*Volutopsius stefanssoni*
94	74983	0.0416	0.0289	0.0000	0.0993	0.0004	0.9881	*Clinocardium ciliatum*
95	43110	0.0368	0.0318	0.0000	0.1003	0.0003	0.9884	*Actinostola* sp.
96	43010	0.0363	0.0221	0.0000	0.0806	0.0003	0.9887	*Metridium* sp.
97	74436	0.0351	0.0191	0.0000	0.0733	0.0003	0.9891	*Nuculana pernula*
98	71025	0.0345	0.0186	0.0000	0.0717	0.0003	0.9894	*Tritonia* sp.
99	95036	0.0314	0.0146	0.0022	0.0606	0.0003	0.9897	*Alcyonidium pedunculatum*
100	43082	0.0311	0.0263	0.0000	0.0837	0.0003	0.9900	*Cribrinopsis fernaldi*
101	98310	0.0291	0.0146	0.0000	0.0583	0.0003	0.9902	*Aplidium* sp.
102	24185	0.0287	0.0117	0.0054	0.0521	0.0003	0.9905	*Lycodes palearis*
103	43040	0.0277	0.0199	0.0000	0.0676	0.0003	0.9908	*Urticina* sp.
104	23807	0.0276	0.0105	0.0065	0.0486	0.0003	0.9910	*Lumpenus fabricii*
105	50010	0.0272	0.0165	0.0000	0.0602	0.0003	0.9913	tube worm unident.
106	43113	0.0270	0.0170	0.0000	0.0610	0.0003	0.9915	*Actinostola groenlandica*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
107	50000	0.0262	0.0194	0.0000	0.0651	0.0002	0.9918	Polychaeta
108	75285	0.0256	<0.0001	0.0151	0.0361	0.0002	0.9920	*Serripes groenlandicus*
109	91074	0.0255	0.0194	0.0000	0.0642	0.0002	0.9922	*Polymastia* sp.
110	71537	0.0249	<0.0001	0.0101	0.0397	0.0002	0.9925	*Cryptonatica* (=*Natica*)
111	24184	0.0235	0.0124	0.0000	0.0484	0.0002	0.9927	*Lycodes raridens*
112	85012	0.0227	0.0221	0.0000	0.0668	0.0002	0.9929	*Ocnus* sp.
113	10211	0.0224	0.0161	0.0000	0.0545	0.0002	0.9931	*Limanda proboscidea*
114	71580	0.0217	<0.0001	0.0112	0.0323	0.0002	0.9933	*Euspira pallida*
115	66045	0.0212	0.0101	0.0010	0.0413	0.0002	0.9935	*Pandalus goniurus*
116	22238	0.0208	<0.0001	0.0070	0.0345	0.0002	0.9937	*Liparis tunicatus*
117	98214	0.0203	0.0203	0.0000	0.0609	0.0002	0.9939	*Distaplia* sp.
118	74646	0.0202	0.0103	0.0000	0.0408	0.0002	0.9941	*Astarte arctica*
119	21388	0.0194	<0.0001	0.0022	0.0367	0.0002	0.9942	*Enophrys diceraus*
120	74311	0.0192	0.0190	0.0000	0.0572	0.0002	0.9944	*Hiatella arctica*
121	98200	0.0191	0.0191	0.0000	0.0572	0.0002	0.9946	*Halocynthia* sp.
122	74065	0.0190	0.0190	0.0000	0.0569	0.0002	0.9948	*Mytilus* sp.
123	69322	0.0184	0.0145	0.0000	0.0475	0.0002	0.9949	*Paralithodes camtschaticus*
124	83348	0.0180	0.0180	0.0000	0.0541	0.0002	0.9951	*Ophiacantha bidentata*
125	21371	0.0165	<0.0001	0.0000	0.0333	0.0002	0.9953	*Myoxocephalus jaok*
126	95038	0.0160	0.0159	0.0000	0.0478	0.0001	0.9954	*Alcyonidium* sp.
127	80546	0.0153	<0.0001	0.0000	0.0305	0.0001	0.9955	*Henricia tumida*
128	85000	0.0151	0.0149	0.0000	0.0449	0.0001	0.9957	Holothuroidea
129	43100	0.0142	<0.0001	0.0000	0.0332	0.0001	0.9958	Actinostolidae
130	23041	0.0139	<0.0001	0.0028	0.0250	0.0001	0.9959	*Mallotus villosus*
131	71731	0.0136	<0.0001	0.0052	0.0221	0.0001	0.9961	*Colus halli*
132	71710	0.0134	0.0133	0.0000	0.0399	0.0001	0.9962	*Colus* sp.
133	24188	0.0130	<0.0001	0.0010	0.0249	0.0001	0.9963	*Lycodes polaris*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
134	74561	0.0126	0.0125	0.0000	0.0375	0.0001	0.9964	*Musculus niger*
135	72305	0.0124	0.0106	0.0000	0.0336	0.0001	0.9965	*Trichotropis bicarinata*
136	99902	0.0120	<0.0001	0.0000	0.0256	0.0001	0.9967	*Molgula griffithsii*
137	83336	0.0117	<0.0001	0.0000	0.0250	0.0001	0.9968	*Amphiophiura nodosa*
138	85200	0.0115	0.0115	0.0000	0.0345	0.0001	0.9969	*Cucumaria* sp.
139	66170	0.0104	<0.0001	0.0032	0.0176	<0.0001	0.9970	*Eualus* sp.
140	56311	0.0102	<0.0001	0.0038	0.0167	<0.0001	0.9971	*Eunoe nodosa*
141	69090	0.0090	<0.0001	0.0000	0.0211	<0.0001	0.9971	*Pagurus ochotensis*
142	62020	0.0088	<0.0001	0.0000	0.0231	<0.0001	0.9972	*Saduria entomon*
143	56312	0.0086	<0.0001	0.0000	0.0193	<0.0001	0.9973	*Eunoe depressa*
144	65201	0.0073	<0.0001	0.0000	0.0213	<0.0001	0.9974	*Balanus* sp.
145	71886	0.0072	<0.0001	0.0027	0.0117	<0.0001	0.9974	*Clinopegma magnum*
146	71720	0.0071	<0.0001	0.0000	0.0181	<0.0001	0.9975	*Colus sabini*
147	66175	0.0071	<0.0001	0.0003	0.0138	<0.0001	0.9976	*Eualus gaimardii*
148	80597	0.0069	<0.0001	0.0003	0.0134	<0.0001	0.9976	*Henricia beringiania*
149	21377	0.0067	<0.0001	0.0000	0.0169	<0.0001	0.9977	*Myoxocephalus quadricornis*
150	56310	0.0067	<0.0001	0.0000	0.0149	<0.0001	0.9978	*Eunoe* sp.
151	94500	0.0066	<0.0001	0.0000	0.0143	<0.0001	0.9978	Echiura
152	94001	0.0066	<0.0001	0.0000	0.0134	<0.0001	0.9979	*Golfingia margaritacea*
153	78013	0.0065	<0.0001	0.0013	0.0117	<0.0001	0.9979	*Benthoctopus sibiricus*
154	71726	0.0065	<0.0001	0.0004	0.0126	<0.0001	0.9980	*Colus spitzbergensis*
155	21314	0.0061	<0.0001	0.0000	0.0179	<0.0001	0.9981	*Gymnocanthus pistilliger*
156	95105	0.0060	<0.0001	0.0000	0.0172	<0.0001	0.9981	*Dendrobeania* sp.
157	21740	0.0054	<0.0001	0.0014	0.0094	<0.0001	0.9982	*Gadus chalcogrammus*
158	92500	0.0052	<0.0001	0.0000	0.0135	<0.0001	0.9982	Nemertea
159	23809	0.0052	<0.0001	0.0000	0.0155	<0.0001	0.9983	*Acantholumpenus mackayi*
160	72535	0.0051	<0.0001	0.0013	0.0088	<0.0001	0.9983	*Margarites costalis*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
161	71590	0.0050	<0.0001	0.0019	0.0081	<0.0001	0.9984	*Onchidiopsis* sp.
162	71597	0.0050	<0.0001	0.0000	0.0109	<0.0001	0.9984	*Onchidiopsis carnea*
163	10155	0.0049	<0.0001	0.0000	0.0132	<0.0001	0.9984	*Liopsetta glacialis*
164	71751	0.0047	<0.0001	0.0000	0.0135	<0.0001	0.9985	*Volutopsius* sp.
165	71027	0.0044	<0.0001	0.0000	0.0114	<0.0001	0.9985	*Calycidoris guentheri*
166	81315	0.0042	<0.0001	0.0000	0.0127	<0.0001	0.9986	*Pteraster tesselatus*
167	21355	0.0042	<0.0001	0.0011	0.0073	<0.0001	0.9986	*Triglops pingeli*
168	74640	0.0042	<0.0001	0.0000	0.0125	<0.0001	0.9986	*Astarte* sp.
169	66570	0.0041	<0.0001	0.0000	0.0123	<0.0001	0.9987	*Argis* sp.
170	74648	0.0041	<0.0001	0.0000	0.0089	<0.0001	0.9987	*Astarte esquimalti*
171	20041	0.0039	<0.0001	0.0013	0.0065	<0.0001	0.9988	*Podothecus veternus*
172	66193	0.0038	<0.0001	0.0000	0.0077	<0.0001	0.9988	*Eualus suckleyi*
173	10212	0.0037	<0.0001	0.0000	0.0085	<0.0001	0.9988	*Limanda sakhalinensis*
174	43008	0.0036	<0.0001	0.0000	0.0081	<0.0001	0.9989	*Ptychodactis patula*
175	21334	0.0035	<0.0001	0.0011	0.0060	<0.0001	0.9989	*Artediellus scaber*
176	72759	0.0033	<0.0001	0.0000	0.0089	<0.0001	0.9989	*Buccinum tenellum*
177	21387	0.0033	<0.0001	0.0000	0.0068	<0.0001	0.9990	*Enophrys lucasi*
178	71840	0.0032	<0.0001	0.0000	0.0097	<0.0001	0.9990	*Neptunea middendorffii*
179	72766	0.0028	<0.0001	0.0000	0.0063	<0.0001	0.9990	*Buccinum ectomycina*
180	71902	0.0028	<0.0001	0.0005	0.0050	<0.0001	0.9990	*Plicifusus johanseni*
181	95070	0.0028	<0.0001	0.0000	0.0074	<0.0001	0.9991	*Rhamphostomella costata*
182	21932	0.0027	<0.0001	0.0000	0.0066	<0.0001	0.9991	*Hexagrammos stelleri*
183	72751	0.0025	<0.0001	0.0000	0.0049	<0.0001	0.9991	*Buccinum plectrum*
184	71585	0.0025	<0.0001	0.0000	0.0059	<0.0001	0.9991	*Onchidiopsis glacialis*
185	71535	0.0024	<0.0001	0.0000	0.0071	<0.0001	0.9992	*Cryptonatica* (=*Natica*)
186	71722	0.0024	<0.0001	0.0002	0.0046	<0.0001	0.9992	*Colus hypolispus*
187	72737	0.0024	<0.0001	0.0008	0.0039	<0.0001	0.9992	*Buccinum obsoletum*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
188	83400	0.0023	<0.0001	0.0000	0.0048	<0.0001	0.9992	*Ophiopholis aculeata*
189	71021	0.0021	<0.0001	0.0000	0.0061	<0.0001	0.9992	*Dendronotus frondosus*
190	60107	0.0021	<0.0001	0.0000	0.0054	<0.0001	0.9993	*Stegocephalus inflatus*
191	66179	0.0021	<0.0001	0.0000	0.0051	<0.0001	0.9993	*Eualus macilentus*
192	98210	0.0021	<0.0001	0.0000	0.0064	<0.0001	0.9993	*Distaplia* sp.
193	80000	0.0021	<0.0001	0.0000	0.0064	<0.0001	0.9993	Asteroidea
194	95030	0.0021	<0.0001	0.0000	0.0062	<0.0001	0.9993	*Flustra serrulata*
195	71589	0.0020	<0.0001	0.0000	0.0054	<0.0001	0.9994	*Onchidiopsis* sp.
196	81322	0.0020	<0.0001	0.0000	0.0048	<0.0001	0.9994	*Pteraster octaster*
197	45005	0.0017	<0.0001	0.0000	0.0046	<0.0001	0.9994	*Beroe* sp.
198	94000	0.0017	<0.0001	0.0000	0.0037	<0.0001	0.9994	Sipuncula
199	40500	0.0016	<0.0001	0.0000	0.0046	<0.0001	0.9994	Scyphozoa
200	66203	0.0016	<0.0001	0.0000	0.0040	<0.0001	0.9994	*Lebbeus groenlandicus*
201	66502	0.0016	<0.0001	0.0000	0.0042	<0.0001	0.9995	*Crangon* sp.
202	60100	0.0016	<0.0001	0.0000	0.0035	<0.0001	0.9995	Amphipoda
203	74654	0.0016	<0.0001	0.0000	0.0037	<0.0001	0.9995	*Cyclocardia crassidens*
204	75242	0.0016	<0.0001	0.0000	0.0041	<0.0001	0.9995	*Macoma calcarea*
205	71584	0.0015	<0.0001	0.0000	0.0045	<0.0001	0.9995	*Lamellaria* sp.
206	66580	0.0015	<0.0001	0.0000	0.0045	<0.0001	0.9995	*Argis dentata*
207	82755	0.0014	<0.0001	0.0000	0.0043	<0.0001	0.9995	*Heliometra glacialis*
208	71010	0.0014	<0.0001	0.0000	0.0039	<0.0001	0.9995	Nudibranchia
209	66605	0.0014	<0.0001	0.0000	0.0028	<0.0001	0.9996	*Sabinea septemcarinata*
210	23843	0.0014	<0.0001	0.0000	0.0041	<0.0001	0.9996	*Chirolophis snyderi*
211	83310	0.0013	<0.0001	0.0000	0.0039	<0.0001	0.9996	*Ophiura* sp.
212	22265	0.0013	<0.0001	0.0005	0.0021	<0.0001	0.9996	*Liparis marmoratus*
213	74658	0.0013	<0.0001	0.0000	0.0037	<0.0001	0.9996	*Cyclocardia* sp.
214	71012	0.0012	<0.0001	0.0000	0.0037	<0.0001	0.9996	*Tochuina tetraquetra*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
215	24186	0.0012	<0.0001	0.0000	0.0030	<0.0001	0.9996	*Lycodes mucosus*
216	21397	0.0012	<0.0001	0.0000	0.0031	<0.0001	0.9996	*Blepsias bilobus*
217	71018	0.0012	<0.0001	0.0000	0.0025	<0.0001	0.9997	*Dendronotus* sp.
218	21348	0.0012	<0.0001	0.0000	0.0022	<0.0001	0.9997	*Hemilepidotus papilio*
219	98212	0.0011	<0.0001	0.0000	0.0033	<0.0001	0.9997	*Distaplia occidentalis*
220	75287	0.0011	<0.0001	0.0000	0.0032	<0.0001	0.9997	*Serripes notabilis*
221	66515	0.0010	<0.0001	0.0000	0.0031	<0.0001	0.9997	*Crangon communis*
222	21376	0.0010	<0.0001	0.0000	0.0030	<0.0001	0.9997	*Megalocottus platycephalus*
223	66516	0.0010	<0.0001	0.0000	0.0029	<0.0001	0.9997	*Crangon* sp.
224	75333	0.0010	<0.0001	0.0000	0.0029	<0.0001	0.9997	*Mya truncata*
225	43081	0.0009	<0.0001	0.0000	0.0028	<0.0001	0.9997	*Cribrinopsis* sp.
226	71716	0.0009	<0.0001	0.0002	0.0017	<0.0001	0.9997	*Colus martensi*
227	71634	0.0009	<0.0001	0.0000	0.0024	<0.0001	0.9997	*Tachyrhynchus erosus*
228	66530	0.0009	<0.0001	0.0000	0.0018	<0.0001	0.9998	*Crangon dalli*
229	74333	0.0008	<0.0001	0.0000	0.0025	<0.0001	0.9998	*Nucula tenuis*
230	60111	0.0008	<0.0001	0.0000	0.0018	<0.0001	0.9998	*Rachotropis* sp.
231	21378	0.0008	<0.0001	0.0000	0.0023	<0.0001	0.9998	*Myoxocephalus scorpioides*
232	97120	0.0008	<0.0001	0.0000	0.0018	<0.0001	0.9998	*Hemithiris psittacea*
233	75240	0.0007	<0.0001	0.0000	0.0019	<0.0001	0.9998	*Macoma* sp.
234	21441	0.0007	<0.0001	0.0000	0.0018	<0.0001	0.9998	*Icelus spatula*
235	71723	0.0007	<0.0001	0.0000	0.0014	<0.0001	0.9998	*Colus ombronius*
236	56300	0.0007	<0.0001	0.0000	0.0013	<0.0001	0.9998	Polynoidae
237	75111	0.0007	<0.0001	0.0000	0.0020	<0.0001	0.9998	*Mactromeris polynyma*
238	72421	0.0006	<0.0001	0.0001	0.0011	<0.0001	0.9998	*Boreotrophon pacificus*
239	74985	0.0006	<0.0001	0.0000	0.0019	<0.0001	0.9998	*Clinocardium californiense*
240	60112	0.0006	<0.0001	0.0000	0.0012	<0.0001	0.9998	*Rhachotropis aculeata*
241	50001	0.0006	<0.0001	0.0001	0.0011	<0.0001	0.9998	worm unident.

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
242	21405	0.0006	<0.0001	0.0001	0.0010	<0.0001	0.9998	*Nautichthys pribilovius*
243	20051	0.0006	<0.0001	0.0002	0.0010	<0.0001	0.9999	*Ulcina olrikii*
244	72403	0.0006	<0.0001	0.0002	0.0010	<0.0001	0.9999	*Boreotrophon coronatus*
245	80542	0.0006	<0.0001	0.0000	0.0017	<0.0001	0.9999	*Henricia sanguinolenta*
246	98079	0.0005	<0.0001	0.0000	0.0014	<0.0001	0.9999	*Pelonaia corrugata*
247	71739	0.0005	<0.0001	0.0000	0.0011	<0.0001	0.9999	*Volutopsius attenuatus*
248	10001	0.0005	<0.0001	0.0000	0.0016	<0.0001	0.9999	*Pleuronectiformes*
249	72736	0.0005	<0.0001	0.0000	0.0012	<0.0001	0.9999	*Buccinum normale*
250	71777	0.0005	<0.0001	0.0000	0.0012	<0.0001	0.9999	*Beringius* sp.
251	92900	0.0005	<0.0001	0.0000	0.0011	<0.0001	0.9999	*Maldanidae unid.*
252	21370	0.0005	<0.0001	0.0000	0.0011	<0.0001	0.9999	*Myoxocephalus polyacanthocephalus*
253	23806	0.0004	<0.0001	0.0000	0.0009	<0.0001	0.9999	*Lumpenus medius*
254	66031	0.0004	<0.0001	0.0000	0.0012	<0.0001	0.9999	*Pandalus eous*
255	20202	0.0004	<0.0001	0.0000	0.0010	<0.0001	0.9999	*Ammodytes hexapterus*
256	60118	0.0004	<0.0001	0.0000	0.0011	<0.0001	0.9999	*Nototropis* sp.
257	43050	0.0004	<0.0001	0.0000	0.0012	<0.0001	0.9999	*Oractis diomedeae*
258	69316	0.0004	<0.0001	0.0000	0.0011	<0.0001	0.9999	*Hapalogaster grebnitzkii*
259	21720	0.0004	<0.0001	0.0000	0.0008	<0.0001	0.9999	*Gadus macrocephalus*
260	23804	0.0004	<0.0001	0.0000	0.0009	<0.0001	0.9999	*Stichaeus punctatus*
261	85211	0.0003	<0.0001	0.0000	0.0010	<0.0001	0.9999	*Psolus phantapus*
262	22201	0.0003	<0.0001	0.0000	0.0010	<0.0001	0.9999	*Liparis* sp.
263	93102	0.0003	<0.0001	0.0000	0.0009	<0.0001	0.9999	*Priapulus caudatus*
264	73186	0.0003	<0.0001	0.0000	0.0006	<0.0001	0.9999	*Admete regina*
265	60115	0.0003	<0.0001	0.0000	0.0009	<0.0001	0.9999	*Arctolembos arcticus*
266	53700	0.0003	<0.0001	0.0000	0.0007	<0.0001	0.9999	*Nephtyidae*
267	74420	0.0003	<0.0001	0.0000	0.0008	<0.0001	0.9999	*Yoldia hyperborea*
268	66500	0.0003	<0.0001	0.0000	0.0008	<0.0001	0.9999	*Crangonidae*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
269	40049	0.0003	<0.0001	0.0000	0.0008	<0.0001	0.9999	*Sertulariidae unid.*
270	83000	0.0002	<0.0001	0.0000	0.0007	<0.0001	1.0000	Ophiuroidea
271	98319	0.0002	<0.0001	0.0000	0.0007	<0.0001	1.0000	*Trididemnum* sp.
272	60109	0.0002	<0.0001	0.0000	0.0005	<0.0001	1.0000	*Anonyx nugax*
273	71635	0.0002	<0.0001	0.0000	0.0006	<0.0001	1.0000	*Tachyrhynchus reticulatus*
274	66161	0.0002	<0.0001	0.0000	0.0006	<0.0001	1.0000	*Spirontocaris arcuata*
275	71911	0.0002	<0.0001	0.0000	0.0005	<0.0001	1.0000	*Liomesus ooides*
276	474	0.0002	<0.0001	0.0000	0.0006	<0.0001	1.0000	*Bathyraja parmifera*
277	71733	0.0002	<0.0001	0.0000	0.0006	<0.0001	1.0000	*Colus bristolensis*
278	74647	0.0002	<0.0001	0.0000	0.0005	<0.0001	1.0000	*Astarte montagui*
279	95103	0.0002	<0.0001	0.0000	0.0005	<0.0001	1.0000	*Heteropora* sp.
280	74414	0.0002	<0.0001	0.0000	0.0005	<0.0001	1.0000	*Yoldia* sp.
281	98070	0.0002	<0.0001	0.0000	0.0005	<0.0001	1.0000	Thaliacea
282	50220	0.0002	<0.0001	0.0000	0.0005	<0.0001	1.0000	*Travisia* sp.
283	1	0.0002	<0.0001	0.0000	0.0005	<0.0001	1.0000	fish eggs unident.
284	72756	0.0001	<0.0001	0.0000	0.0003	<0.0001	1.0000	*Buccinum solenum*
285	71524	0.0001	<0.0001	0.0000	0.0004	<0.0001	1.0000	*Cryptonatica* sp.
286	22212	0.0001	<0.0001	0.0000	0.0004	<0.0001	1.0000	*Liparis fabricii*
287	71713	0.0001	<0.0001	0.0000	0.0004	<0.0001	1.0000	*Colus capponius*
288	20001	0.0001	<0.0001	0.0000	0.0003	<0.0001	1.0000	*Pallasina barbata*
289	50005	0.0001	<0.0001	0.0000	0.0003	<0.0001	1.0000	*Eunice valens*
290	70150	0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	*Stenosemus albus*
291	72406	0.0001	<0.0001	0.0000	0.0003	<0.0001	1.0000	*Boreotrophon clathratus*
292	71250	0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	Dorididae
293	66548	<0.0001	<0.0001	0.0000	0.0003	<0.0001	1.0000	*Crangon septemspinosa*
294	95081	<0.0001	<0.0001	0.0000	0.0003	<0.0001	1.0000	*Costazia ventricosa*
295	72302	<0.0001	<0.0001	0.0000	0.0003	<0.0001	1.0000	*Trichotropis borealis*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
296	66613	<0.0001	<0.0001	0.0000	0.0003	<0.0001	1.0000	*Argis levior*
297	72740	<0.0001	<0.0001	0.0000	0.0003	<0.0001	1.0000	*Buccinum* sp.
298	23805	<0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	*Lumpenus maculatus*
299	74560	<0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	*Musculus* sp.
300	72800	<0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	*Velutina undata*
301	45000	<0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	*Ctenophora*
302	85170	<0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	*Pentamera* sp.
303	71020	<0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	*Dendronotus dalli*
304	66160	<0.0001	<0.0001	0.0000	0.0001	<0.0001	1.0000	*Spirontocaris* sp.
305	10115	<0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	*Reinhardtius hippoglossoides*
306	71724	<0.0001	<0.0001	0.0000	0.0001	<0.0001	1.0000	*Colus roseus*
307	92502	<0.0001	<0.0001	0.0000	0.0002	<0.0001	1.0000	*Emplectonema* sp.
308	74000	<0.0001	<0.0001	0.0000	0.0001	<0.0001	1.0000	Bivalvia
309	97010	<0.0001	<0.0001	0.0000	0.0001	<0.0001	1.0000	*Hemithyridae*
310	72757	<0.0001	<0.0001	0.0000	0.0001	<0.0001	1.0000	*Buccinum ciliatum*
311	57000	<0.0001	<0.0001	0.0000	0.0001	<0.0001	1.0000	*Sabellidae*
312	60140	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Anonyx* sp.
313	75220	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Pandora glacialis*
315	60105	<0.0001	<0.0001	0.0000	0.0001	<0.0001	1.0000	*Eusirus cuspidatus*
314	71405	<0.0001	<0.0001	0.0000	0.0001	<0.0001	1.0000	limpet unident.
316	74656	<0.0001	<0.0001	0.0000	0.0001	<0.0001	1.0000	*Cyclocardia* sp.
317	72804	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Velutina prolongata*
318	72806	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Velutina* sp.
319	74565	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Musculus glacialis*
320	92802	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Cerebratulus californienesis*
321	66174	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Eualus fabricii*
322	72533	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Margarites giganteus*

Appendix B.--Continued.

Rank	Species code	Mean CPUE (kg/ha)	Standard error	95% Confidence limits		Proportion	Cumulative proportion	Scientific name
323	64000	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	Mysida
324	55900	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Phyllodocidae unid.*
325	72100	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Oenopota* sp.
326	56313	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Eunoe senta*
327	60130	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Melita dentata*
328	72531	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Margarites* sp.
329	72372	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Neoiphinoe echinata*
330	95016	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Bugula* sp.
331	92510	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Tubulanus* sp.
332	72541	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Solariella obscura*
333	60131	<0.0001	<0.0001	0.0000	<0.0001	<0.0001	1.0000	*Quasimelita formosa*

Appendix C.--Fish species encountered, in alphabetical order by family, during the 2012 Chukchi Sea bottom trawl survey.

				Bottom depth (m)			Latitude range	
Family	Scientific name	Common name	Number stations present	Min. depth	Max. depth	Avg. depth	Southern	Northern
Agonidae	*Pallasina barbata*	tubenose poacher	3	12	14	13	66.48	69.01
	Podothecus veternus	veteran poacher	15	12	56	35	66.48	71.00
	Ulcina olrikii	Arctic alligatorfish	20	29	90	45	66.48	72.00
Ammodytidae	*Ammodytes hexapterus*	Pacific sand lance	4	12	51	29	69.01	69.99
Clupeidae	*Clupea pallasi*	Pacific herring	17	12	56	30	66.00	70.50
Cottidae	*Gymnocanthus pistilliger*	threaded sculpin	2	14	14	14	66.49	66.98
	Gymnocanthus tricuspis	Arctic staghorn sculpin	51	12	90	40	66.00	73.00
	Artediellus scaber	hamecon	18	12	86	46	68.00	73.04
	Hemilepidotus papilio	butterfly sculpin	7	37	59	51	66.03	72.48
	Triglops pingeli	ribbed sculpin	14	21	90	46	66.03	72.50
	Myoxocephalus verrucosus	warty sculpin	28	12	58	38	66.03	71.11
	Myoxocephalus polyacanthocephalus	great sculpin	2	37	52	45	66.51	66.99
	Myoxocephalus jaok	plain sculpin	5	14	24	17	66.00	66.99
	Megalocottus platycephalus	belligerent sculpin	1	14	14	14	66.98	66.98
	Myoxocephalus quadricornis	fourhorn sculpin	4	14	17	15	66.00	66.98
	Myoxocephalus scorpioides	Arctic sculpin	1	12	12	12	69.01	69.01
	Enophrys lucasi	leister sculpin	4	14	30	23	66.48	67.50
	Enophrys diceraus	antlered sculpin	9	12	56	32	68.00	69.99
	Icelus spatula	spatulate sculpin	3	50	90	66	71.52	72.48
Gadidae	*Gadus macrocephalus*	Pacific cod	3	29	47	41	67.50	69.50
	Boreogadus saida	Arctic cod	71	12	90	42	66.00	73.04
	Eleginus gracilis	saffron cod	24	12	53	33	66.00	72.50
	Gadus chalcogrammus	walleye pollock	24	17	59	38	66.48	72.50

Appendix C.--Continued.

Family	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Hemitripteridae	*Blepsias bilobus*	crested sculpin	2	29	42	36	66.48	70.50
	Nautichthys pribilovius	eyeshade sculpin	9	27	90	42	66.48	71.52
Hexagrammidae	*Hexagrammos stelleri*	whitespotted greenling	2	12	14	13	66.98	69.01
Liparidae	*Liparis* sp.		2	41	47	44	69.50	70.99
	Liparis gibbus	variegated snailfish	26	29	59	45	66.03	72.51
	Liparis fabricii	gelatinous seasnail	1	44	44	44	71.50	71.50
	Liparis tunicatus	kelp snailfish	36	21	86	44	66.48	73.04
	Liparis marmoratus	festive snailfish	11	23	53	40	69.50	72.50
Osmeridae	*Mallotus villosus*	capelin	30	12	58	40	66.03	72.50
	Osmerus mordax	rainbow smelt	11	12	30	21	66.00	70.50
Pleuronectidae	*Reinhardtius hippoglossoides*	Greenland turbot	1	50	50	50	70.50	70.50
	Hippoglossoides robustus	Bering flounder	40	24	86	47	66.03	73.04
	Liopsetta glacialis	Arctic flounder	2	14	14	14	66.48	66.98
	Limanda aspera	yellowfin sole	16	12	56	26	66.00	70.50
	Limanda proboscidea	longhead dab	5	15	37	23	66.00	69.01
	Limanda sakhalinensis	Sakhalin sole	6	29	56	45	66.03	70.50
	Platichthys stellatus	starry flounder	10	14	30	22	66.00	69.01
	Pleuronectes quadrituberculatus	Alaska plaice	13	14	47	26	66.00	69.50
	Pleuronectiformes	flatfish unident.	1	15	15	15	66.00	66.00
Rajidae	*Bathyraja parmifera*	Alaska skate	1	52	52	52	66.51	66.51
	Bathyraja parmifera egg case	Alaska skate egg case	1	49	49	49	71.50	71.50
Stichaeidae	*Stichaeus punctatus*	Arctic shanny	2	14	52	33	66.03	66.98
	Lumpenus maculatus	daubed shanny	2	47	84	66	70.01	73.04
	Lumpenus medius	stout eelblenny	5	35	59	44	69.50	72.48
	Lumpenus fabricii	slender eelblenny	30	14	58	39	66.03	71.11

Appendix C.--Continued.

Family	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
	Acantholumpenus mackayi	pighead prickleback	1	14	14	14	66.98	66.98
	Chirolophis snyderi	bearded warbonnet	1	29	29	29	68.00	68.00
Zoarcidae	*Lycodes raridens*	marbled eelpout	12	35	51	43	68.50	72.50
	Lycodes palearis	wattled eelpout	15	21	56	38	66.48	69.50
	Lycodes mucosus	saddled eelpout	2	47	51	49	68.50	70.01
	Lycodes polaris	Canadian eelpout	12	35	86	51	66.51	73.00
	Lycodes turneri	polar eelpout	11	14	58	38	66.48	71.11
Other		fish eggs unident.	1	39	39	39	70.49	70.49

Appendix D.--Invertebrate species, in alphabetical order by phylum or subphylum, encountered during the 2012 Chukchi Sea bottom trawl survey.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m) Min. depth	Max. depth	Avg. depth	Latitude range Southern	Northern
Annelida	Polychaeta	polychaete worm unid.	30	14	90	47	66.98	73.04
		worm unid.	10	28	84	49	70.00	73.04
	Eunice valens		1	46	46	46	67.52	67.52
		tube worm unid.	6	42	86	56	71.49	72.48
	Travisia sp.		1	58	58	58	68.01	68.01
	Nephtyidae	cat worm unid.	4	42	59	49	71.50	72.48
	Phyllodocidae unid.		2	46	50	48	71.50	71.50
	Polynoidae	scale worm unid.	7	39	53	46	68.50	72.50
	Eunoe sp.		6	37	59	50	66.03	72.48
	Eunoe nodosa	giant scale worm	28	23	90	49	67.51	73.04
	Eunoe depressa	depressed scale worm	15	24	53	42	66.99	72.50
	Eunoe senta		1	41	41	41	70.99	70.99
	Sabellidae	sabellid unid.	1	53	53	53	72.01	72.01
	Maldanidae unid.	bamboo worm unid.	5	39	84	51	71.50	73.04
	Polychaete tubes		3	23	42	31	68.00	71.00
	Polychaete tubes		3	23	42	31	68.00	71.00
Arthropoda	Amphipoda	amphipod unid.	9	21	90	43	69.99	72.04
	Eusirus cuspidatus		1	42	42	42	70.00	70.00
	Stegocephalus inflatus		4	35	90	52	70.00	71.52
	Anonyx nugax	riddick amphipod	3	28	44	38	71.50	72.04
	Rachotropis sp.		5	28	53	43	71.50	72.04
	Rhachotropis aculeata		8	28	86	45	70.00	72.04
	Arctolembos arcticus		2	35	35	35	69.50	71.11

Appendix D.--Invertebrate species, in alphabetical order by phylum or subphylum, encountered during the 2012 Chukchi Sea bottom trawl survey.

				Bottom depth (m)			Latitude range	
Phylum/ subphylum	Scientific name	Common name	Number stations present	Min. depth	Max. depth	Avg. depth	Southern	Northern
Annelida	Polychaeta	polychaete worm unid.	30	14	90	47	66.98	73.04
		worm unid.	10	28	84	49	70.00	73.04
	Eunice valens		1	46	46	46	67.52	67.52
		tube worm unid.	6	42	86	56	71.49	72.48
	Travisia sp.		1	58	58	58	68.01	68.01
	Nephtyidae	cat worm unid.	4	42	59	49	71.50	72.48
	Phyllodocidae unid.		2	46	50	48	71.50	71.50
	Polynoidae	scale worm unid.	7	39	53	46	68.50	72.50
	Eunoe sp.		6	37	59	50	66.03	72.48
	Eunoe nodosa	giant scale worm	28	23	90	49	67.51	73.04
	Eunoe depressa	depressed scale worm	15	24	53	42	66.99	72.50
	Eunoe senta		1	41	41	41	70.99	70.99
	Sabellidae	sabellid unid.	1	53	53	53	72.01	72.01
	Maldanidae unid.	bamboo worm unid.	5	39	84	51	71.50	73.04
	Polychaete tubes		3	23	42	31	68.00	71.00
	Polychaete tubes		3	23	42	31	68.00	71.00
Arthropoda	Amphipoda	amphipod unid.	9	21	90	43	69.99	72.04
	Eusirus cuspidatus		1	42	42	42	70.00	70.00
	Stegocephalus inflatus		4	35	90	52	70.00	71.52
	Anonyx nugax	riddick amphipod	3	28	44	38	71.50	72.04
	Rachotropis sp.		5	28	53	43	71.50	72.04
	Rhachotropis aculeata		8	28	86	45	70.00	72.04
	Arctolembos arcticus		2	35	35	35	69.50	71.11

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Arthropoda cont.	*Nototropis* sp.		2	47	51	49	68.99	69.50
	Melita dentata		2	39	46	43	71.00	72.00
	Quasimelita formosa		1	46	46	46	71.00	71.00
	Anonyx sp.		2	21	35	28	70.50	71.11
	Saduria entomon		4	46	59	51	71.50	72.48
	Mysida	opossum shrimps	2	28	45	37	71.01	72.04
	Thoracica	barnacle unid.	14	29	52	42	66.03	72.50
	Balanus sp.		2	31	42	37	69.99	71.00
	Pandalus eous (=*borealis*)	Alaskan pink (=northern) shrimp	5	39	59	48	69.50	73.00
	Pandalus goniurus	humpy shrimp	33	21	58	42	66.03	72.50
	Spirontocaris sp.		2	29	90	60	68.00	71.52
	Spirontocaris arcuata	Rathbun blade shrimp	3	14	42	33	66.49	71.00
	Eualus sp.		37	12	90	46	67.50	73.00
	Eualus fabricii	Arctic eualid	1	50	50	50	72.00	72.00
	Eualus gaimardii		18	39	53	46	68.50	72.50
	Eualus macilentus	Greenland shrimp	2	43	51	47	69.50	70.50
	Eualus suckleyi	shortscale eualid	6	40	56	48	68.00	70.50
	Lebbeus groenlandicus	spiny lebbeid	6	12	56	33	68.00	69.99
	Crangonidae	crangonid shrimp unid.	2	45	46	46	71.00	71.50
	Crangon sp.		4	14	90	49	66.98	71.52
	Crangon communis	twospine crangon	1	43	43	43	70.50	70.50
	Crangon sp. cf. *communis* (CAS)		1	29	29	29	66.48	66.48
	Crangon dalli	ridged crangon	12	14	53	41	66.48	72.50
	Crangon septemspinosa	sevenspine bay shrimp	1	17	17	17	66.48	66.48

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Arthropoda cont.	*Argis* sp.		2	29	50	40	66.48	72.51
	Argis dentata	Arctic argid	2	17	46	32	66.48	72.48
	Sclerocrangon boreas	sculptured shrimp	17	12	59	33	66.49	72.48
	Sabinea septemcarinata		13	38	86	51	71.00	73.00
	Argis lar	kuro argid	63	12	59	40	66.00	73.00
	Argis levior	Nelson's argid	1	42	42	42	70.00	70.00
	Hyas coarctatus	circumboreal toad crab	66	14	90	44	66.03	73.04
	Chionoecetes opilio	snow crab	61	14	90	44	66.00	73.04
	Telmessus cheiragonus	helmet crab	18	12	40	24	66.00	71.11
	Labidochirus splendescens	splendid hermit	65	12	90	41	66.00	73.00
	Pagurus trigonocheirus	fuzzy hermit crab	66	14	90	44	66.03	73.04
	Pagurus ochotensis	Alaskan hermit	3	14	17	15	66.00	66.48
	Pagurus rathbuni	longfinger hermit	37	37	86	49	66.99	73.04
	Pagurus capillatus	hairy hermit crab	24	14	58	36	66.48	71.01
	Hapalogaster grebnitzkii	soft crab	2	37	37	37	68.52	71.00
	Paralithodes camtschaticus	red king crab	2	27	40	34	66.99	67.51
	Paralithodes platypus	blue king crab	8	35	56	45	66.03	70.51
Brachiopoda	Hemithyridae	hemithyrid brachiopods	1	45	45	45	70.99	70.99
	Hemithiris psittacea	black brachiopod	3	39	56	46	68.00	70.49
Bryozoa	Bryozoa	bryozoan unid.	35	12	84	39	66.00	73.04
Cnidaria		hydroid unid.	26	21	86	43	69.01	72.51
	Sertulariidae unid.	Sertulariid hydroid	2	37	46	42	68.52	72.48
	Scyphozoa	jellyfish unid.	2	37	50	44	71.00	71.50
	Chrysaora melanaster		48	12	90	40	66.00	73.04

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Cnidaria cont.	*Cyanea capillata*	lion's mane	32	12	86	40	66.00	72.01
	Gersemia sp.	sea raspberry	20	14	90	40	66.48	71.52
	Gersemia fruticosa		21	28	86	50	70.00	73.04
	Actiniaria	sea anemone unid.	29	12	90	41	66.03	72.48
	Ptychodactis patula		5	39	56	47	68.00	71.50
	Metridium sp.		7	14	30	20	66.48	67.50
	Stomphia sp.		3	21	52	37	66.03	70.50
	Stomphia coccinea	swimming anemone	4	29	56	40	68.00	71.11
	Urticina sp.		4	27	40	33	66.48	70.00
	Urticina crassicornis	mottled anemone	53	12	90	44	66.49	73.04
	Oractis diomedeae	grape anemone	1	58	58	58	68.01	68.01
	Cribrinopsis sp.		1	49	49	49	71.50	71.50
	Cribrinopsis fernaldi	chevron-tentacled anemone	2	21	35	28	70.50	71.11
	Actinostolidae		4	24	86	52	66.99	71.99
	Actinostola sp.		2	47	56	52	68.00	70.01
	Actinostola groenlandica		3	21	37	29	68.00	70.50
Ctenophora	Ctenophora	comb jelly unid.	1	53	53	53	72.50	72.50
	Beroe sp.		3	42	59	49	71.00	73.00
Echinodermata	Asteroidea	sea star unid.	1	47	47	47	69.50	69.50
	Evasterias echinosoma	giant sea star	13	12	46	27	66.48	71.00
	Urasterias lincki		17	39	86	51	68.50	73.00
	Leptasterias groenlandica		41	28	86	47	66.99	73.00
	Lethasterias nanimensis	blackspined sea star	15	12	46	25	66.48	71.00
	Henricia sanguinolenta	sanguine sea star	1	29	29	29	68.00	68.00

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Echinodermata cont.	*Henricia tumida*	tumid sea star	15	12	52	34	66.03	71.00
	Leptasterias polaris		48	12	58	39	66.00	72.04
	Leptasterias arctica		42	12	56	37	66.00	72.04
	Henricia beringiania	Bering Henricia	7	29	90	55	68.00	73.04
	Solaster arcticus		12	29	90	54	66.03	73.04
	Crossaster papposus	rose sea star	43	12	90	44	66.03	73.04
	Pteraster tesselatus		1	29	29	29	68.00	68.00
	Pteraster octaster		2	30	37	34	67.50	68.52
	Pteraster obscurus	obscure sea star	22	21	86	47	66.51	73.00
	Asterias amurensis	purple-orange sea star	26	12	51	30	66.00	71.00
	Ctenodiscus crispatus	common mud star	21	28	86	51	71.00	73.04
	Strongylocentrotus droebachiensis	green sea urchin	38	12	90	38	66.00	71.52
	Echinarachnius parma	parma sand dollar	4	21	35	28	69.50	70.51
	Heliometra glacialis		1	90	90	90	71.52	71.52
	Ophiuroidea	brittlestar unid.	1	50	50	50	72.00	72.00
	Gorgonocephalus eucnemis	basketstar	6	42	52	47	66.51	72.48
	Gorgonocephalus sp. cf. *arcticus*		35	17	84	43	66.48	73.04
	Ophiura sp.		2	50	50	50	72.48	72.51
	Ophiura sarsi	notched brittlestar	35	14	90	45	66.48	73.04
	Stegophiura nodosa		13	15	56	36	66.00	72.04
	Ophiacantha bidentata		1	90	90	90	71.52	71.52
	Ophiopholis aculeata	ubiquitous brittle star	8	29	56	42	68.00	71.11
	Holothuroidea	sea cucumber unid.	2	21	29	25	68.00	70.50
	Ocnus sp.		2	35	90	63	71.11	71.52

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Echinodermata cont.	*Ocnus glacialis*		16	35	86	51	69.50	73.04
	Myriotrochus rinkii		16	23	86	46	69.50	72.51
	Pentamera sp.		1	14	14	14	66.98	66.98
	Cucumaria sp.		1	37	37	37	71.00	71.00
	Psolus phantapus		1	45	45	45	70.99	70.99
	Psolus fabricii	brownscaled sea cucumber	21	14	84	44	66.03	73.04
Echiura	Echiura	echiuroid worm unid.	7	14	90	50	66.98	73.00
Ectoprocta	*Bugula* sp.		1	47	47	47	72.01	72.01
	Flustra serrulata	leafy bryozoan	1	50	50	50	71.50	71.50
	Alcyonidium pedunculatum		14	21	84	39	67.51	73.04
	Alcyonidium sp.		2	23	31	27	69.50	69.99
	Alcyonidium disforme		11	14	59	41	66.98	73.00
	Alcyonidium enteromorpha	noodle bryozoan	6	31	90	49	69.99	71.52
	Rhamphostomella costata	ribbed bryozoan	3	37	56	46	68.00	70.99
	Costazia ventricosa	rusty bryozoan	1	45	45	45	70.99	70.99
	Heteropora sp.		1	45	45	45	70.99	70.99
	Dendrobeania sp.		5	29	86	51	68.00	72.01
Mollusca	*Amicula vestita*		10	21	90	46	68.00	71.52
	Stenosemus albus	northern white chiton	4	37	47	43	70.00	71.00
	gastropod eggs	snail eggs	13	14	58	40	66.49	72.01
	Buccinum sp. Eggs		33	21	90	47	68.00	73.04
	Neptunea sp. eggs		6	21	90	43	69.01	71.52
	Nudibranchia	nudibranch unid.	4	23	53	45	68.50	72.50
	Tochuina tetraquetra	giant orange tochui	1	23	23	23	69.50	69.50

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Mollusca cont.	*Dendronotus* sp.		6	37	90	58	66.99	72.50
	Dendronotus dalli	Dall's dendronotid	1	58	58	58	68.01	68.01
	Dendronotus frondosus	frond-aeolis	2	21	43	32	70.50	70.50
	Tritonia sp.		8	35	47	42	69.50	71.11
	Calycidoris guentheri		7	28	59	45	70.51	73.00
	Tritonia diomedea	rosy tritonia	3	14	30	22	66.49	70.50
	Dorididae	dorid nudibranch unid.	2	37	38	38	66.99	66.99
		limpet unident.	1	42	42	42	70.00	70.00
	Naticidae eggs	moonsnail eggs unid.	28	28	90	50	67.50	73.04
	Cryptonatica sp.		1	28	28	28	72.04	72.04
	Cryptonatica (=*Natica*) *aleutica*	Aleutian moonsnail	2	37	46	42	66.99	67.52
	Cryptonatica (=*Natica*) *russa*	rusty moonsnail	32	38	90	49	67.50	73.00
	Euspira pallida	pale moonsnail	35	14	90	47	66.49	73.00
	Lamellaria sp.		1	47	47	47	70.01	70.01
	Onchidiopsis glacialis	icy lamellaria	5	31	47	41	69.50	70.99
	Onchidiopsis sp. B (Clark & McLean)		2	31	35	33	69.99	70.51
	Onchidiopsis sp.		13	21	59	41	68.50	72.48
	Onchidiopsis carnea		6	31	47	40	69.99	71.50
	Tachyrhynchus erosus	eroded turretsnail	5	40	51	46	69.50	71.50
	Tachyrhynchus reticulatus	reticulated turretsnail	3	28	51	40	69.50	72.04
	Colus sp.		3	21	52	39	66.03	71.01
	Colus capponius		1	58	58	58	68.01	68.01
	Colus martensi		8	42	53	48	71.00	72.51
	Colus sabini		2	84	86	85	71.99	73.04

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Mollusca cont.	*Colus hypolispus*		8	42	58	49	68.01	72.51
	Colus ombronius	shady whelk	5	14	51	40	66.49	71.50
	Colus roseus	rosy whelk	5	41	50	45	70.50	71.50
	Colus spitzbergensis	thick-ribbed whelk	15	35	90	52	68.00	73.04
	Colus halli	shrew whelk	22	14	84	47	66.49	73.04
	Colus bristolensis		1	40	40	40	67.51	67.51
	Volutopsius attenuatus	attenuate melon whelk	3	43	51	46	69.50	71.00
	Volutopsius sp. eggs		3	42	90	72	71.00	73.04
	Pyrulofusus deformis	warped whelk	16	14	90	49	66.49	73.04
	Volutopsius fragilis	fragile whelk	17	14	90	51	66.49	73.04
	Volutopsius stefanssoni	shouldered whelk	8	21	56	42	66.03	71.11
	Beringius beringii		29	14	90	46	66.03	73.04
	Beringius stimpsoni		9	21	90	46	66.03	71.52
	Beringius sp. eggs		2	59	84	72	72.48	73.04
	Neptunea borealis		55	14	90	46	66.48	73.04
	Neptunea middendorffii		1	45	45	45	70.99	70.99
	Neptunea ventricosa	fat whelk	24	14	56	38	66.03	72.00
	Neptunea heros		60	14	90	44	66.00	73.04
	Clinopegma magnum	helmet whelk	13	41	86	52	68.50	72.50
	Plicifusus kroyeri		25	21	90	49	66.51	73.04
	Plicifusus johanseni		15	42	90	50	68.01	72.51
	Liomesus ooides	egg whelk	2	23	24	24	66.99	69.50
	Oenopota sp.		1	39	39	39	72.00	72.00
	Trichotropis borealis		2	44	59	52	71.50	73.00

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Mollusca cont.	*Trichotropis bicarinata*	two-keel hairysnail	3	21	37	31	68.52	71.11
	Neoiphinoe echinata		1	50	50	50	71.50	71.50
	Boreotrophon coronatus		9	35	56	47	68.00	72.50
	Boreotrophon clathratus	clathrate trophon	2	42	44	43	70.00	71.50
	Boreotrophon pacificus		8	39	90	50	69.50	71.52
	Margarites sp.		1	42	42	42	71.00	71.00
	Margarites giganteus	giant margarite	2	46	58	52	68.01	71.50
	Margarites costalis	boreal rosy margarite	14	28	59	44	70.50	72.48
	Solariella obscura	obscure solarelle	1	46	46	46	71.50	71.50
	Buccinum normale		2	28	58	43	68.01	72.04
	Buccinum obsoletum		13	35	86	49	68.50	72.51
	Buccinum sp.		1	45	45	45	71.01	71.01
	Buccinum angulosum	angular whelk	29	21	90	45	66.48	71.99
	Buccinum plectrum	sinuous whelk	5	35	84	50	70.00	73.04
	Buccinum scalariforme	ladder whelk	39	23	90	46	66.99	72.50
	Buccinum polare	polar whelk	39	29	90	48	66.48	73.00
	Buccinum solenum		2	38	90	64	66.99	71.52
	Buccinum ciliatum		1	45	45	45	71.00	71.00
	Buccinum glaciale	glacial whelk	7	35	56	46	66.03	71.11
	Buccinum tenellum		2	14	29	22	66.48	66.49
	Buccinum ectomycina		3	39	45	42	70.00	70.99
	Velutina undata	wavy lamellaria	2	24	29	27	66.48	66.99
	Velutina prolongata	elongate lamellaria	1	37	37	37	66.99	66.99
	Velutina sp.		1	21	21	21	70.50	70.50
	Admete regina	noble admete	5	14	56	40	66.49	70.50

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Mollusca cont.	Bivalvia	bivalve unid.	2	46	50	48	71.50	72.00
	Mytilus sp.		1	37	37	37	71.00	71.00
	Chlamys behringiana	Iceland scallop	11	37	90	54	68.00	73.04
	Hiatella arctica	Arctic hiatella	6	37	51	44	68.99	71.50
	Nucula tenuis	smooth nutclam	1	46	46	46	71.50	71.50
	Yoldia sp.		1	59	59	59	72.48	72.48
	Yoldia hyperborea	northern yoldia	3	35	46	42	71.11	71.50
	Nuculana pernula	northern nutclam	17	28	59	46	69.50	73.00
	Musculus sp.		1	50	50	50	71.50	71.50
	Musculus niger	black mussel	2	45	90	68	71.01	71.52
	Musculus discors	discordant mussel	10	21	90	40	69.01	71.52
	Musculus glacialis	corrugate mussel	2	39	47	43	72.00	72.50
	Astarte sp.		2	59	90	75	71.52	72.48
	Astarte arctica		20	14	90	42	66.49	72.51
	Astarte montagui		1	14	14	14	66.49	66.49
	Astarte esquimalti		8	28	86	52	71.49	73.04
	Cyclocardia crassidens	thick carditid	4	21	47	38	70.01	71.00
	Cyclocardia sp.		1	35	35	35	70.51	70.51
	Cyclocardia sp. cf. *borealis* (Clark 2006)	northern carditid	3	21	50	39	70.50	71.50
	Clinocardium ciliatum	hairy cockle	27	14	56	41	66.49	72.51
	Clinocardium californiense	California cockle	2	21	49	35	69.01	71.50
	Mactromeris polynyma	Arctic surfclam	1	12	12	12	69.01	69.01
	Pandora glacialis	glacial pandora	2	46	50	48	71.50	71.50
	Macoma sp.		3	44	47	46	67.50	71.50

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Mollusca cont.	*Macoma calcarea*	chalky macoma	2	14	84	49	66.98	73.04
	Serripes groenlandicus	Greenland cockle	30	14	59	41	66.00	73.00
	Serripes laperousii	broad cockle	6	12	52	30	66.03	71.00
	Serripes notabilis	oblique smoothcockle	1	39	39	39	72.00	72.00
	Mya truncata	truncate softshell	1	12	12	12	69.01	69.01
	Benthoctopus sibiricus		8	38	84	53	66.03	73.04
		empty bivalve shells	58	12	90	41	66.00	73.00
		empty gastropod shells	34	14	90	39	66.00	72.50
Nemertea	Nemertea	nemertean worm unid.	10	42	90	49	67.50	72.50
	Emplectonema sp.		1	46	46	46	67.52	67.52
	Tubulanus sp.		1	46	46	46	67.52	67.52
	Cerebratulus californienesis		1	46	46	46	67.52	67.52
Porifera	Porifera	sponge unid.	11	14	84	42	66.03	73.04
	Suberites sp.		2	37	90	64	71.00	71.52
	Halichondria sp.		4	12	37	25	68.00	71.00
	Polymastia sp.		3	59	86	76	71.99	73.04
	Halichondria sitiens	black papillate sponge	6	12	52	37	66.51	70.99
	Stylissa sp.	drumstick sponge	10	23	90	51	67.50	73.04
Priapula	*Priapulus caudatus*		2	37	47	42	67.50	71.00
Sipuncula	Sipuncula	peanut worm unid.	4	14	90	46	66.98	71.52
	Golfingia margaritacea		10	38	59	48	68.00	73.00
Tunicata	Ascidiacea	tunicate unid.	21	12	90	40	66.99	73.04
	Thaliacea	salp unid.	1	90	90	90	71.52	71.52
	Pelonaia corrugata		3	37	47	43	66.99	72.01
	Styela rustica	sea potato	28	15	56	38	66.00	71.50

Appendix D.--Continued.

Phylum/ subphylum	Scientific name	Common name	Number stations present	Bottom depth (m)			Latitude range	
				Min. depth	Max. depth	Avg. depth	Southern	Northern
Tunicata cont.	*Boltenia ecinata*		12	21	56	39	66.99	71.50
	Boltenia ovifera		22	21	90	44	68.52	72.48
	Halocynthia sp.	sea peach unid.	1	45	45	45	70.99	70.99
	Halocynthia aurantium	sea peach	10	21	90	46	68.00	71.52
	Distaplia sp.		1	56	56	56	68.00	68.00
	Distaplia occidentalis		1	29	29	29	68.00	68.00
	Distaplia sp. A (Clark 2006)		1	29	29	29	68.00	68.00
		compound ascidian unid.	2	29	37	33	68.00	68.52
	Aplidium sp. A (Clark 2006)	sea glob	9	15	53	33	66.00	72.01
	Trididemnum sp.		1	21	21	21	70.50	70.50
	Chelyosoma productum		8	21	59	40	68.52	72.48
	Molgula sp.		1	27	27	27	66.99	66.99
	Molgula griffithsii	sea grape	6	23	59	43	68.00	72.48

Appendix I.

Variability in the summer diet of juvenile polar cod (*Boreogadus saida*) in the northeastern Chukchi and western Beaufort Seas

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March 7, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)
Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
BASIS	U.S. Bering-Aluetian Salmon International Survey
CCA	Canonical correspondence analysis
nMDS	Non-metric multidimensional scaling
$\%\overline{N}$	Percent mean number of prey
%O	Percent occurrence of prey
$\%\overline{W}$	Percent mean weight of prey

List of Oral and Poster Presentations

Gray BP., Norcross BL. Characterizing the diets of three abundant fishes in the Chukchi and Beaufort seas. Poster presented at the Alaska Marine Science Symposium in Anchorage, Alaska from January 21–25, 2013.

Gray BP., Norcross BL. Comparing the diets of three abundant fishes across the Chukchi and Beaufort seas. Poster presented at the 28th Lowell Wakefield Fisheries Symposium: Responses of Arctic Marine Ecosystems to Climate Change in Anchorage, Alaska from March 26–29, 2013.

Gray BP., Norcross BL. Fish diets across the Chukchi and Beaufort seas. Oral Presentation at the American Fisheries Society meeting in Fairbanks, Alaska on October 10, 2013.

Gray BP., Norcross BL. Fish diets across the Chukchi and Beaufort seas. Oral Presentation at the Alaska Marine Science Symposium in Anchorage, Alaska on January 20, 2014.

Gray BP., Norcross BL. Region and size-based comparisons of three fish species' diets across the Chukchi and Beaufort seas. Poster presented at the Ocean Sciences Meeting in Honolulu, Hawaii on February 26, 2014.

Gray BP., Norcross BL. Comparisons of Arctic cod, Arctic staghorn sculpin, and shorthorn sculpin diets across the northeastern Chukchi and western Beaufort Seas. Oral presentation component of Benjamin Gray's MS thesis defense in Fairbanks, Alaska on October 10, 2014.

Gray BP., Norcross BL. A comparison of fish diets between regions of the northeastern Chukchi and western Beaufort Seas. Poster presentation at the American Fisheries Society meeting in Juneau, Alaska from October 20–24, 2014.

Proposed Objectives and Study Chronology

The objectives of our research were to 1) describe the summer diets of juvenile polar cod within the Chukchi and Beaufort Seas, 2) determine the potential drivers of variation in juvenile polar cod diet, and 3) compare juvenile polar cod diets within and between the Chukchi and Beaufort Seas. To meet these objectives, polar cod stomach contents were identified, grouped by order, and analyzed using two multivariate methods: canonical correspondence analysis and non-metric multidimensional scaling.

Polar cod were collected via bottom trawl over three summers in the northeastern Chukchi Sea (2010–2012) and one summer in the western Beaufort Sea (2011). Chukchi Sea polar cod were collected during the Alaska Monitoring and Assessment Program (AKMAP) cruises in 2010 and 2011, and the Arctic Ecosystem Integrated Survey (Arctic Eis) bottom trawl segment in 2012. Beaufort Sea polar cod were collected during the 2011 Central Beaufort Sea Fisheries Survey (Beaufish).

Laboratory and data analysis took place at the University of Alaska Fairbanks. All processes associated with polar cod stomach contents analysis occurred from fall 2011 to fall 2013. Data analysis took place from fall 2013 to spring 2015. The data used to develop this report, along with an associated manuscript published in the Arctic gadids special issue of Polar Biology (October 2015), can be found on AOOS Arctic Eis Ocean Workspace in the "Diets – Fish and Snow Crab" folder. These products will be made publically available through the Alaska Ocean Observing System (AOOS) Arctic Data Portal at the conclusion of the Arctic Eis Project.

1. Abstract

Polar cod (*Boreogadus saida*) is an important link between top predators and lower trophic levels in high-latitude marine ecosystems. Previous findings describe differences in its diet throughout the western Arctic; however, the causes of this variation are not well known. This study examined the diets of juvenile polar cod collected via demersal trawling methods over three summers in the northeastern Chukchi Sea (2010–2012) and one summer in the western Beaufort Sea (2011) to determine the amount of variability explained by biological, spatial, and interannual factors. Prey were identified, measured for length, and aggregated by percent mean weight into taxonomically-coarse prey categories for analysis. Within seas, variation in juvenile polar cod diet composition was significantly related to body size, latitude, longitude, depth, and interannual (Chukchi Sea only) factors. Canonical correspondence analysis indicated body size was the most important factor contributing to the total variance in juvenile polar cod diet in the Chukchi and Beaufort Seas. Body size-based diet differences between the Chukchi and Beaufort Seas were evaluated using non-metric multidimensional scaling. This method revealed that similar-sized polar cod consumed similar-sized prey in both seas, but their diets were more benthically-influenced in the Chukchi Sea and more pelagically-influenced in the Beaufort Sea. Juvenile polar cod diet compositions vary by body size and region of inhabitance throughout their distribution. Here, we show that body size was the primary factor explaining variation in the summer diet of juvenile polar cod within the Chukchi and Beaufort Seas.

2. Introduction

Polar cod is an abundant (Lowry and Frost 1981; Welch et al. 1992; Mecklenburg et al. 2011), zooplanktivorous (Welch et al. 1992; Walkusz et al. 2011) forage fish found throughout high-latitude marine systems. It is an important prey source for marine mammals, seabirds, and other fishes (Lowry and Frost 1981; Welch et al. 1992; Walkusz et al. 2011), linking lower trophic levels to higher level predators (Welch et al. 1992). Polar cod has been observed to inhabit shallower surface waters as juveniles or deeper continental slope regions as adults (Parker-Stetter et al. 2011; Benoit et al. 2014). Polar cod has been found under ice in winter (Benoit et al. 2008; Geoffroy et al. 2011) and in ice-free waters in summer (Barber et al. 1997; Walkusz et al. 2011; Norcross et al. 2013). It typically consumes pelagic prey (Lowry and Frost 1981) including calanoid copepods, ice-associated amphipods, hyperiid amphipods, euphausiids, and other fishes (Lowry and Frost 1981; Craig et al. 1982; Coyle et al. 1997; Rand et al. 2013). In addition to feeding on pelagic organisms, polar cod may inhabit shallower regions (Bluhm and Gradinger 2008) and feed on bottom-associated (i.e., benthic and epibenthic) prey such as benthic amphipods, cumaceans, and mysids (Craig et al. 1982; Coyle et al. 1997; Cui et al. 2012). This study describes the summer diets of juvenile (i.e., 31–230 mm; approximately age 0–2) polar cod sampled from the northeastern Chukchi Sea (hereafter, Chukchi Sea) and western Beaufort Sea (hereafter, Beaufort Sea). It further quantifies variation in diets attributed to body size, location, depth, and year.

Body size is expected to be a major source of variability in juvenile polar cod diet. Ontogenetic shifts in morphology are common among fishes (Labropoulou and Eleftheriou 1997) and influence the size range and types of prey eaten by juvenile fishes (Werner and Gilliam 1984). Size-based shifts in prey use have been documented in polar cod populations; larval polar cod consume smaller stages of calanoid copepods (Walkusz et al. 2011), while juvenile and adult individuals consume larger prey, including larger calanoid copepods, amphipods, mysids, and other fishes (Lowry and Frost 1981; Craig et al. 1982; Jensen et al. 1991). Although body size has been described as influencing polar cod diet, its importance relative to other potential sources of variability is not well documented in polar cod diet literature.

In addition to body size, interannual (Scharf et al. 2000; Renaud et al. 2012) and spatial variability in prey abundance and distribution (Nahrgang et al. 2014) may account for within- and between-sea diet differences. Prey availability and the sizes of prey available to juvenile polar cod could vary in relation to the timing of sea ice retreat, water mass formation, terrestrial hydrographic conditions (Walkusz et al. 2013), and other factors that create spatial variability in habitat within and between seas. Here, we examine the effects of spatial variation on juvenile polar cod diet compositions using latitude, longitude, and depth as proxies for habitat. Combinations of these factors influence the spatial distributions of fish communities (Norcross et al. 2013) along with their potential prey, i.e., benthic macroinvertebrates (Iken et al. 2010, Blanchard et al. 2013) and pelagic zooplankton (Ashjian et al. 2005, Hopcroft et al. 2010) in the western Arctic.

We analyzed polar cod stomach contents and used multivariate statistics to 1) describe the summer diets of juvenile polar cod within the Chukchi and Beaufort Seas, 2) determine the potential drivers of variation in juvenile polar cod diet, and 3) compare juvenile polar cod diets within and between the Chukchi and Beaufort Seas. This study advances our understanding of how biological and environmental factors influence the feeding ecology of polar cod and provides comprehensive information on polar cod diets, which can be used to parameterize food web models for the Arctic.

3. Methods

3.1 Study area and fish sampling

The Chukchi and Beaufort Seas are governed by unique physical and biological processes. Regions of the Chukchi Sea are supplemented with warmer water, nutrients (Weingartner 1997), and fauna from the Bering Sea (Walsh et al. 1989). These flow across the Chukchi Sea shelf into the Arctic Ocean, effectively bypassing benthic habitats of the Beaufort Sea, which are largely influenced by colder Arctic and warmer Atlantic waters from the eastern Beaufort Sea (Carey 1991). In the Chukchi Sea, nutrient-rich subsidies of Bering Sea origin (Walsh et al. 1989), along with matter from high local productivity (Grebmeier et al 2006), are deposited to the benthos resulting in positive growth conditions for macrofauna (Feder et al. 1994; Blanchard et al. 2013; Blanchard and Feder 2014). In contrast, the Beaufort Sea receives fewer nutrient subsidies and only about 1–10% of locally generated primary productivity is estimated to enrich the benthos (Carey and Ruff 1977; Carey 1987). Consequently, macrofaunal biomass and diversity is lower in regions of the western Beaufort Sea (Carey 1991).

Sampling occurred during the ice-free months of August and September in both the Chukchi and Beaufort Seas (Fig. 1). Polar cod in the Chukchi Sea were collected during three cruises, two that were in conjunction with the Alaska Monitoring and Assessment Program (AKMAP; 23 August–03 September, 2010 and 05 September–16 September, 2011) on the R/V *Norseman II*, and one that was part of the Arctic Ecosystem Integrated Survey (Arctic EIS; 13 August–20 September, 2012) on the F/V *Alaskan Knight*. Three types of bottom trawling gear were used: a standard plumb staff beam trawl (2.26 x 1.20 m opening, 4 mm mesh codend, towed at 2 kts for 2–5 minutes), an otter trawl (variable dimensions, 19 mm mesh codend, towed at 2–2.5 kts for 5–10 minutes), or an 83-112 NOAA net (2.5 x 15 m opening, 40 mm codend, towed at 4 kts for 15 min). Geographically, the Chukchi Sea cruises covered the area between Point Hope and the western side of Point Barrow trawling at depths of 17–90 m (Fig. 1). In the Beaufort Sea, polar cod were collected aboard the R/V *Norseman II* from 17 August−03 September, 2011, during the Beaufish 2011 survey, from the eastern side of Point Barrow to Camden Bay at depths of 13−223 m (Fig. 1). Fish were captured with either a plumb-staff beam trawl or otter trawl. Fish collected from both seas were given a lethal dose of MS-222 fish anesthetic (i.e., 250mg l^{-1}) mixed with seawater (University of Alaska Fairbanks [UAF] Institutional Animal Care and Use Committee protocol number 13465). Euthanized fish were frozen and transported to the UAF Fisheries Oceanography Laboratory where total length was measured to the nearest 1mm.

3.2 Stomach contents analysis

Whole stomachs (defined here as esophagus to pyloric valve) were removed, placed in petri dishes, and frozen in fresh water until their contents were examined. Stomachs were opened and prey was identified using a dissecting microscope. At 6x to 100x magnification, all recognizable prey were identified to the lowest taxonomic level using taxonomic keys (Barnard 1969; Gardner and Szabo 1982; Vassilenko and Petryashov 2009) or through consultation with invertebrate specialists. Once identified, the wet weight of each prey item was recorded to the nearest 0.0001 g.

Due to the diversity of prey consumed by juvenile polar cod, all identifiable prey were aggregated into broader taxonomic groups at the level of order or sub-order for descriptive and statistical comparisons. These coarse taxonomic groups were defined as: benthic amphipods, calanoid copepods, crabs, cumaceans, euphausiids, fish prey, hyperiid amphipods, mysids, polychaetes, shrimps, and "other prey" (Table 1). Benthic prey included benthic amphipods, cumaceans, mysids, and polychaetes, and pelagic prey included calanoid copepods, euphausiids, and hyperiid amphipods. Crabs were either benthic or pelagic depending on life stage, i.e., juveniles and adult crabs were benthic and larval crabs pelagic. Fish prey, shrimps, and "other prey" were either benthic or pelagic depending on the type consumed. "Other prey" were rare (e.g., unidentified amphipods and decapods, barnacle cyprids, and mollusks). Unidentifiable tissues were excluded from analyses as they may have been a variety of soft-bodied prey or stomach lining.

Three diet indices were used to characterize polar cod diets: percent mean weight ($\%\overline{W}$), percent mean number ($\%\overline{N}$), and percent occurrence (%O). Percent mean weight was calculated as: $\%\overline{W}_i=1/P\times(\sum[W_{ij}/\sum W_{ij}])\times100$, where ($\%\overline{W}_i$) is the percent mean weight of prey *i* consumed by a predator,

W_{ij} is the weight of prey i in a single predator j, and ΣW_{ij} is the sum of all prey weights in the stomach of a single predator j. The sums of this calculation for each prey item over the entire sample were divided by the number of fish with food in their stomachs (P). Percent mean number ($\%\overline{N}$) was calculated similarly. Percent occurrence (%O) was calculated as: $\%O=[O_i/P] \times 100$, where %O is defined as the occurrence of a prey group i divided by the sum of non-empty stomachs (P). Each diet index offers unique information about fish diet composition within a category of interest. Percent mean weight values can be used as an indicator of the energetic importance of prey types to a fish population (Hyslop 1980; Chipps and Garvey 2007). Alternatively, $\%\overline{N}$ gives information about the numerical importance of prey in the diets, while %O indicates the percentage of individuals in the sampled population that ate a specific prey type (Hyslop 1980; Chipps and Garvey 2007, Baker et al. 2014). We ultimately chose $\%\overline{W}$ for statistical comparisons because it represented prey energetic importance and was the most comparable method.

For polar cod in both seas, cumulative prey curves were generated at both fine and broad taxonomic levels to determine how adequately diets were described by our sample sizes and to visualize overall differences in diet diversity. This method plotted the occurrence of novel prey taxa or prey groups against a running total of examined stomachs (Chipps and Garvey 2007). When the curve was close to reaching an asymptote, fish diet diversity was said to be adequately described. Cumulative prey curves were constructed using the species-accumulation plot function in PRIMER v6 multivariate statistics package. Following the methods outlined in Hallett and Daley (2011), we randomized polar cod stomach contents data across 999 permutations using a bootstrap method. This removed biases associated with plotting the accumulation of prey types by sample order and allowed for a visualization of any major trends in prey use.

3.3 Multivariate analyses

Two multivariate methods, i.e., canonical correspondence analysis (CCA) and non-metric multidimensional scaling (nMDS), were used to examine differences in polar cod diet compositions within and between the Chukchi and Beaufort Seas. Using CCA, each polar cod stomach was treated as an individual sampling unit, with the coarse taxonomic prey groups representing multivariate response variables. Biological data (i.e., body size), along with environmental data (i.e., latitude, longitude, depth, and cruise year [Chukchi Sea only]) were assigned to each polar cod stomach and included as continuous predictor variables in our analysis. As outlined in Jaworski and Ragnarsson (2006) and Blanchard et al. (2013), we used CCA to generate ordination plots for polar cod in either sea by regressing the selected predictor variables against axes from a correspondence analysis on the multivariate diet data. The resulting ordinations show prey groups consumed by polar cod as weighted averages with vectors indicating the correlation between our environmental and biological predictor variables and each axis (Quinn and Keough 2002). The significance of the predictor variables was determined using a permutation test at a 5% significance level. All statistical tests associated with CCA were conducted in the vegan library of R. For the nMDS analysis, polar cod diet data was pooled by sea into 10 mm size bins and examined both by changes in the $\%\overline{W}$ of prey groups consumed and the $\%\overline{N}$ of the sizes of prey consumed (i.e., small <5 mm, medium 5–10 mm, and large >10 mm). This Bray-Curtis distance based ordination method was used to show relationships between polar cod size bins in multidimensional space, with size bins closer together being more similar than those further apart (Quinn and Keough 2002). Vectors were overlaid to show the specific prey groups or prey sizes that drove differences between larger and smaller sized polar cod. The degree to which the nMDS ordination fit relationships between the 10 mm size bins was evaluated by a stress statistic, with a value less than 0.20 considered a good fit and a value under 0.10 to be an even better fit (Clarke 1993). All statistical tests associated with nMDS were conducted in Primer v6.

4. Results

A total of 614 polar cod stomachs (Chukchi Sea=273 and Beaufort Sea=341) containing identifiable prey were used in descriptive and multivariate diet analyses. Of the stomachs analyzed, 10 were empty in the Chukchi Sea compared to 20 empty in the Beaufort Sea. Overall, a wider size range of larger specimens were available for diet study in the Chukchi Sea (Fig. 2). Consequently, Chukchi Sea polar cod included in this analysis were on average larger than Beaufort Sea conspecifics (Table 1). The initial analysis, which pooled all polar cod by sea to determine overall diet differences by descriptive indices %$\overline{\text{W}}$, %$\overline{\text{N}}$, and %O, indicated that of all prey consumed, calanoid copepods (especially *Calanus* spp.) was the dominant prey item, with the highest percentages found in the diets of Beaufort Sea polar cod (Table 1). Other prey types varied in importance between the two seas with notable diet contributors (i.e., values of prey categories ≥5% by %$\overline{\text{W}}$, %$\overline{\text{N}}$, or %O) being benthic amphipods, crabs, cumaceans, euphausiids, fish prey, hyperiid amphipods, and other prey in the Chukchi Sea, and euphausiids, hyperiid amphipods, and other prey in the Beaufort Sea (Table 1).

Polar cod inhabiting both seas consumed diverse prey, and consequently, when prey taxa were analyzed to the lowest possible taxon, cumulative prey curves did not reach an asymptote (i.e., more stomachs were needed to describe polar cod diets; Fig. 3). Polar cod diets in both seas were better described when prey taxa were aggregated into the broad, 11 taxonomic groups based on order and sub-order. At this level of identification, cumulative prey curves appeared to attain an asymptote at <50 stomachs (Fig. 3). The lowest taxon curves indicated that, at our level of prey identification, Chukchi Sea polar cod consumed a more diverse diet with over 80 unique prey taxa consumed compared to <50 unique taxa consumed by Beaufort Sea conspecifics. While the taxonomically-broad curves revealed that polar cod in both seas consumed fairly similar prey groups at about the same rate, more unique prey species, genera, and families per prey group were consumed by Chukchi Sea polar cod. It is important to note that rare prey taxa and rare prey groups were included in these analyses to account for all identifiable prey in polar cod diets. If rare prey were removed from our analysis, cumulative prey curves would have reached an asymptote at smaller stomach sample sizes, meaning polar cod diets would be adequately described by fewer stomachs.

Overall, the continuous predictors of body size, depth, latitude, longitude, and cruise year (Chukchi Sea only) accounted for 8–9% of the total variance explained in juvenile polar cod diets (Table 2). The first two canonical axes (i.e., CCA1 and CCA2, respectively) accounted for 80.8% (CCA1=56.3%; CCA2=24.5%) of the total variance in Chukchi Sea polar cod diets (i.e., 9%) and 90.1% (CCA1=79.2%; CCA2=10.9%) of the total variance in Beaufort Sea polar cod diets (i.e., 8%). In both seas, all variables considered were significant predictors of polar cod diets (p=0.03–0.01; Table 2). Year was included as an explanatory variable in the Chukchi Sea CCA because there were three years of cruise data available; it was not included in the Beaufort Sea CCA due to only one collection year at this location (Table 2).

In the Chukchi Sea, body size was most correlated with CCA1 and year was most correlated with CCA2 (Table 2; Fig. 4A). All other predictor variables, especially longitude, were only slightly correlated with either axis (Table 2). CCA1 highlighted a gradient in polar cod diet composition with smaller individuals consuming the largest proportions of calanoid copepods and larger individuals consuming increasingly varied diets including cumaceans, hyperiid amphipods, benthic amphipods, mysids, fishes, and shrimps (Fig. 4A; 6A). CCA2 displayed an increase in crab and euphausiid proportions in polar cod diets in later cruise years; consequently, both prey types were consumed in highest proportions by polar cod during the 2012 Arctic EIS cruise (Fig. 4A; 6B). Additionally, a higher %$\overline{\text{W}}$ of other prey and cumaceans in polar cod diet appeared negatively correlated with depth and latitude (Fig 4A; 6C and D).

Similarly, body size was strongly correlated with CCA1 in the Beaufort Sea analysis although latitude and longitude were also moderately correlated with CCA1 (Table 2). Depth was nearly evenly correlated with both axes (Table 2). CCA1, again, indicated a gradient of less diverse (i.e., diets composed of calanoid copepods only) to more diverse diet compositions with an increase in body size;

however, the proportions of prey groups consumed were more noticeably influenced by multiple predictor variables and not only body size (Fig. 4B). The %$\overline{W}$ of hyperiid amphipods in polar cod diet was positively correlated with body size and latitude (Fig 4B; 7A and B). Fish prey was positively correlated with body size and longitude (Fig. 4B; 7A and C). Mysids were correlated positively with longitude and negatively with depth (Fig 4A; 7C and D). Euphausiids, polychaetes, crabs, and shrimps were positively correlated with longitude (Fig. 4B); however, the latter three prey groups were consumed very rarely and were not reported in the %$\overline{W}$ longitude figure (Fig. 7C). Cumaceans were consumed rarely but were positively correlated with body size (Fig 4A; 7A).

While depth, latitude, longitude, and year each explained polar cod diet variability, body size showed the strongest correlation with CCA1 in both seas; therefore, we chose to further examine body size-related shifts in diet compositions using nMDS. Similar to CCA, a gradual increase in diet variability was apparent with an increase in body size (Fig. 5A) although for nMDS analyses polar cod diets were pooled by 10 mm size bins rather than analyzed individually. Along with an increase in variability, there was a noticeable difference in the diet compositions of larger polar cod (i.e., >50 mm) between the Chukchi and Beaufort Seas, with Chukchi Sea polar cod diets containing more benthic prey and Beaufort Sea conspecific's more pelagic prey (Fig. 5A). Smaller polar cod (i.e., 31–50 mm) in both seas consumed similar diets composed mainly of pelagic, calanoid copepods; however, polar cod >50 mm displayed differences in diets between seas, driven mostly by a higher %$\overline{W}$ of benthic amphipods or cumaceans in Chukchi Sea fish and pelagic, hyperiid amphipods in Beaufort Sea fish (Fig. 5A). When accounting for sizes of prey consumed (Fig. 5B), there was less differentiation between the diets of similar-sized Chukchi or Beaufort Sea polar cod. In general, polar cod 31–60 mm in length consumed mostly small (<5 mm) prey, fish 71–100 mm in length consumed mostly medium (5–10 mm) prey, and fish ≥111 mm in length consumed higher proportions of large (>10 mm) prey (Fig. 5B).

5. Discussion

Juvenile polar cod diets are diverse and vary along body size, spatial, and interannual gradients. Our findings confirm that polar cod function as generalist zooplanktivores (Renaud et al. 2012), whose diets may differ according to body size (Lowry and Frost 1981) and food availability within different habitats (Lønne and Gulliksen 1989). In this study, we used multivariate methods to explain some of the factors and prey types responsible for variation in the summer diets of juvenile polar cod within and between the Chukchi and Beaufort Seas.

The factors influencing variation in Chukchi and Beaufort Sea polar cod diets are comparable to those of another high-latitude gadid, Atlantic cod (*Gadus morhua*). Canonical correspondence analysis of Atlantic cod diets along the United States continental shelf (Link and Garrison 2002) and regions surrounding Iceland (Jaworski and Ragnarsson 2006) explained 8–10% of the total variation in observed diets, similar to the patterns observed here. The Atlantic cod studies used a combination of predictor variables comparable to ours: depth, latitude, longitude, season, and year, and found that variation in Atlantic cod diet compositions was most strongly correlated with body size. Similarly, we found juvenile polar cod diets in this study were most influenced by body size. The amount of variance in a prey matrix captured through CCA is generally low making it important to realize that the objective of CCA is not to explain 100% of the variance (Ter Braak 1986). A portion of the total variance is due to noise in the data (Ter Braak 1986) which is caused, in part, by the large amount of zero values characteristic of ecological data sets (Bennion 1994; Reeves et al. 2007). The patterns highlighted by CCA in this study contribute to a weight of evidence in association with descriptive methods presented here supporting the influence of body size on polar cod diets.

As body size increased, juvenile polar cod diet compositions became more complex within the Chukchi and Beaufort Seas. This was expected because as fish grow larger, they generally become more proficient at eating larger, more energetically-profitable prey (Werner and Hall 1974). Similar to accounts of polar cod diets in the Bering (Lowry and Frost 1981; Cui et al. 2012), Chukchi (Lowry and Frost 1981), and Beaufort Seas (Lowry and Frost 1981; Craig et al. 1982), we observed a body size-related gradual shift in diet composition from consuming only small zooplankton (e.g., calanoid copepods) to integrating larger benthic amphipods, euphausiids, mysids, shrimps, and fishes.

Polar cod diet compositions are known to become more benthic-associated with an increase in body size (Walkusz et al. 2013). This pattern held true for larger Chukchi Sea individuals in our study, but not for larger Beaufort Sea conspecifics. A between-sea difference in diets became noticeable in polar cod >50 mm, roughly the size at which these fish began consuming other prey species in addition to calanoid copepods. As size of polar cod increased, Chukchi Sea diets became more bottom-associated while similar-sized Beaufort Sea conspecifics continued to feed within the water column. Despite differences in overall prey groups consumed, the size ranges of prey consumed by similar-sized polar cod in both seas was fairly consistent. This suggests juvenile polar cod diet compositions in the Chukchi and Beaufort Seas may follow a pattern of prey availability rather than size selectivity. Given that regions of the Chukchi Sea are much more benthically productive (Walsh et al. 1989; Weingartner 1997; Blanchard et al. 2013; Blanchard and Feder 2014) than the Beaufort Sea (Carey and Ruff 1977; Carey 1987, 1991) the presence of benthic or pelagic prey groups in juvenile polar cod diets is likely closely related to regional, oceanographic processes occurring within each sea acting upon prey availability. In the Chukchi Sea zooplankton assemblages are associated with the temperature and salinity characteristics of specific water masses (Hopcroft et al. 2010), and food webs of benthic communities within individual water masses indicate a direct coupling to pelagic productivity (Iken et al. 2010). Additionally, the distribution of polar cod itself is related to water masses in the Chukchi and Beaufort Seas (Crawford et al. 2012; Gleason in review).

Geographic location and depth had differing effects on juvenile polar cod diets within the Chukchi and Beaufort Seas. This could be due in part to study design. The two study areas were different in spatial extent and depth with the shallower Chukchi Sea stations covering large south-to-north and east-to-west gradients relative to the deeper Beaufort Sea stations, which had a noticeably stronger east-to-west gradient than south-to-north. Ultimately, the diets of juvenile polar cod in the Beaufort Sea showed more variation related to location and depth than those in the Chukchi Sea. Longitudinal effects were especially noticeable in the Beaufort Sea analysis, with juvenile polar cod diets being more diverse and slightly more benthically-influenced at the westernmost stations. This may be due to the influence of Chukchi Sea waters in areas of the Beaufort Sea adjacent to Barrow Canyon (Ashijian et al. 2005), where the westernmost sampling stations were located. It follows that the influence of these Chukchi Sea waters would decrease moving eastward where Atlantic and Arctic waters would begin exerting a stronger influence upon invertebrate communities (Carey 1991). This west-to-east gradient appears reflected in the diets of juvenile polar cod collected in the furthest east Beaufort Sea regions, which were composed of nearly entirely pelagic zooplankton.

Interannual variability in juvenile polar cod diet was only quantifiable in the Chukchi Sea. The most obvious pattern was increased crab and euphausiid consumption by juvenile polar cod collected during the Arctic EIS 2012 cruise. While this finding could be related to interannual variability in crab and euphausiid production, the patterns seen here may be due to gear selectivity and overall differences in sampling extent. In 2012, the larger-meshed NOAA 83–112 net captured a larger size range of individuals (43–230 mm), compared to collections made by both the smaller-meshed plumb-staff beam trawl and otter trawl in 2010 (42–175 mm) and 2011 (45–162 mm). Additionally, the 2012 Arctic EIS stations covered a much larger continental shelf area than the nearshore extents of the other two Chukchi Sea cruises. This heavier coverage increased the probability of sampling offshore prey groups that were not captured in nearshore cruises.

Due to data limitations, prey density information was not included in this research; therefore, it is not known whether diet differences highlighted within and between the Chukchi and Beaufort Seas are a result of regional prey abundance or prey selectivity by juvenile polar cod. Gadids have been described as generalist 'samplers' of the prey available in their environments (Lilly and Parsons 1991; Fahrig et al. 1993), but they also have been described as selective foragers in nearshore regions of the western Beaufort Sea (Craig et al. 1982). Our research suggests that, during the summer months, juvenile polar cod diet composition within the Chukchi and Beaufort Seas reflects the available prey spectrum that fish of a given size are capable of consuming given that there are well-known differences in processes that affect regional prey availability within both seas. Additional biological factors not considered here could lead to increased statistical variation in polar cod diets, including age, maturity stage, and sex. Likewise, environmental data such as water density, salinity, and temperature (proxies for water masses), or sediment grain size (proxy for habitat) could explain a larger portion of variance in polar cod diets than we report here in the CCA.

The variability in juvenile polar cod diet composition documented in this study has implications for food web modeling. Historically, there has been a lack of quantitative, region-specific diet data for all life stages of polar cod in the Chukchi and Beaufort Seas. As a result, food web models for this area have relied on conspecific diet data collected in the eastern Bering Sea (Whitehouse 2014). A recent model parameterized polar cod diet composition as follows: 23% benthic amphipods, 17% copepods, 48% other zooplankton, 6% miscellaneous crustaceans, and 2% shrimps, with the remaining 2% made up of fishes, bivalves, miscellaneous crabs, and polychaetes (Whitehouse 2014). Comparing the model diet composition with diet compositions of the size ranges of polar cod collected in our study indicates that applying these model parameters would underestimate the importance of calanoid copepods in both seas (Chukchi Sea = 59%; Beaufort Sea = 74%; pooled $\%\overline{W}$), and would overestimate the amount of benthic amphipods eaten in the Beaufort Sea (0.65%; pooled $\%\overline{W}$). Our study confirms that juvenile polar cod diet varies as a function of body size, spatial, and temporal factors. Because polar cod is a vital link in the Arctic food chain, parameterizing a model that accounts for these factors could enhance our knowledge of trophic pathways in the Arctic.

6. Acknowledgements

We thank the crewmembers aboard the R/V *Alaska Knight* and R/V *Norseman II* for their help and fishing expertise along with all past and present UAF Fisheries Oceanography lab technicians for their help in processing fish stomach contents. We also thank Crystal Cano, Max Hoberg, Hillary Nichols, and Chris Stark for their assistance in prey identification. This study was funded in part with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior. It was also funded by the Bureau of Ocean and Energy Management (BOEM) Award # M10AC20004 and BOEM Award # M12PG00018. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of the U.S. Government. Mention of trade names or commercial products does not constitute their endorsement by the U.S. Government.

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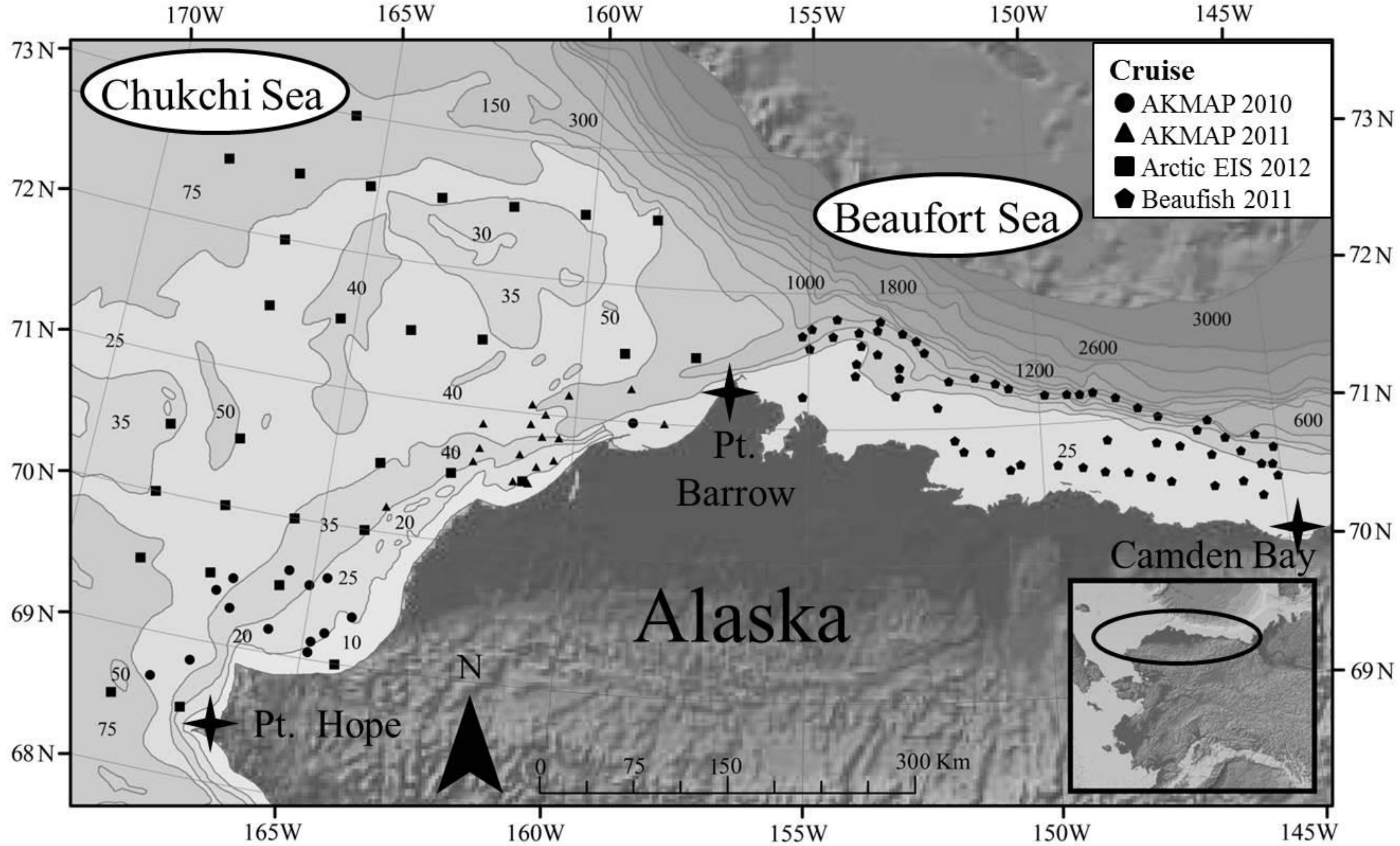
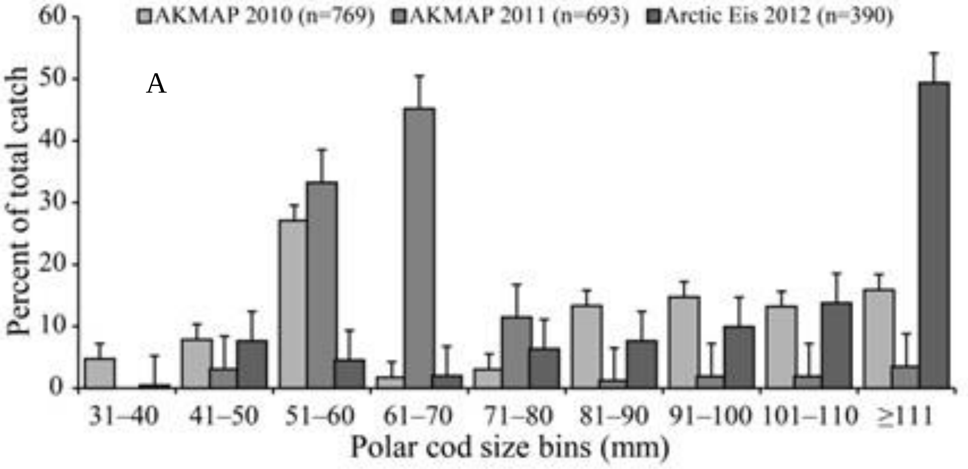


Fig. 1 Polar cod diet analysis sampling locations in the Chukchi and Beaufort Seas. Fish were collected over four cruises, three in the Chukchi Sea (AKMAP10–11 and ArcticEIS12), and one in the Beaufort Sea (Beaufish11).



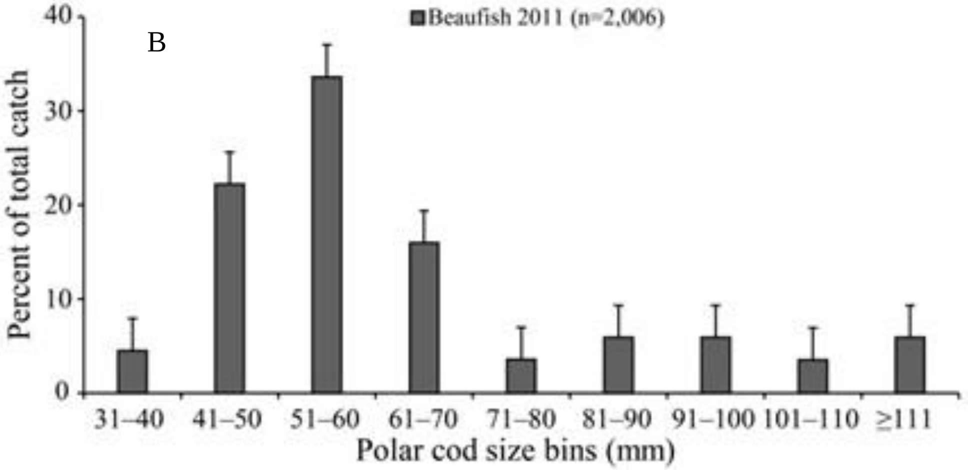


Fig. 2 Size distribution of all polar cod collected during 3 cruises in the A) Chukchi and one cruise in the B) Beaufort Sea. Solid bars represent the percentage of polar cod within 10 mm size bins relative to the total catch of polar cod within a respective cruise. Error bars represent +1 standard deviation from the mean.

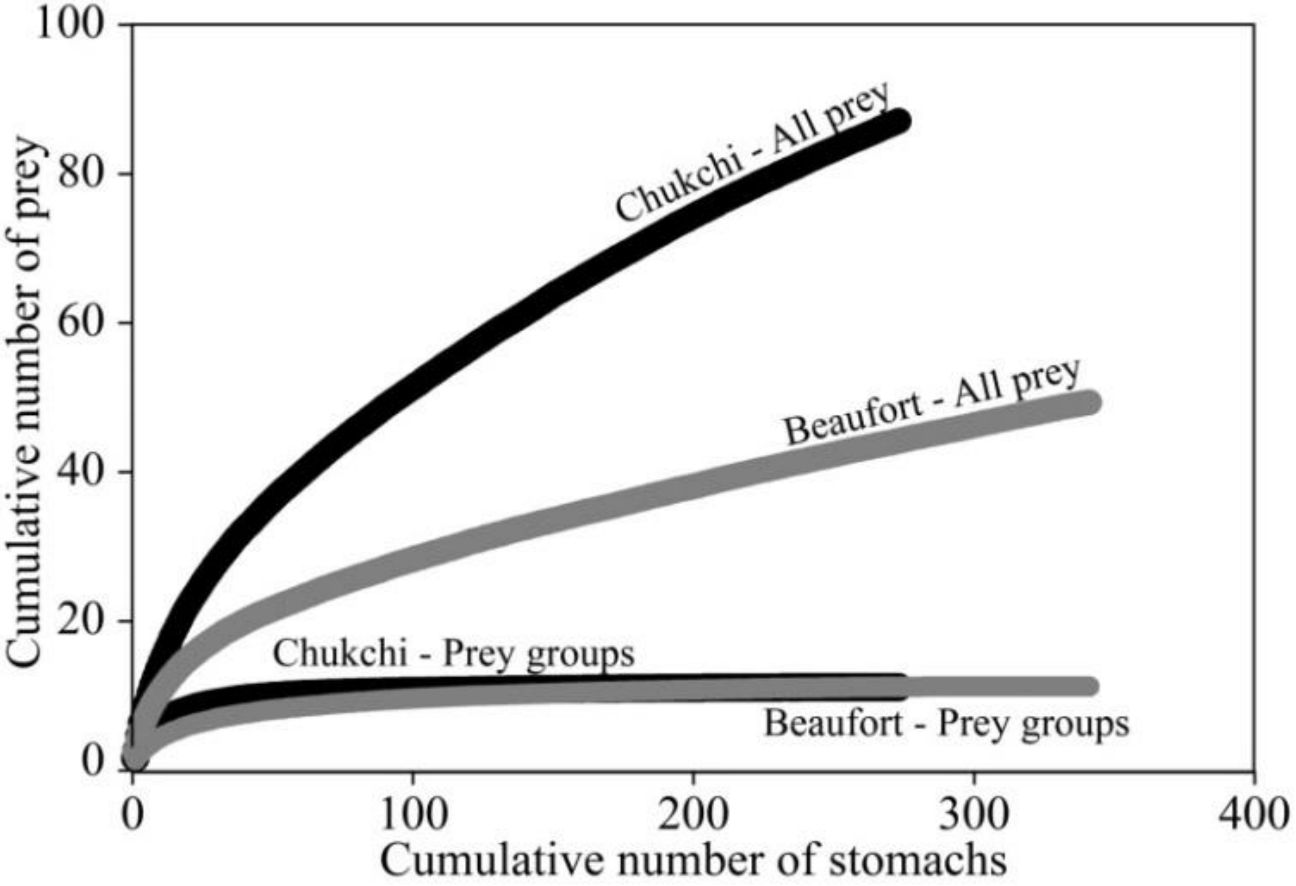


Fig. 3 Cumulative prey curves of polar cod diets in the Chukchi and Beaufort Seas showing the accumulation of prey taxa or groups relative to a running total of stomachs. Curves were generated at both low taxonomic clarity (all prey) and coarse taxonomic groups (prey groups) to show the effectiveness of aggregating prey groups and to visualize differences in conspecific diet diversity.

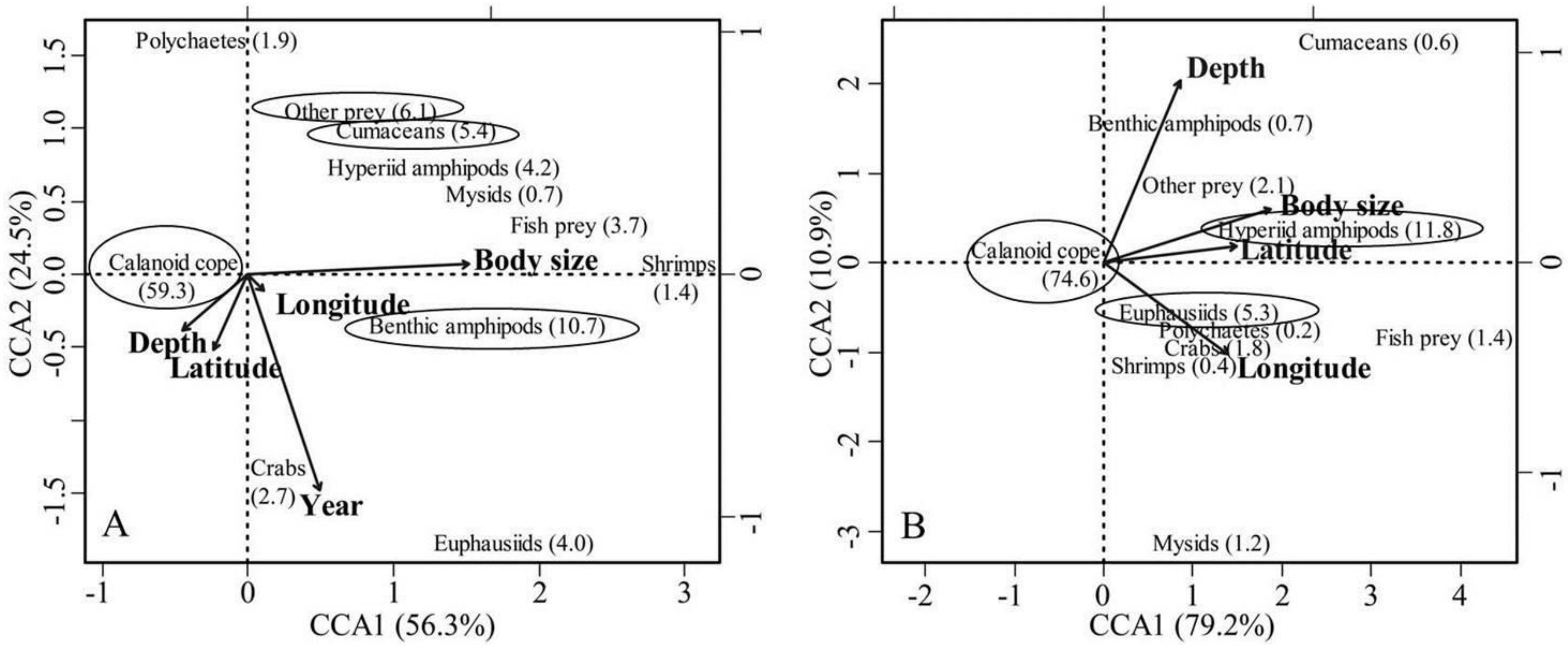


Fig. 4 Canonical correspondence analysis (CCA) ordinations generated to relate biological (i.e., body size) and environmental (i.e., depth, latitude, longitude, and year) factors as continuous predictors of polar cod diets in the A) Chukchi and B) Beaufort Seas. Numbers in parenthesis next to prey categories signify their contribution to pooled polar cod diet by %$\overline{W}$. Prey categories that contributed ≥5% by %$\overline{W}$ are circled within the ordinations.

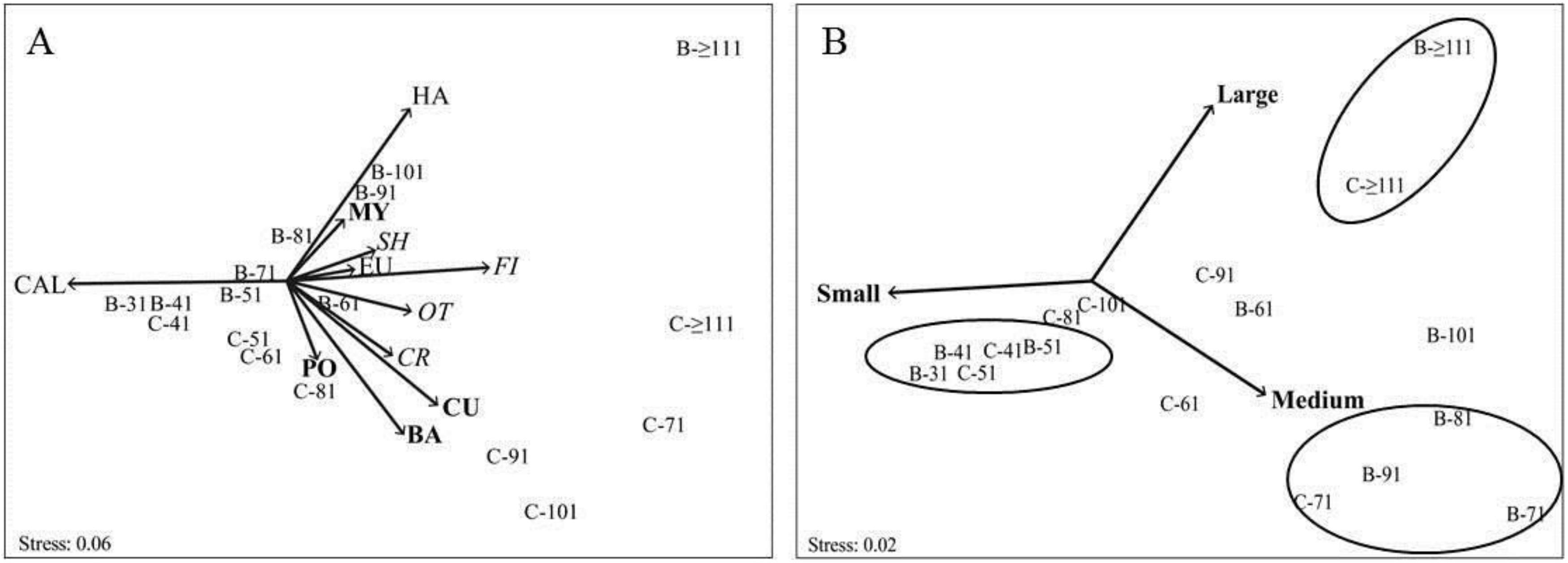


Fig. 5 Non-metric multidimensional scaling (nMDS) ordinations used to explain differences among 10 mm size bins of polar cod between the Chukchi and Beaufort Seas considering both, A) prey groups each consumed, and B) the sizes of prey each consumed. Abbreviations of prey groups in Fig. 4A are defined as follows: CAL = calanoid copepods, BA = benthic amphipods, EU = euphausiids, CR = crabs, CU = cumaceans, FI = fish prey, HA = hyperiid amphipods, MY = mysids, SH = shrimps, and OT = other prey. A non-bolded, bolded, or italicized abbreviation signifies a benthic, pelagic, or benthic/pelagic prey group, respectively. Circles in Fig. 5B were drawn to indicate groups of similar sizes of polar cod consuming similar sized prey irrespective of the sea each inhabited.

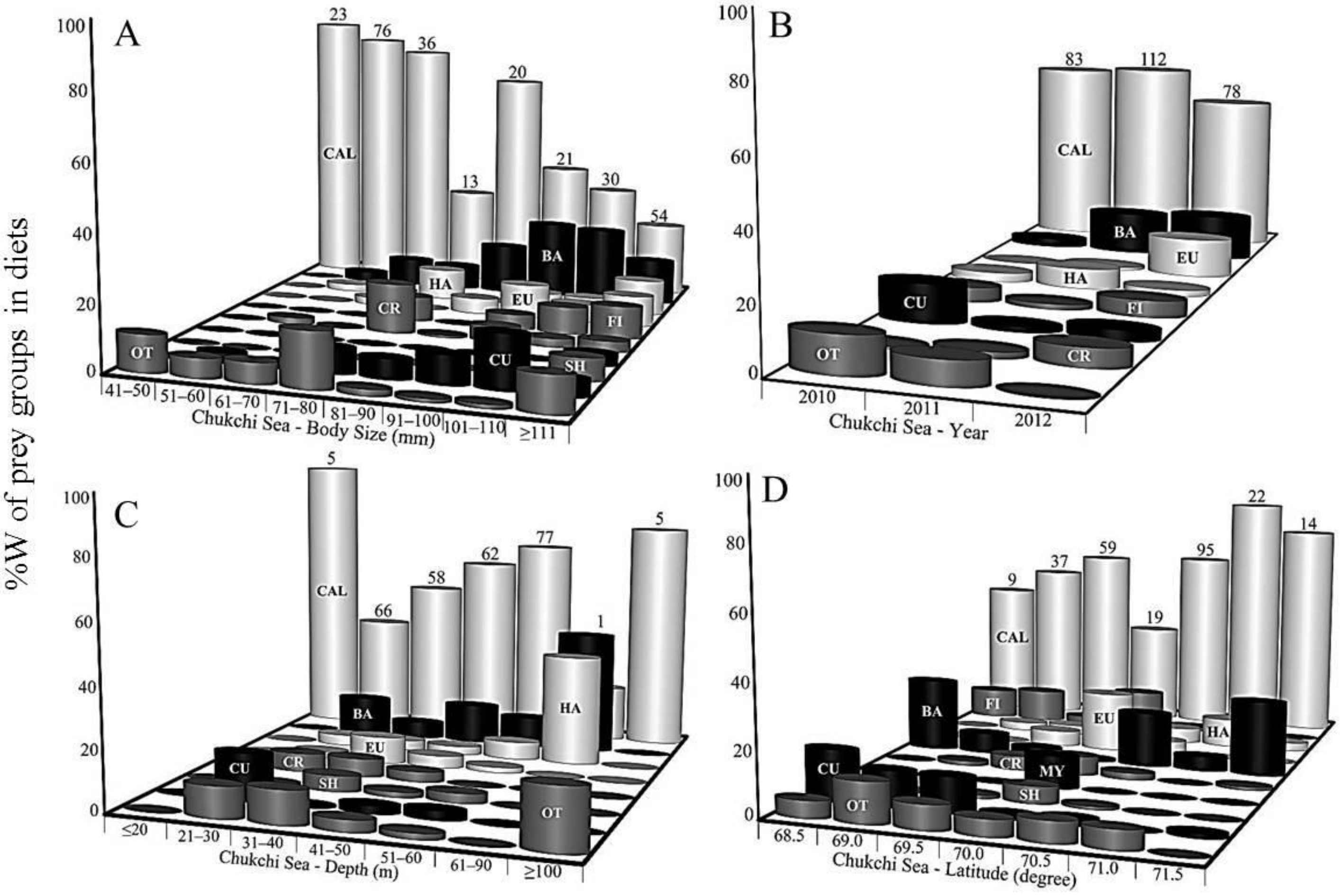


Fig. 6 Plots of major prey items (defined as prey ≥5% by %$\overline{W}$ in a respective category) consumed by polar cod in the Chukchi Sea. Plots are in order from highest to lowest correlation with CCA1, i.e., A) body size, B) year, C) depth, and D) latitude. Longitude was not reported due to its low correlation with both CCA axes. The colors gray, dark-gray, and black represent pelagic, benthic/pelagic, and benthic prey, respectively. Prey groups are abbreviated as follows, CAL = calanoid copepods, BA = benthic amphipods, EU = euphausiids, CR = crabs, CU = cumaceans, FI = fish prey, HA = hyperiid amphipods, MY = mysids, SH = shrimps, and OT = other prey. Sample sizes are listed above the calanoid copepod column in each figure. Depth was pooled into 10 m bins and latitude and longitude were binned to nearest 0.5 degrees or into ranges as needed for visual purposes.

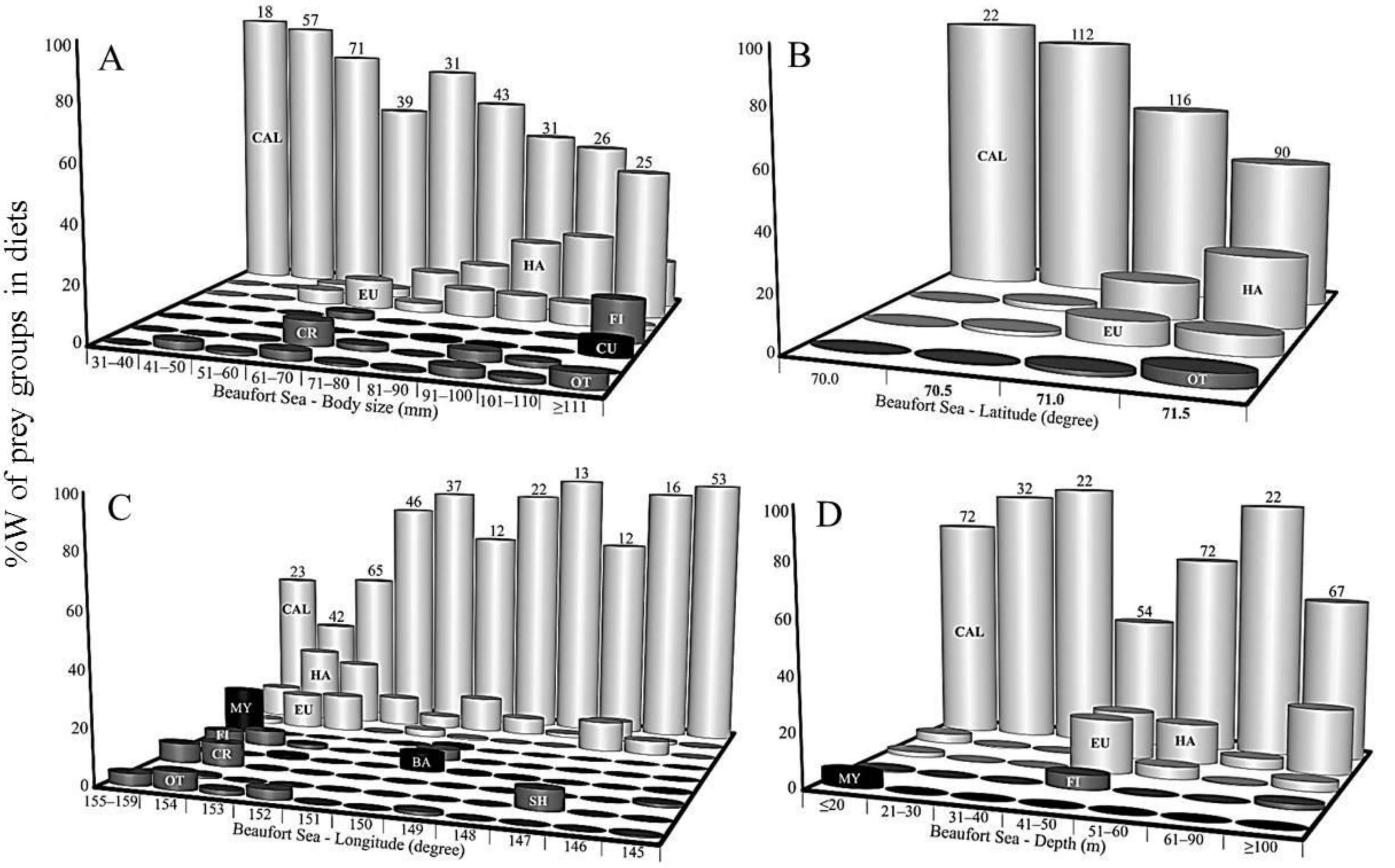


Fig. 7 Plots of major prey items (defined as prey ≥5% by %W̄ in a respective category) consumed by polar cod in the Beaufort Sea. Plots are in order from highest to lowest correlation with CCA1, i.e., A) body size, B) latitude, C) longitude, and D) depth. The colors gray, dark-gray, and black represent pelagic, benthic/pelagic, and benthic prey, respectively. Prey groups are abbreviated as follows, CAL = calanoid copepods, BA = benthic amphipods, EU = euphausiids, CR = crabs, CU = cumaceans, FI = fish prey, HA = hyperiid amphipods, MY = mysids, SH = shrimps, and OT = other prey. Sample sizes are listed above the calanoid copepod column in each figure. Depth was pooled into 10 m bins and latitude and longitude were binned to nearest 0.5 degrees or into ranges as needed for visual purposes.

Table 1. Juvenile polar cod diet summarized by $\%\overline{W}$, $\%\overline{N}$, and %O in the Chukchi and Beaufort Seas. Major prey categories used in the analysis are in boldface; prey items contributing to the major categories are listed underneath. Summary information including total number of prey, total prey weight (g), total stomachs, along with body size ranges and averages are listed at the end of the table.

	Chukchi (2010–2012)			Beaufort (2011)		
	$\%\overline{W}$	$\%\overline{N}$	%O	$\%\overline{W}$	$\%\overline{N}$	%O
Benthic amphipods	**10.72**	**7.96**	**24.18**	**0.65**	**0.53**	**1.47**
Ampelescidae	1.47	0.86	2.20	0.04	0.01	0.29
Atylidae	0.14	0.26	1.83	0.00	0.00	0.00
Oedicerotidae	0.75	0.28	6.23	0.01	0.01	0.29
Other benthic amphipods	8.35	6.56	18.68	0.60	0.51	1.17
Calanoid copepods	**59.26**	**65.73**	**76.19**	**74.63**	**77.91**	**86.51**
Calanus glacialis	28.16	33.37	59.34	26.25	32.70	58.36
Calanus hyperboreus	2.82	2.01	8.06	24.05	19.28	38.42
Metridia longa	0.17	0.26	1.47	2.46	2.55	15.25
Other calanoid copepods	28.12	30.10	57.14	21.87	23.39	48.39
Crabs	**2.71**	**1.95**	**5.13**	**1.79**	**1.30**	**4.40**
Hyas coarctatus	0.28	0.02	0.37	0.00	0.00	0.00
Paguridae	0.94	0.89	2.93	1.30	0.93	2.64
Other crabs	1.49	1.04	2.20	0.50	0.37	1.76
Cumaceans	**5.41**	**6.08**	**17.95**	**0.60**	**0.51**	**2.05**
Diastylidae	0.73	0.64	1.83	0.00	0.00	0.00
Leuconidae	1.62	2.01	6.96	0.58	0.30	1.47
Nannastacidae	0.99	1.33	3.66	0.00	0.00	0.00
Other cumaceans	2.08	2.11	9.16	0.01	0.21	0.88
Euphausiids	**4.00**	**3.66**	**7.33**	**5.25**	**5.01**	**8.50**
Thysanoessa raschi	4.00	3.66	7.33	5.25	5.01	8.50
Fish prey	**3.65**	**2.99**	**5.13**	**1.41**	**0.83**	**2.93**
Gadidae	0.33	0.18	0.37	0.00	0.00	0.00
Stichaeidae	0.32	0.09	0.37	0.00	0.00	0.00
Other fish prey	3.00	2.71	4.40	1.41	0.83	2.93
Hyperiid amphipods	**4.18**	**2.81**	**9.52**	**11.81**	**9.39**	**21.11**
Themisto abysorrum	1.13	1.02	4.03	1.67	1.88	7.33
Themisto libellula	2.13	1.03	4.03	4.89	3.74	6.45
Themisto spp.	0.90	0.70	1.83	5.25	3.76	12.02
Other hyperiids	0.03	0.05	1.47	0.00	0.00	0.00
Mysids	**0.72**	**0.55**	**0.73**	**1.23**	**0.66**	**2.35**
Mysis sp.	0.72	0.55	0.73	1.23	0.66	2.35
Polychaetes	**1.87**	**1.25**	**4.03**	**0.17**	**0.16**	**0.59**
Shrimps	**1.42**	**0.73**	**3.66**	**0.37**	**0.13**	**0.59**
Other prey	**6.06**	**6.29**	**19.05**	**2.09**	**3.58**	**9.38**
Unid. Amphipoda	3.94	2.73	6.59	1.18	1.01	2.93
Barnacle cyprid	0.26	0.82	2.93	0.80	2.19	4.40
Copepod nauplii	0.52	1.39	5.86	0.08	0.03	0.59
Decapoda	0.40	0.16	1.47	0.01	0.03	0.29
Mollusca	0.04	0.17	0.73	0.02	0.19	0.59
All other prey	0.89	1.02	4.40	0.01	0.13	1.17
Total number of prey	7,054			4,519		
Total prey weight (g)	12.1			15.3		
Total stomachs	273			341		
Size range (mm)	42–230			31–182		
Average size (mm)	83			72		

Table 2 Correlations of the explanatory variables body size, depth, latitude, longitude, and year (Chukchi Sea only) with the first two axes of the canonical correspondence analysis (CCA) of juvenile polar cod diet compositions within the Chukchi and Beaufort Seas. The significance of each variable is listed next to its corresponding axes correlation value. The cumulative percent variance explained by the first two CCA axes is listed underneath.

Chukchi Sea – polar cod diet				Beaufort Sea – polar cod diet			
Variables	CCA1	CCA2	p	Variables	CCA1	CCA2	p
Body size	0.62	0.02	0.01	Body size	0.58	0.08	0.01
Depth	-0.18	-0.11	0.01	Depth	0.27	0.25	0.01
Latitude	-0.10	-0.15	0.01	Latitude	0.46	0.02	0.01
Longitude	0.04	-0.03	0.02	Longitude	0.43	-0.13	0.03
Year	0.20	-0.42	0.01	Year	Not applicable		
Cumul.(%)	4.97	7.14		Cumul.(%)	6.41	7.30	
Total (%)		8.83		Total (%)		8.10	

Appendix J.

Food habits of Arctic staghorn sculpin (*Gymnocanthus tricuspis*) and shorthorn sculpin (*Myoxocephalus scorpius*) in the northeastern Chukchi and western Beaufort Seas

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March 7, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)
Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

nMDS	Non-metric multidimensional scaling
PERMANOVA	Permutational multivariate analysis of variance
SFI	Stomach fullness index
SCS	South Chukchi Sea
NCS	North Chukchi Sea
WBS	Western Beaufort Sea
$\%\overline{N}$	Percent mean number of prey
%O	Percent occurrence of prey
$\%\overline{W}$	Percent mean weight of prey

List of Oral and Poster Presentations

Gray BP., Norcross BL. Characterizing the diets of three abundant fishes in the Chukchi and Beaufort seas. Poster presented at the Alaska Marine Science Symposium in Anchorage, Alaska from January 21–25, 2013.

Gray BP., Norcross BL. Comparing the diets of three abundant fishes across the Chukchi and Beaufort seas. Poster presented at the 28th Lowell Wakefield Fisheries Symposium: Responses of Arctic Marine Ecosystems to Climate Change in Anchorage, Alaska from March 26–29, 2013.

Gray BP., Norcross BL. Fish diets across the Chukchi and Beaufort seas. Oral Presentation at the American Fisheries Society meeting in Fairbanks, Alaska on October 10, 2013.

Gray BP., Norcross BL. Fish diets across the Chukchi and Beaufort seas. Oral Presentation at the Alaska Marine Science Symposium in Anchorage, Alaska on January 20, 2014.

Gray BP., Norcross BL. Region and size-based comparisons of three fish species’ diets across the Chukchi and Beaufort seas. Poster presented at the Ocean Sciences Meeting in Honolulu, Hawaii on February 26, 2014.

Gray BP., Norcross BL. Comparisons of Arctic cod, Arctic staghorn sculpin, and shorthorn sculpin diets across the northeastern Chukchi and western Beaufort Seas. Oral presentation component of Benjamin Gray’s MS thesis defense in Fairbanks, Alaska on October 10, 2014.

Gray BP., Norcross BL. A comparison of fish diets between regions of the northeastern Chukchi and western Beaufort Seas. Poster presentation at the American Fisheries Society meeting in Juneau, Alaska from October 20–24, 2014.

Proposed Objectives and Study Chronology

The objectives of our research were to 1) describe and compare Arctic staghorn sculpin and shorthorn sculpin diets in the Chukchi and Beaufort Seas, 2) examine variation in their diets related to body size, 3) analyze differences in their mouth morphologies, and 4) relate those morphological differences to variability in sizes of prey consumed. To meet these objectives, sculpin stomach contents were identified, grouped by order, and analyzed using a suite of univariate and multivariate methods.

Sculpins were collected via bottom trawl over three summers in the northeastern Chukchi Sea (2010–2012) and one summer in the western Beaufort Sea (2011). In the Chukchi Sea, sculpins were collected during the Alaska Monitoring and Assessment Program (AKMAP) cruises in 2010 and 2011, and the Arctic Ecosystem Integrated Survey (Arctic Eis) bottom trawl segment in 2012. Beaufort Sea sculpins were collected during the 2011 Central Beaufort Sea Fisheries Survey (Beaufish).

Laboratory and data analysis took place at the University of Alaska Fairbanks. All processes associated with sculpin stomach contents analysis occurred from fall 2011 to fall 2013. Data analysis took place from fall 2013 to spring 2015. The data used to develop this report, along with an associated manuscript submitted for publication in the Arctic Eis special issue of Deep Sea Research Part II, can be found on AOOS Arctic Eis Ocean Workspace in the “Diets – Fish and Snow Crab” folder. These products will be made publically available through the Alaska Ocean Observing System (AOOS) Arctic Data Portal at the conclusion of the Arctic Eis Project.

1. Abstract

Arctic staghorn sculpin (*Gymnocanthus tricuspis*) and shorthorn sculpin (*Myoxocephalus scorpius*) belong to Cottidae, the second most abundant fish family in the western Arctic. Although considered important in food webs, little is known about their food habits throughout this region. To address this knowledge gap, we examined and compared the diets of 515 Arctic staghorn sculpin and 422 shorthorn sculpin using stomachs collected over three summers in the northeastern Chukchi Sea (2010–2012) and one summer in the western Beaufort Sea (2011). We used permutational multivariate analysis of variance (PERMANOVA) and non-metric multidimensional scaling (nMDS) to compare sculpin diets between regions and selected size classes. Differences in mouth morphologies and predator size versus prey size relationships were examined using regression techniques. Arctic staghorn sculpin and shorthorn sculpin diet compositions differed greatly throughout the Chukchi and Beaufort Seas. Regardless of body size, the smaller-mouthed Arctic staghorn sculpin consumed mostly benthic amphipods and polychaetes, whereas the larger-mouthed shorthorn sculpin shifted from a diet composed of benthic and pelagic macroinvertebrates as smaller individuals to shrimps and fish prey as larger individuals. Within shared habitats, the sculpins appear to partition prey, either by taxa, size, or proportion, in a manner that suggests no substantial overlap occurs between species. This study increases knowledge of sculpin feeding ecology in the western Arctic and offers regional, quantitative diet information that could support current and future food web modeling efforts.

2. Introduction

Sculpins (family Cottidae) are commonplace in the western Arctic (Barber et al. 1997; Norcross et al. 2013) and are important in the northeastern Chukchi and western Beaufort Seas as both prey and predators (Lowry et al. 1980; Smith et al. 1997; Rand et al. 2013); Two abundant cottids are the Arctic staghorn sculpin (*Gymnocanthus tricuspis*) and shorthorn sculpin (*Myoxocephalus scorpius*) (Mecklenburg et al. 2011). Each is considered an important part of Arctic food webs, yet little is known regarding their food habits. Arctic staghorn sculpin is prey for seals (Lowry et al. 1980; Smith et al. 1997) and other fishes (Coyle et al. 1997). As planktonic larvae, shorthorn sculpin is important prey for Arctic cod (Rand et al. 2013), while juvenile and adult individuals are likely eaten by other fishes and marine mammals. As predators, both sculpins are considered benthic generalists (Moore and Moore 1974; Atkinson and Percy 1992; Coyle et al. 1997; Cui et al. 2012). Arctic staghorn sculpin in the eastern Bering Sea (Cui et al. 2012), Chukchi (Coyle et al. 1997), and Canadian Beaufort Seas (Atkinson and Percy 1992) consume fairly similar diets consisting of benthic amphipods, bivalve siphons, cumaceans, and polychaetes. There is no published diet information for shorthorn sculpin in the Chukchi and Beaufort Seas, however, this species consumes mostly crabs and benthic amphipods in the eastern Bering Sea (Cui et al. 2012), benthic crustaceans, decapods, polychaetes, and zooplankton in the Labrador Sea (Moore and Moore 1974; Atkinson and Percy 1992), and benthic crustaceans and fishes in the southwestern Baltic Sea (Cardinale 2000). These previous studies indicate the possibility of similarities between the two species' diets, and that shorthorn sculpin diet may be more regionally variable than that of Arctic staghorn sculpin.

Arctic staghorn sculpin and shorthorn sculpin differ in body morphology, which should influence each species' patterns of prey consumption. Shorthorn sculpin can achieve larger sizes than Arctic staghorn sculpin (Mecklenburg et al. 2002) and body size is known to influence fish foraging success (Scharf et al. 2000). As fishes attain greater body sizes, gape width and height increase (Scharf et al.

2000) and greatly influence the maximum size of prey eaten (Keast and Webb 1966; Werner and Gilliam 1984; Juanes et al. 2002). Typically, the size range of prey consumed by larger fishes overlaps that of smaller individuals and could give larger fishes a competitive advantage (Scharf et al. 2000).

Habitat features in the Chukchi and Beaufort Seas could influence sculpin diets by affecting prey availability. The Chukchi Sea is a productive (Grebmeier et al. 2006), shallow system that is supplemented by nutrients (Weingartner 1997; Weingartner et al. 2013) and fauna (Walsh et al. 1989) of Bering Sea origin. The high local production, external nutrient input, and small-scale oceanographic processes drive the strong delivery of carbon to the benthos in the Chukchi Sea (Grebmeier et al. 2006), which creates positive growth conditions for benthic macrofauna (Feder et al. 1994a; Blanchard et al. 2013; Blanchard and Feder 2014). Comparatively, macrofaunal biomass and diversity is lower in regions of the Beaufort Sea (Carey 1991). This is likely because the deeper, narrower western Beaufort Sea shelf receives fewer nutrient subsidies (Crawford et al. 2012), with only about 10% of the locally originated nutrients reaching the benthos (Carey and Ruff 1977; Carey 1987). These broad differences in productivity should be reflected in the sculpins' diets, with possibly more unique prey taxa consumed by both species in the Chukchi Sea.

Given the few studies available regarding sculpin food habits, there is a lack of quantitative, region-specific diet information available for Arctic staghorn sculpin and shorthorn sculpin (Whitehouse et al. 2014), which could have implications for ecosystem-based food web models. Recently, Whitehouse et al. (2014) included Arctic staghorn sculpin and shorthorn sculpin in two separate functional groups, i.e., "other sculpins" and "large-mouth sculpins," respectively, in a food web model constructed for the eastern Chukchi Sea. Dietary compositions within these functional groups were parameterized using diet information from eastern Bering Sea studies. Because fishes' diets can be quite variable throughout ontogeny and habitat (Chipps and Garvey 2007), using spatially-distant, confamilial diet information as a proxy for sculpin's diets in food web models could misrepresent their ecological impact. While the present study does not directly contribute to the implementation of food web models, it offers regional diet information for both sculpin species that could supplement the current Chukchi Sea food web model and aid in parameterizing a model for the Beaufort Sea.

The objectives of this research were to 1) describe and compare Arctic staghorn sculpin and shorthorn sculpin diets in the Chukchi and Beaufort Seas, 2) examine variation in their diets related to body size, 3) analyze differences in their mouth morphologies, and 4) relate those morphological differences to variability in sizes of prey consumed. Using stomach contents analysis and other quantitative techniques, this research shows that within similar Chukchi and Beaufort Sea habitats, differences in body size and morphology may enhance intra- and interspecific resource partitioning between these confamilial sculpins.

3. Methods

3.1. Study area and fish sampling

Fish collection occurred during the ice-free, summer months of August and September in the Chukchi and Beaufort Seas (Fig. 1). Arctic staghorn sculpin and shorthorn sculpin were collected during three cruises in the Chukchi Sea, two that were a part of the Alaska Monitoring and Assessment Program (AKMAP) during 23 August–03 September 2010 and 05 September–16 September, 2011 and one cruise that was a part of the Arctic Ecosystem Integrated Survey (Arctic Eis) during 13 August–20 September 2012. Sampling occurred during daylight hours at stations located between Point Hope and the western side of Point Barrow (Fig. 1). Chukchi Sea regions were divided at 70°N, with the south Chukchi study area (hereafter, SCS) falling below 70˚N and the north Chukchi (hereafter, NCS) above 70˚N. The AKMAP 2010 cruise transects occurred in the SCS region, whereas the AKMAP 2011 cruise occurred in the NCS region. Both AKMAP cruises operated in fairly shallow waters (17−60 m water depth). The Arctic Eis cruise surveyed about the same latitudinal extent as both AKMAP cruises but included some deeper stations (20−90 m water depth). Sculpins were collected in the western Beaufort Sea (WBS) during the Beaufish 2011 cruise (17 August–03 September; 24 hour sampling) between the eastern side of Point Barrow and Camden Bay at depths of 13−223 m. (Fig. 1).

Regions (i.e., SCS, NCS, and WBS) were demarked to isolate unique oceanographic conditions within the Chukchi and Beaufort Seas. Within the Chukchi Sea, frontal boundaries were expected to increase benthic productivity by concentrating and exporting pelagic nutrients to the benthos (Feder et al. 1994b). Frontal boundaries occur in the SCS near Point Hope and in the NCS near Point Franklin (Weingartner 1997; approximate locations Fig. 1). Additionally, in the NCS, benthic productivity may have been increased by the hydrographic and topographic features associated with Hanna Shoal (Blanchard et al. 2013) and Barrow Canyon (Blanchard and Feder 2014; approximate locations Fig. 1). Unlike the SCS and NCS regions, sculpins collected in the WBS were not divided further by spatial location due to sample size limitations and because, within our study area, there were no well-defined processes affecting benthic productivity with which to demark regions. Thus, the WBS was included to account for the differences in physical and biological oceanography between the Chukchi and Beaufort Seas and to describe how those differences might influence the regional diet compositions of each species.

Arctic staghorn sculpin and shorthorn sculpin were captured by towing either a standard plumb staff beam trawl (PSBT) or two types of otter trawls. Nets differed in dimension and tow speed. The PSBT had a 3 m beam, a 4 mm mesh codend, and was towed at 1 to 2 knots for 2 to 5 minutes. The smaller otter trawl had a 9.1 m opening, a 19 mm codend and was towed at 2 to 2.5 knots for 5 to 10 minutes. The larger otter trawl (NOAA 83–112 net) had on average a 15 m opening, a 40 mm codend, and was towed at about 4 knots for 15 minutes. All three nets were used throughout the Chukchi Sea study area, while the PSBT and smaller otter trawl were used for Beaufort Sea collections.

Captured fishes were given a lethal dose of MS-222 (i.e., 250 mg/l) mixed with seawater (University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol) then subsampled both *in* and *ex situ* in a manner that maximized the distribution of sculpins throughout juvenile and adult life stages and throughout the sculpin's respective spatial distributions. Because sculpins were collected using bottom-trawling methods, they were assumed to be captured near the benthos; therefore, for the purposes of these analyses, we pooled all captured sculpins across gear types. The trawling methods used mostly captured ≤60 mm fishes (Fig. 2), therefore we subsampled smaller individuals more often than larger individuals. This subsampling style did not necessarily reflect the size distributions of the overall catches (Fig. 2), it was rather meant to account for what is eaten by each species across multiple life stages. Spatially, sculpins for diet analysis were selected from various stations within the SCS, NCS, and WBS (Supplemental 1–3). This subsampling method did not necessarily reflect population-level patterns in either species' spatial distributions, it was employed rather to increase the probability that sculpins included in diet analyses encountered all prey types unique to a respective region.

3.2. Laboratory methods

Arctic staghorn sculpin and shorthorn sculpin were measured to the nearest 1 mm and their stomachs (i.e., esophagus to pyloric valve) were removed, placed in petri dishes, and frozen in fresh water until examined. All recognizable prey items were identified to the lowest possible taxon, depending on condition. Once identified, the blotted wet weight of each prey item was recorded to the nearest 0.0001 g.

Sculpin diets were diverse (Supplemental 4), therefore, all identifiable prey were aggregated into nine functional groups: benthic amphipods, calanoid copepods, crabs, cumaceans, fish prey, hyperiid amphipods, polychaetes, shrimps, and "other prey" (Table 1). Benthic amphipods, cumaceans, and polychaetes were classified as benthic prey, while calanoid copepods and hyperiid amphipods were considered pelagic prey. Crabs were either benthic or pelagic depending on life stage, i.e., juveniles and adult crabs were benthic and larval crabs were pelagic. Fish prey, shrimps, and “other prey” were either benthic or pelagic depending on type consumed. “Other prey” included small prey items (e.g., harpacticoid copepods and barnacle cyprids, each <1 mm in length) or rare prey types (e.g., euphausiids, isopods, and mollusks). Unidentifiable tissues were not included as a functional group as they may have been a variety of different prey.

All measurable prey were used to determine relationships between predator size and prey size. The total length of all intact prey items was measured to the nearest 0.1 mm. Approximately 42% of identifiable prey items were unmeasurable due to mastication. This was most noticeable for soft-bodied prey such as polychaetes and fishes although fragmented specimens of each functional group were commonly encountered.

3.3. Descriptive diet analyses

Sculpin diets were initially characterized by region using three diet indices: percent mean weight ($\%\overline{W}$), percent mean number ($\%\overline{N}$), and percent occurrence (%O). Percent mean weight for a fish group *i* was calculated as:

$$\%\overline{W}_i = 1/P \times \sum_{j=1}^{P} \left(W_{ij} \Big/ \sum_{i=1}^{Q} W_{ij} \right) \times 100$$

where $\%\overline{W}_i$ is the percent mean weight of prey type *i* eaten a by a group of fishes, W_{ij} is the weight of prey *i* in a single fish stomach *j*, and ΣW_{ij} is the sum of the weights of all Q prey types present in a fish stomach *j*. For each prey item, the sum of this calculation over all *j* stomachs was then divided by the number of non-empty stomachs, P. The same formula was used to calculate $\%\overline{N}$ by substituting prey count data for prey weight data. Percent occurrence (%O) was calculated as:

$$\%O_i = [O_i/P] \times 100$$

where $\%O_i$ is defined as the occurrence of a prey group *i* divided by the sum of non-empty stomachs, P. Each diet index offers different information about fish diet composition. In the absence of prey energetic data, $\%\overline{W}$ values can be used to estimate the energetic importance of different prey types to a fish population (Hyslop 1980; Chipps and Garvey 2007). Alternatively, $\%\overline{N}$ gives information about the abundance of various prey types in fish diets, while %O shows the percentage of fish that ate a specific prey type (Hyslop 1980; Chipps and Garvey 2007, Baker et al. 2014). We ultimately chose $\%\overline{W}$ for selected graphics and statistical comparisons as it represented prey energetic importance and was the most comparable method.

To facilitate same-size, interspecific diet comparisons within regions, Arctic staghorn sculpin and shorthorn sculpin food habits were evaluated by five size classes: ≤50 mm, 51–75 mm, 76–100 mm, 101–125 mm, and ≥126 mm. These size classes were chosen to maximize the amount of comparisons between different sizes of each species. To the best of our knowledge, there exists no information for either species regarding specific size intervals of ontogenetic shifts in diets with which to structure this study.

For each species, region, and size class, we generated $\%\overline{W}$ plots of the nine shared prey groups, along with plots of a stomach fullness index and the percent occurrence (%O) of empty stomachs. The stomach fullness index was adapted from Walter and Austin (2003) and calculated as:

$$SFI = \frac{Stomach\ content\ weight}{Fish\ weight} \text{ x } 100$$

The %O of empty stomachs was calculated using the previously defined %O equation by substituting the amount of empty stomachs within a sculpin size class for O_i and all stomachs available within a sculpin size class for P. The analysis by $\%\overline{W}$ included only the identifiable prey in each sculpin' diet, which meant that individuals that only consumed unidentifiable prey were not included. The analysis by stomach fullness index and %O of empty stomachs took into account those fish that ate unidentified prey (whether exclusively or in addition to identifiable prey) to ensure the importance of all stomach contents of all sculpins were included in this study.

3.4 Statistical analyses

Arctic staghorn sculpin and shorthorn sculpin diet compositions were compared using two, three-way permutational multivariate analysis of variance (PERMANOVA) models, along with two corresponding non-metric multidimensional scaling (nMDS) ordinations. Both PERMANOVA models included species, regions, and size classes as fixed factors. The first model compared the diet compositions of both species within the SCS and NCS regions by all five size classes, while the second model compared diets of both species over all regions by the smallest two size classes. This design structure was used because large sculpins (i.e., ≥75 mm) of both species were scarce in the Beaufort Sea making comparisons across all regions and size classes impossible. Both PERMANOVA and nMDS were conducted using the multivariate statistics package, PRIMER v7 with PERMANOVA. Prior to PERMANOVA and nMDS analyses, stomach contents data were 4th root transformed to down-weight the influence of extreme values and subsequently analyzed using Bray-Curtis distance measures. All PERMANOVA results were evaluated at an α=0.05. If significant interactions between the main effects existed, additional PERMANOVA models were developed for multiple comparisons. The two nMDS ordinations were generated to accompany the PERMANOVA analysis by illustrating differences in sculpin diet compositions in multivariate space. Prey group vectors, based on Pearson correlations, were overlain to show the specific prey groups driving differences between the sculpin's diets. The degree to which the nMDS ordination fit relationships between species, regions, and size bins was evaluated by a stress statistic, with a stress of <0.2 considered a good fit (Clarke and Warwick 2001).

To better understand how the morphological differences between the sculpin species might lead to differences in their diets, mouth gape width and height measurements were made to the nearest

0.1 mm using digital calipers. Gape width was defined as the greatest distance between the corners of both jaws, while gape height was defined as the greatest distance between the top and bottom of the mouth (Scharf et al. 2000). The resulting measurements were meant to represent the maximum size dimensions of prey a fish could ingest at a given body size. The gape measurements were regressed against total length using the Rcmdr package (Fox 2005, 2007) available in R, version 5.19 (R Core Team 2015). If total length was found to be a significant predictor of gape width or height, the slopes were compared between species using paired t-tests to determine interspecific differences in body size-gape size relationships.

The relationship between sculpin body size and the size of prey consumed was quantified using quantile regression. Quantile regression minimizes the sums of the absolute values of residuals to fit lines at specified quantiles ranging from 0 to 100 (Scharf et al. 1998; Scharf et al. 2000). This method was used to fit lines at the 10th and 90th quantiles to determine the lower and upper size ranges of prey consumed by similar-sized Arctic staghorn sculpin and shorthorn sculpin. All quantile regressions were conducted using the quantreg package (Koenker 2015) available in R, version 5.19 (R Core Team 2015). We interpreted the size ranges of prey consumed by both sculpins at a given body size in the context of differences in sculpin mouth morphologies at that given body size.

4. Results

4.1. Descriptive and multivariate diet comparisons

A total of 515 Arctic staghorn sculpin and 422 shorthorn sculpin stomachs were included in the descriptive and multivariate analyses. Throughout the SCS, NCS, and WBS, the major contributors to Arctic staghorn sculpin diet included benthic amphipods (28–69 %$\overline{W}$, 29–67 %$\overline{N}$, 45–83%O), polychaetes (11–35%$\overline{W}$, 9–26 %$\overline{N}$, 23–48 %O), and other prey (8–25 %$\overline{W}$, 14–41 %$\overline{N}$, 26–59 %O) (Table 1). Calanoid copepods, crabs, cumaceans, fish prey, hyperiid amphipods, and shrimps individually accounted for a smaller proportion of Arctic staghorn sculpin diet (≤1–8%$\overline{W}$, ≤1–7%$\overline{N}$, ≤1–13%O). Prey most consistently consumed by shorthorn sculpin throughout all regions included benthic amphipods (12–40%$\overline{W}$, 13–42%$\overline{N}$, 34–61%O) and crabs (14–19%$\overline{W}$, 17–22%$\overline{N}$, 28–38%O) (Table 1). Shorthorn sculpin inhabiting the SCS and WBS consumed the most hyperiid amphipods (18–52%$\overline{W}$, 17–47%$\overline{N}$, 20–60%O), while SCS and NCS conspecifics consumed the most fish prey (16–19 %$\overline{W}$, 11–13 %$\overline{N}$, 24–26 %O) and shrimps (8–18 %$\overline{W}$, 8–14 %$\overline{N}$, 14–27 %O) (Table 1). Calanoid copepods, cumaceans, and polychaetes individually accounted for a smaller proportion of shorthorn sculpin diet (≤1–7%$\overline{W}$, ≤1–6%$\overline{N}$, ≤1–11%O).

When size classes were accounted for, PERMANOVA determined significant differences in sculpin diet compositions within model one (SCS and NCS, all size classes) and model two (SCS, NCS, and WBS, two smallest size classes). In both models, significant differences in sculpin diets were found among the main effects of species ($F=35.105–60.697$; both $p<0.001$), regions ($F=27.331–30.596$; both $p<0.001$), and size classes ($F=7.834–8.012$; both <0.001) and the interactions between species and regions ($F=2.327–7.602$; $p=0.042–0.001$), species and size classes ($F=4.423–7.502$; both $p<0.001$), and species, regions, and size classes ($F=2.148–2.420$; $p=0.031–0.003$) (Supplemental 5 and 6). The regions and size classes interaction was not included in either model because it did not take into account the main effect of species. Overall, model one and two each accounted for about 25% of the total variance ($R^2 = 0.250$ and 0.252, respectively) in Arctic staghorn sculpin and shorthorn sculpin diets, with variance explained by individual components (i.e., partial R^2 values) generally being highest among the main effects (Supplemental 5 and 6). Because the higher-order interactions of species, regions, and size classes accounted for significant differences in sculpin diet compositions, only these interactions were examined further by multiple comparisons using PERMANOVA. At an $\alpha=0.05$, the multiple comparisons tested diet compositions between species, within regions, and at similar size classes and determined all diet comparisons were significantly different in both model one and two (both; $t=1.699–5.736$; $p=0.049–0.001$) (Supplemental 5 and 6).

For both models, nMDS illustrated a strong separation between species generally driven by the consumption of benthic amphipods and polychaetes by Arctic staghorn sculpin, and crabs, hyperiid amphipods, fish prey, and shrimps by shorthorn sculpin (Figs. 3 and 4). For all size classes in the SCS and NCS (i.e., model 1), shorthorn sculpin exhibited more noticeable shifts in their diet compositions with an increase in body size than did Arctic staghorn sculpin (Figs. 3 and 5A-D). Smaller shorthorn sculpin (i.e., ≤75 mm) diet compositions were influenced by prey such as hyperiid amphipods and juvenile crabs, whereas diets of larger shorthorn sculpin (i.e., ≥76 mm) were more influenced by fish prey and shrimps (Figs. 3, 5B and D). Arctic staghorn sculpin generally consumed benthic amphipods and polychaetes throughout all size classes with only minimal contribution of fishes and shrimps in the diets of ≥76 mm individuals (Figs. 3, 5A and C). Model two included the two smaller size classes of each species throughout all regions (Fig. 4). Unlike smaller conspecifics in the SCS and NCS, Arctic staghorn sculpin in the WBS consumed higher proportions of polychaetes than benthic amphipods (Figs. 4, 5A, C, and E). Similar to ≤50 mm SCS shorthorn sculpin, smaller, ≤75 mm WBS conspecific's diets were strongly influenced by hyperiid amphipods (Figs. 4, 5B, C, and D). In both models, the only notable diet similarities between species were in the NCS, where both species consumed the highest proportions of benthic amphipods relative to conspecifics in other regions (Fig. 5C and D).

In all regions, and nearly all size classes, shorthorn sculpin exhibited the highest mean stomach fullness index values, along with the highest mean %O of empty stomachs (Fig. 6). Both species exhibited highest mean SFI values in the WBS region, followed by the NCS and SCS regions (Fig. 6A, C, and E). Sculpins in the NCS region had the highest mean %O empty stomachs, followed by individuals in the WBS and SCS regions (Fig. 6B, D, and F). The majority of empty stomachs occurred within the smallest three size classes (i.e., ≤100 mm) which consequently were the three size classes containing the most available stomachs (Figs. 2, 6B, D, and F).

4.2. Morphological analysis and predator size – prey size relationships

Analysis of gape dimensions relative to body size revealed interspecific differences in sculpin mouth morphologies. Fish body size was a significant predictor of both gape height and width for Arctic staghorn sculpin and shorthorn sculpin (Fig. 7). Shorthorn sculpin gape width (df=49, t=11.870, p<0.001) and height (df=49, t=12.628, p<0.001) were significantly greater than those of Arctic staghorn sculpin at a given length.

Due to the large number of prey length measurements required to conduct quantile regression analysis, data from both seas were pooled for each species with the assumption that conspecifics of a similar size consumed a comparable size range of prey throughout their distributions. Fish body size was a significant predictor of the size of prey consumed by Arctic staghorn sculpin at the 10th (t=2.362, p=0.018) and 90th quantiles (t=10.319, p<0.001) and of the size of prey consumed by shorthorn sculpin at the 10th (t=3.042, p=0.002) and 90th quantiles (t=7.886, p<0.001) (Fig. 8). The slopes of the lines at each quantile showed that at similar body sizes, shorthorn sculpin consumed larger prey than Arctic staghorn sculpin. The fitted lines at the 10th quantile were driven mostly by other prey for Arctic staghorn sculpin and smaller stages of crabs and other prey for shorthorn sculpin (Fig. 8). The fitted lines at the 90th quantiles were driven mostly by consumption of larger benthic amphipods and few shrimps by Arctic staghorn sculpin and an increase in fish prey and shrimps in the diets of shorthorn sculpin (Fig. 8).

5. Discussion

Arctic staghorn sculpin and shorthorn sculpin exhibit generalist feeding strategies in the northeastern Chukchi and western Beaufort Seas by consuming a wide variety of benthic, epibenthic, or pelagic macroinvertebrates and fishes. Arctic staghorn sculpin diets described here resembled those in the eastern Bering (Cui et al. 2012), Chukchi (Coyle et al. 1997), and Canadian Beaufort Seas (Atkinson and Percy 1992) in that benthic amphipods and polychaetes are their key prey. Shorthorn sculpin consume similar prey types as conspecifics in the eastern Bering (e.g., benthic amphipods, crabs; Cui et al. 2012), Labrador (e.g., benthic crustaceans and zooplankton; Moore and Moore 1974; Atkinson and Percy 1992) and Baltic Seas (e.g., benthic crustaceans, fish prey; Cardinale 2000). In this study, intra- and interspecific variability became noticeable when these scuplin's diets were examined beyond the fish species group level by body size-related factors within different habitats.

Fish food habits can vary greatly throughout ontogeny in both size and type of prey consumed (Werner and Gilliam 1984; Chipps and Garvey 2007; Gray et al. 2015). Arctic staghorn sculpin generally shifted towards consuming larger individuals of similar prey groups (i.e., larger benthic amphipods and polychaetes) rather than fish prey or shrimps. In contrast, shorthorn sculpin shifted towards exploiting a wider range of prey taxa by consuming both larger prey of similar groups and by incorporating new prey groups. Smaller shorthorn sculpin (i.e., ≤75 mm) primarily consumed smaller benthic and pelagic crustaceans while larger conspecifics frequently consumed fishes and shrimps. In regions where similarities in size ranges allowed for intraspecific comparisons, these patterns were generally conserved, suggesting little regional variation in diet composition among either species.

Body size appears to be a major factor in defining interspecific interactions between these cottids. In the western Arctic, shorthorn sculpin generally attain a larger body size (usually <350 mm; 223 mm observed here), than Arctic staghorn sculpin (usually <150 mm; 157 mm observed here) (Mecklenburg et al. 2002). For both species, body size was related to mouth gape size, which directly affects the size of prey fish can consume (Keast and Webb 1966; Labropoulou and Eleftheriou 1997; Juanes et al. 2002). Shorthorn sculpin have larger relative gape sizes and are capable of consuming larger prey than Arctic staghorn sculpin of the same length. This allows shorthorn sculpin access to prey Arctic staghorn sculpin cannot consume and allows shorthorn sculpin to become piscivorous at smaller body sizes (first evidence of piscivory; 38 mm shorthorn sculpin, 79 mm Arctic staghorn sculpin).

Theoretically, shorthorn sculpin could consume the same diet as Arctic staghorn sculpin given that they share similar habitats and prey bases. However, these sculpins partition prey by taxa, size, or proportion, and there appears to be little overlap in prey use between these species within the Chukchi and Beaufort Seas.

As benthic fishes, Arctic staghorn sculpin and shorthorn sculpin were expected to consume primarily benthic diets throughout ontogeny; this was not always the case, especially for shorthorn sculpin. While Arctic staghorn sculpin opportunistically consumed some pelagic prey in the Chukchi and Beaufort Seas, small (≤75 mm) shorthorn sculpin frequently consumed hyperiid amphipods (mostly *Themisto libellula*) in the SCS and WBS. Moore and Moore (1974) reported similar patterns of pelagic zooplankton consumption by shorthorn sculpin in regions of the Labrador Sea. Likewise, the confamilial ribbed sculpin (*Triglops pingelli*) is known to consume pelagic zooplankton in the Canadian Beaufort Sea (Atkinson and Percy 1992). Shorthorn and ribbed sculpin could be exhibiting this type of feeding behavior as a means of resource partitioning throughout ontogenetic stages to reduce intra- and interspecific competition for prey resources. Because hyperiid amphipods can occur near the benthos (Auel et al 2002), it is possible that Arctic staghorn sculpin and shorthorn sculpin encounter these prey at a similar rate, but face different size-related feeding constraints. Hyperiid amphipods are among the largest and most commonly consumed prey item by ≤75 mm shorthorn sculpin. In comparison, benthic amphipods were the largest and most commonly consumed prey item by similar-sized Arctic staghorn sculpin. For ≤75 mm sculpins, the average size of hyperiid amphipods (16.7±3.8 mm[SD]) consumed by shorthorn sculpin was larger than the benthic amphipods consumed by Arctic staghorn sculpin (6.4±2.9 mm[SD]). It is possible that most hyperiid amphipods are too large for Arctic staghorn sculpins to feed upon within this size range, but are within the upper size ranges of prey that shorthorn sculpin can consume. Another possibility is that Arctic staghorn sculpin are more benthic-oriented foragers than shorthorn sculpin and are therefore less likely to encounter such pelagic prey even though it may be nearby.

Although sculpin diet compositions were quite different, there were some similarities between species' prey use patterns in the Chukchi Sea, especially in the NCS region. Aggregated at the family, genus, or species level, both sculpins' diets were composed of more unique benthic prey taxa in the Chukchi Sea (Arctic staghorn sculpin=102 taxa, shorthorn sculpin=82 taxa) compared to the Beaufort Sea (Arctic staghorn sculpin=47 taxa, shorthorn sculpin=19). This difference could be due to greater benthic productivity throughout regions of the northeastern Chukchi Sea (Grebmeier et al. 2006; Blanchard et al. 2013; Blanchard and Feder 2014) compared to those in the Beaufort Sea (Carey and Ruff 1977; Carey 1987; 1991) although differences in the sizes of sculpins collected within seas likely influenced these findings as well. Relative to all other regions, both species consumed the highest proportions of benthic amphipods in the NCS. The abundance and distribution of these macroinvertebrates within the NCS were probably influenced in part by broad oceanographic-related habitat characteristics of the region (Blanchard and Feder 2014). For example, the presence of a semi-permanent, bottom-water front located near Point Franklin (Weingartner 1997) supports a high abundance of benthic taxa near the frontal boundary (Feder et al. 1994b; Dunton et al. 2005). Other contributing factors may have included enhanced organic carbon deposition in the NCS near Hanna Shoal and Barrow Canyon, which increases food availability to benthic macroinvertebrate communities (Blanchard et al. 2013; Blanchard and Feder 2014). Whatever the mechanisms responsible, the higher contribution of this prey type to both species' diets in the NCS suggests that locally abundant prey groups can lead to greater similarities in diets between species.

The findings of a higher percentage empty stomachs, yet overall greater stomach fullness for shorthorn sculpin is likely related to its piscivorous feeding style. Empty stomachs are more prevalent in piscivorous fishes because they typically consume fewer, larger meals compared to zooplanktivorous fishes (e.g., Arctic staghorn sculpin) which consume smaller prey more frequently (Vinson and Angradi 2011). Keeping body size constant, it follows that a piscivorous shorthorn sculpin would have a fuller stomach than a zooplanktivorous Arctic staghorn sculpin, which is supported in our size class analyses.

The exact causes of the between-region variability in stomach fullness and percent empty stomachs is difficult to determine. Variability in stomach fullness could arise from a few different sources, such as prey availability within the study area or the degree of prey digestedness in a fishes' stomach. Variation in percent empty stomachs could naturally occur between regions due to prey availability or different feeding styles, however, some fish species are known to regurgitate food after capture by trawl nets (Bowman 1986). Such a scenario could lead to a disproportionate amount of empty stomachs between species were one species more susceptible to regurgitating their food than the other. These sources of error should be kept in mind when interpreting these types of analyses.

Soft-bodied prey (e.g., fish prey, polychaetes, or unidentifiable animal tissues) were an important component of each sculpin's diet, accounting for 50% (1% fish, 20% polychaete, and 29% unidentified) of pooled biomass in Arctic staghorn sculpin diets and 28% (13% fish, 5% polychaete, and 10% unidentified) in shorthorn sculpin diets. Polychaetes and fishes were included in the %$\overline{W}$-based statistical analyses and stomach fullness calculations, however, due to mastication, it was impossible to include each individual in the quantile regression analyses. By excluding all polychaetes and some fishes, the upper slope of the predator length–prey length regression was likely skewed downwards for both species. While additional fish prey measurements may have better defined the maximum lengths of prey consumed by either sculpin, we believe the exclusion of polychaete total lengths was acceptable given that a sculpin's ability to consume these soft-bodied prey is most likely determined by prey width rather prey total length. Unidentifiable tissues were not included in the %$\overline{W}$-based statistical analyses because the tissues lack ecological interpretability and because including such prey decreases the amount quantifiable separation among predator's food habits by increasing dietary overlap (Garrison and Link 2000). Instead, we accounted for the contribution of unidentifiable tissues to sculpin diets using the stomach fullness analysis and determined that even though Arctic staghorn sculpin consumed a higher pooled biomass of unidentified tissues compared to shorthorn sculpin, on average, shorthorn sculpin had fuller stomachs throughout all regions and size classes.

This study suggests that the present Chukchi Sea food web model parameters, which were based on Bering Sea sculpin diet compositions (Whitehouse et al. 2014), are likely acceptable for Arctic staghorn sculpin but should be reconsidered for shorthorn sculpin. In the model, Arctic staghorn sculpin was included in the “other sculpins” functional group along with eight other sculpin genera, including *Artediellus, Blepsias, Enophrys, Gymnocanthus, Icelus, Megalocottus, Microcottus, Nautichthys,* and *Triglops* (Whitehouse et al. 2014). This model was parameterized with benthic amphipods and polychaetes composing >80% of these fishes’ diets. Arctic staghorn sculpin diet composition in our study was quite similar to that used in the model. Benthic amphipods and polychaetes, by pooled biomass, composed approximately 71% of its diet in the Chukchi Sea and 63% in the Beaufort Sea. This suggests that Arctic staghorn sculpin diet could be similar throughout the Arctic and that using diet composition from other regions of the Arctic could adequately represent this species’ feeding habits. Shorthorn sculpin was included in the “large-mouth sculpins” functional group along with two other species belonging to the genera *Myoxocephalus* and *Hemilepidotus* (Whitehouse et al. 2014). Diet composition of shorthorn sculpin in our study did not agree as well with the data used in the model. Shorthorn sculpin in the Bering Sea was characterized as a heavy consumer (>80% of diet composition) of snow crab (*Chionoecetes opilio*) and other crabs, with shrimps and benthic amphipods composing about 2.5 to 4% of the diet (Whitehouse et al. 2014). Our study indicates that the present model would overemphasize the pooled biomass of snow crabs and other crabs in shorthorn sculpin diets by about 60% in the Chukchi and Beaufort Seas. Consequently, the importance of shrimps, benthic amphipods, and hyperiid amphipods as shorthorn sculpin prey would be underestimated in both seas. Therefore, for shorthorn sculpin, we recommend that, where possible, parameters be based upon diet studies from Chukchi and Beaufort Sea regions only.

Overall, greater catches, composed of larger Arctic staghorn sculpin and shorthorn sculpin individuals, were obtained in the Chukchi Sea compared to the Beaufort Sea. It is possible that these differences were influenced by between-sea discrepancies in sculpin biomass and by our use of larger-mesh nets in the Chukchi Sea compared to those used in the Beaufort Sea. These possibilities can be explored, to an extent, by examining two prior cruises within our study area, both of which used the larger 83-112 net (Barbar et al. 1997; Logerwell et al. 2011). The authors reported few distinctions between sculpin species, however, the overall pattern of a higher catch per unit effort (CPUE) of sculpins in the Chukchi Sea (0.76 kg/ha) than that in the Beaufort Sea (0.03 kg/ha) would explain the noticeable differences in Arctic staghorn sculpin and shorthorn catches between seas. Unfortunately, the authors did not report the size distributions of the sculpins collected by the 83-112 net, therefore we were unable to determine whether using this net would have allowed us access to larger individuals in the Beaufort Sea. In future Beaufort Sea studies, the collection of larger Arctic staghorn sculpin and shorthorn sculpin individuals, if possible, would allow for a more comprehensive description of ontogenetic shifts in sculpin food habits.

6. Conclusions

Over 30 species of sculpins inhabit Arctic marine waters (Mecklenburg et al. 2011), yet, to our knowledge, there is only one published study regarding cottid diets within the western Arctic (Arctic staghorn sculpin; Coyle et al. 1997). The lack of ecological data available for the second largest Arctic fish family is quite remarkable and creates a gap in our knowledge of trophic pathways within Arctic food webs. As explained here, sculpins may function as benthivores or pelagivores depending on species, habitat, and body sizes. As ecosystem models continue to be developed throughout the Arctic, more detailed diet analyses regarding sculpin species in the Arctic would serve to better determine their role within food webs.

7. Acknowledgements

We thank the crewmembers aboard the R/V *Alaska Knight* and R/V *Norseman II* for their help and fishing expertise. We also thank all past and present UAF Fisheries Oceanography lab technicians for their help in processing fish stomach contents. This study was funded in part with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior. It was also funded by the Bureau of Ocean and Energy Management (BOEM) Award # M10AC20004 and BOEM Award # M12PG00018. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of the U.S. Government. Mention of trade names or commercial products does not constitute their endorsement by the U.S. Government.

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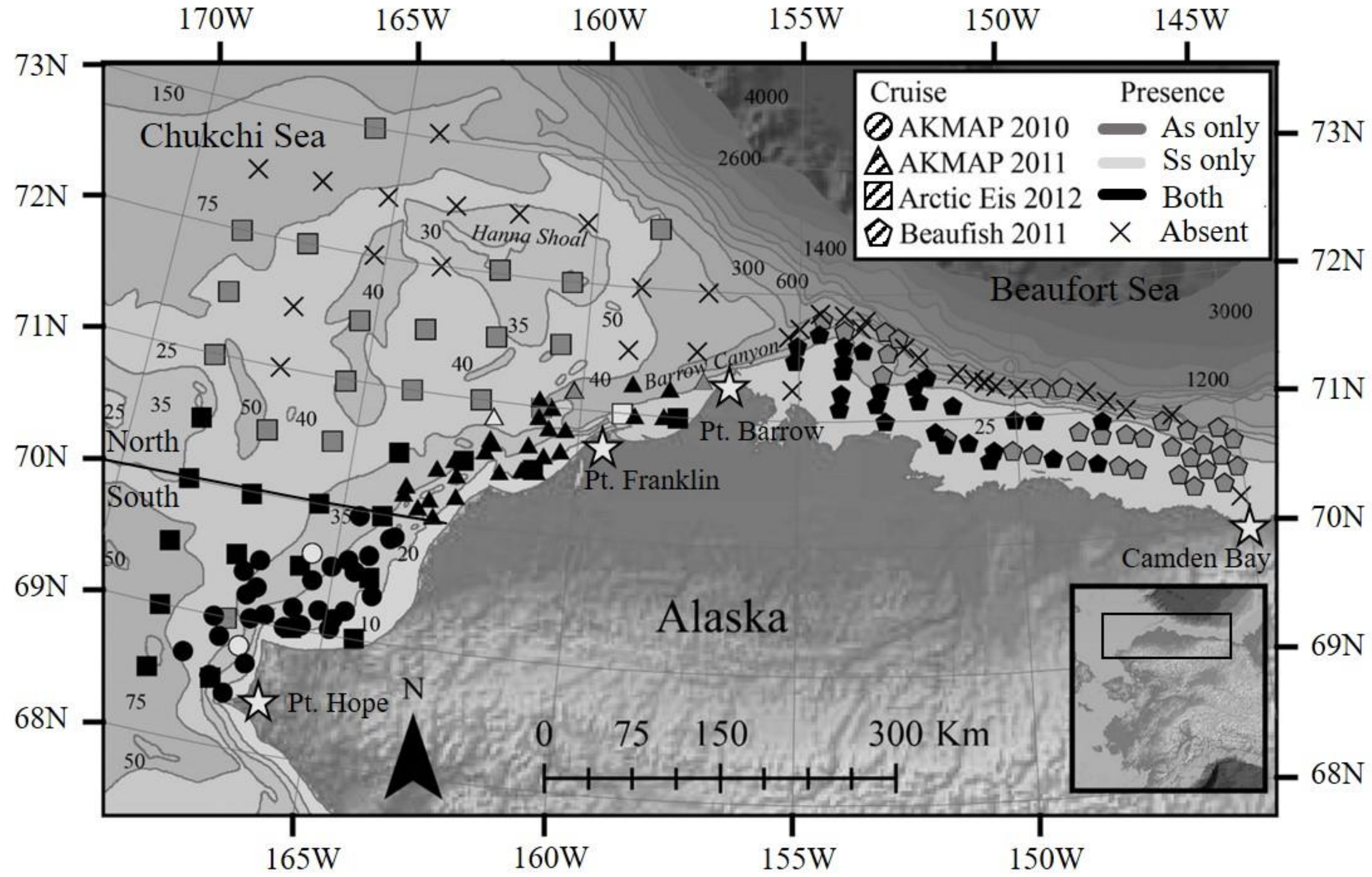

Fig. 1 Chukchi and Beaufort Sea bottom-trawl sampling locations, shape and color-coded to indicate the specific cruise in which collections took place, and whether or not Arctic staghorn sculpin (As) and shorthorn sculpin (Ss) were present at a given location. Fishes were collected over three Chukchi Sea cruises (AKMAP10–11 and Arctic Eis12) and one Beaufort Sea cruise (Beaufish11). North and south Chukchi Sea regions were divided at 70˚N. Barrow Canyon served as the boundary between Chukchi and Beaufort Sea sculpins. Station locations are symbolized by four shapes, one for each cruise. Sculpin presence at a given station is denoted by three colors: dark-gray represents the presence of only Arctic staghorn sculpin, light-gray represents only shorthorn sculpin presence, and black represents presence of both species. An “X” signifies an absence of both species at a station.

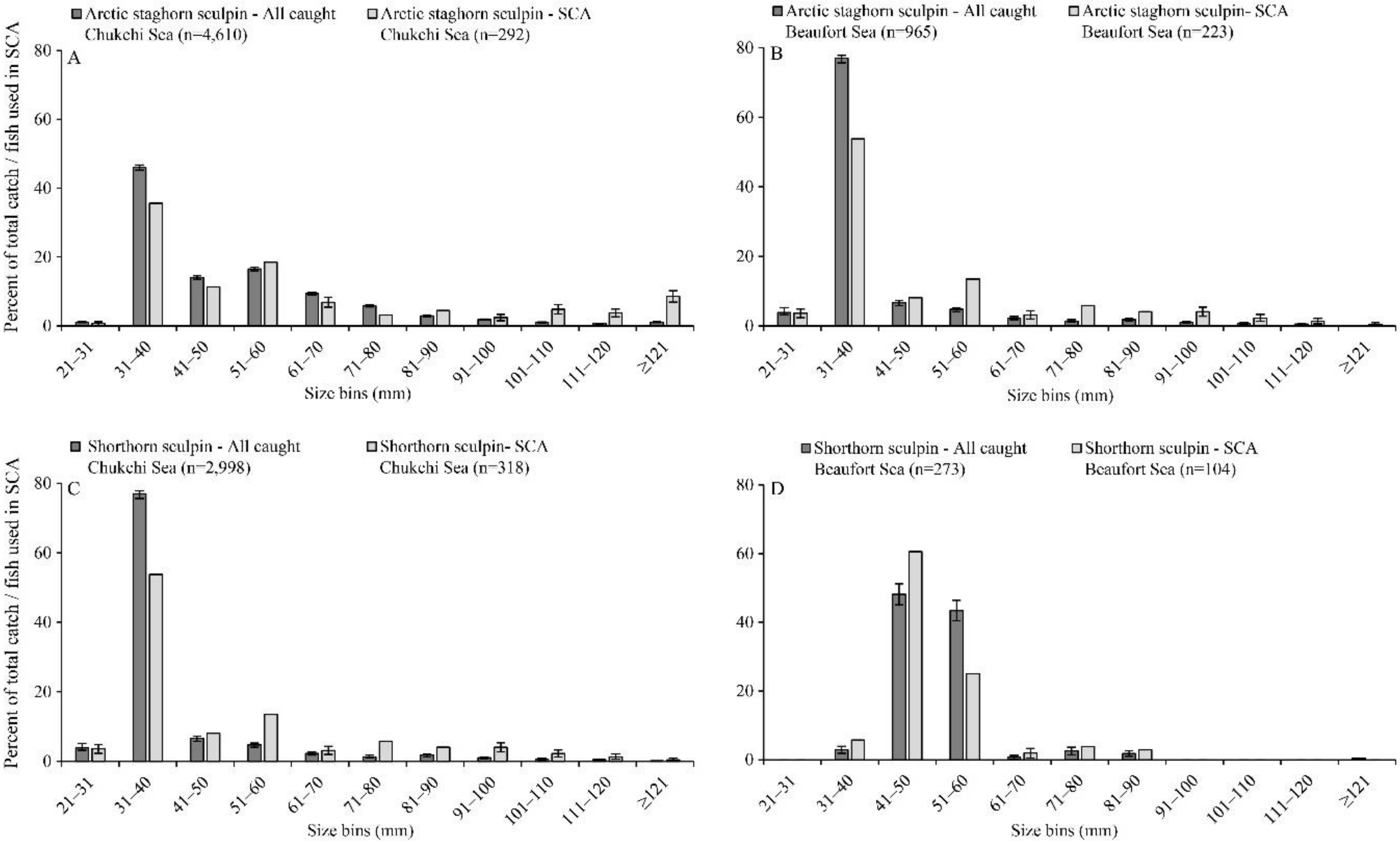

Fig. 2 Size distributions, based on fish total length (TL), of Arctic staghorn sculpin (2A and B) and shorthorn sculpin (2C and D) collected using bottom trawls (dark bars) and those used in stomach contents analysis (SCA; light bars) throughout the Chukchi (2A and C) and Beaufort (2B and D) Seas. Error bars represent ±1 standard error from the mean.

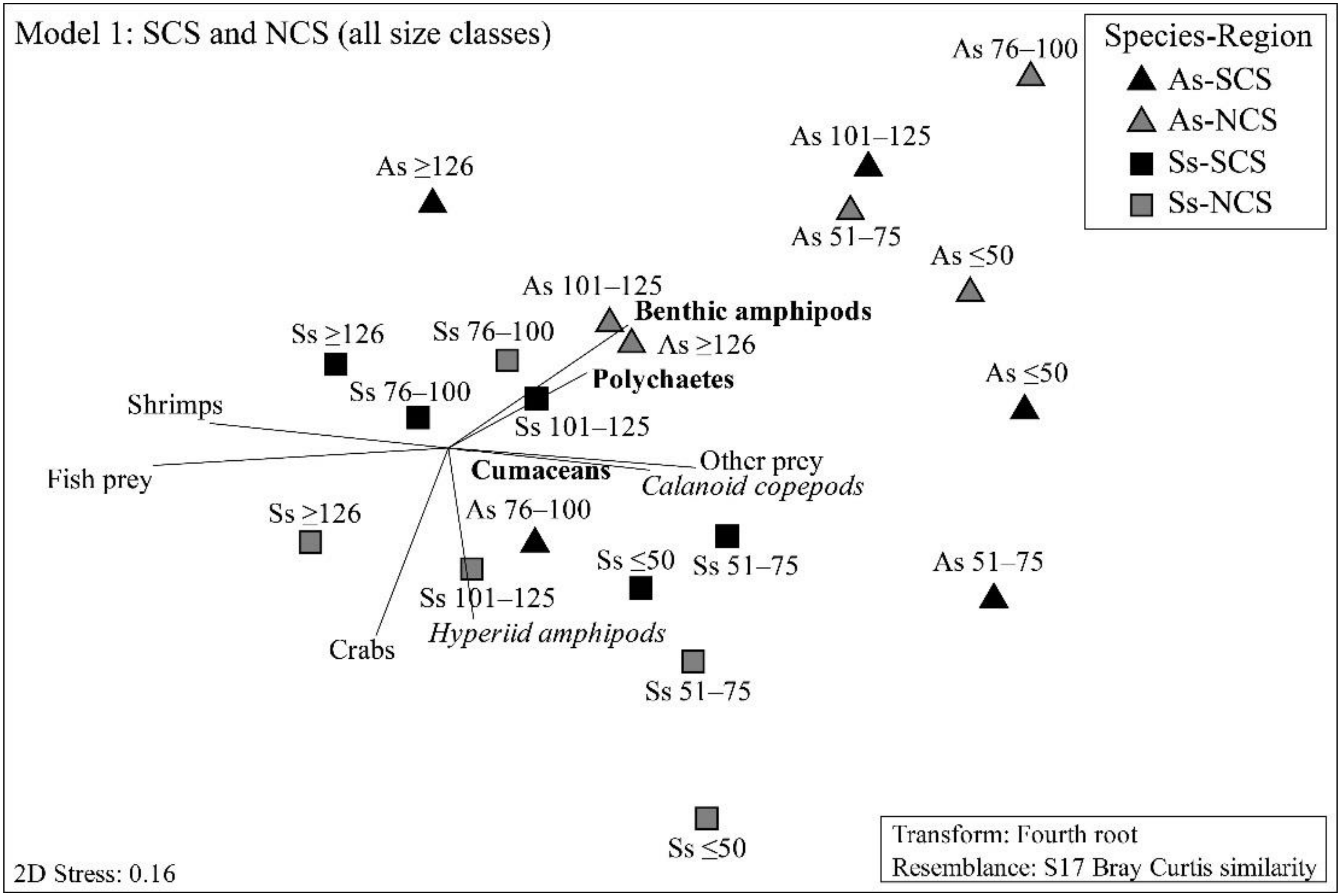

Fig. 3 Non-metric multidimensional scaling (nMDS) plot illustrating the differences among the diets of all five size classes of Arctic staghorn sculpin (As) and shorthorn sculpin (Ss) within the south Chukchi (SCS) and north Chukchi (NCS) regions (i.e., PERMANOVA model 1). Prey group names, listed near their corresponding vectors, are bolded for benthic prey, non-bolded for benthic/pelagic prey, or italicized for pelagic prey.

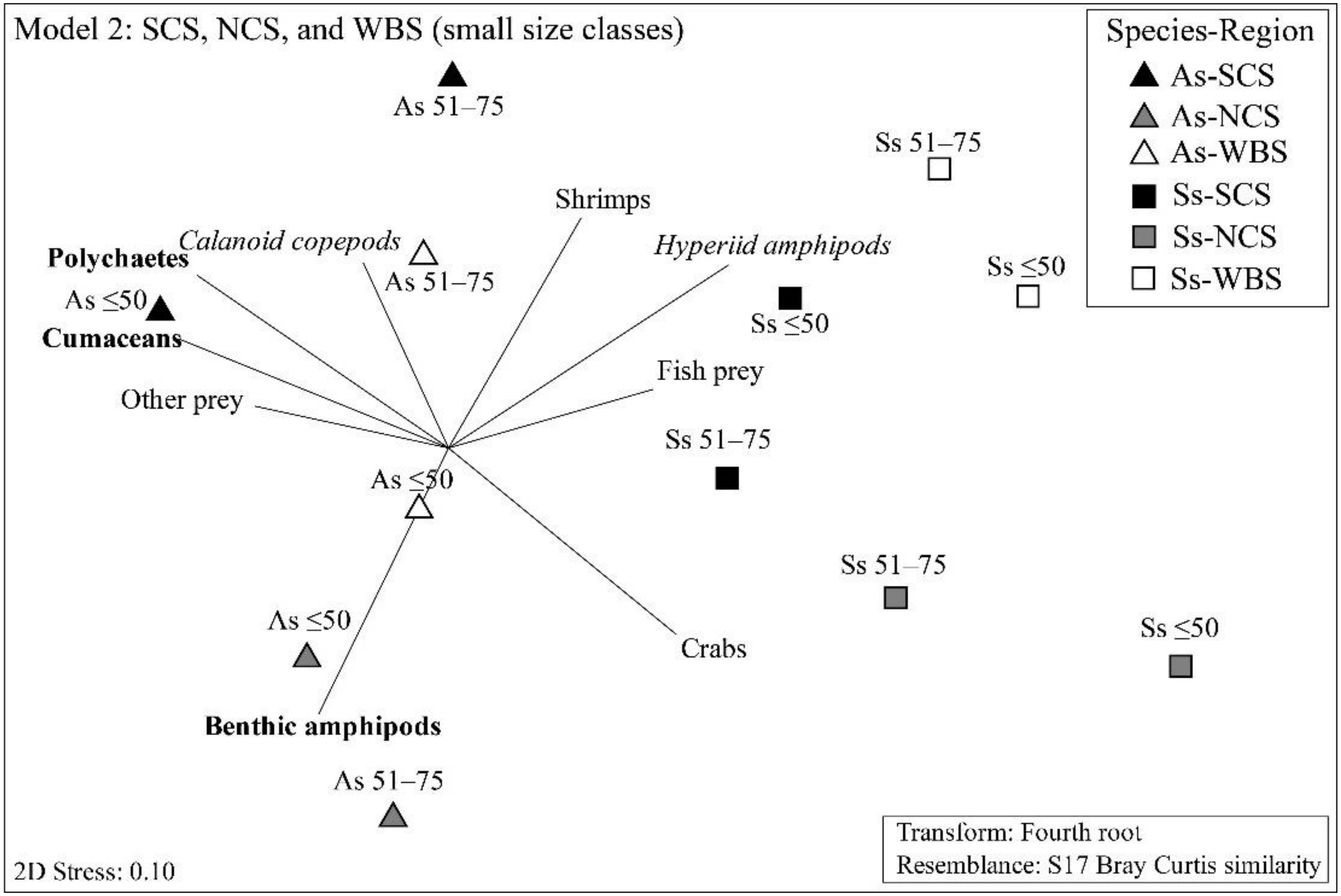

Fig. 4 Non-metric multidimensional scaling (nMDS) plot illustrating the differences among the diets of the two smallest size classes (≤50 mm and 51–75 mm) of Arctic staghorn sculpin (As) and shorthorn sculpin (Ss) within the south Chukchi (SCS), north Chukchi (NCS), and west Beaufort (WBS) regions (i.e., PERMANOVA model 2). Prey group names, listed near their corresponding vectors, are bolded for benthic prey, non-bolded for benthic/pelagic prey, or italicized for pelagic prey.

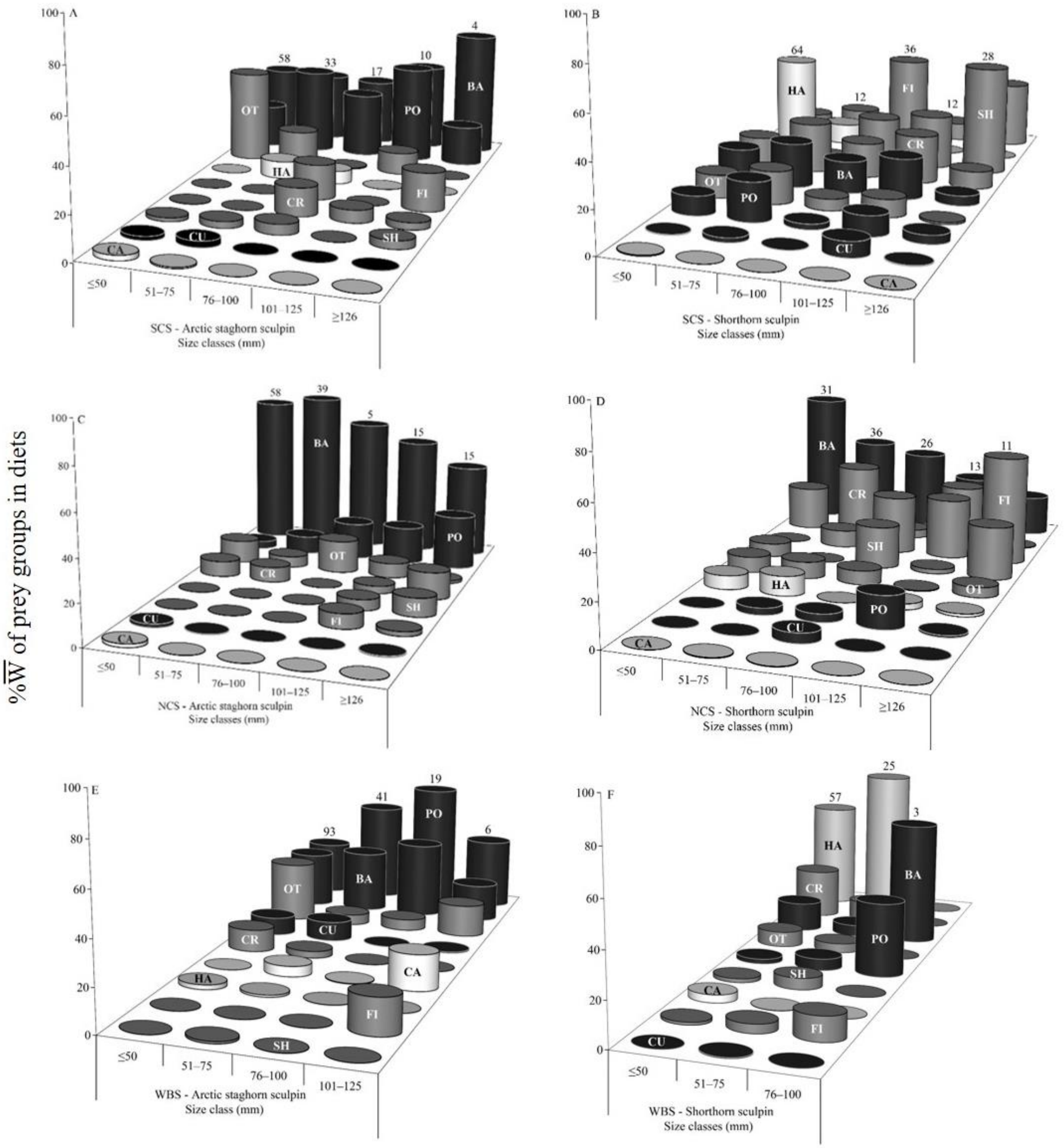

Fig. 5 Diet compositions of Arctic staghorn sculpin (5A, C, and E) and shorthorn sculpin (5B, D, and F) summarized by size classes in the south Chukchi (SCS; 5A and B), north Chukchi (NCS; 5C and D), and west Beaufort (WBS; 5E and F) regions. Prey groups along the z-axis are ranked in order from greatest (rear) to least (front) contribution to each species' diet by %$\overline{W}$. The colors black, dark-gray, and gray represent benthic, benthic/pelagic, and pelagic prey, respectively. Prey groups are abbreviated as follows: CA = calanoid copepods, BA = benthic amphipods, CR = crabs, CU = cumaceans, FI = fish prey, HA = hyperiid amphipods, PO = polychaetes, SH = shrimps, and OT = other prey. Stomach sample sizes are listed above the rear column in each figure. The diet compositions of sculpins ≥76 mm in the WBS are included here as a description only; these fishes were not included in the statistical analyses because very few shorthorn sculpin were collected in the WBS at this size.

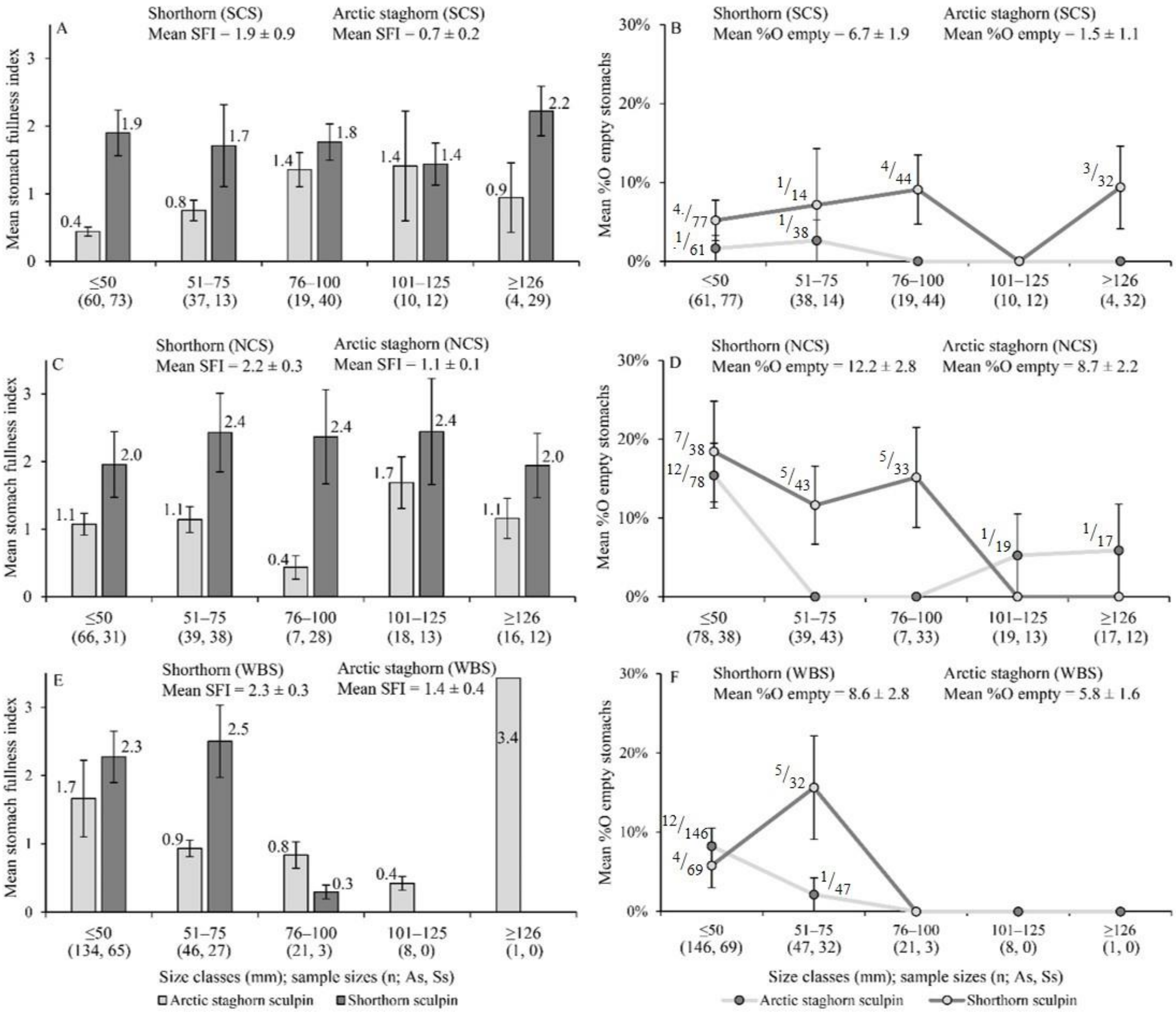

Fig. 6 Plots of mean stomach fullness index (SFI; 6A, C, and E) and mean percent occurrence (%O) of empty stomachs (6B, D, and F) for all sculpin size classes within the south Chukchi (SCS; 6A and B), north Chukchi (NCS; 6C and D), and west Beaufort (WBS; 6E and F) regions. In all plots, Arctic staghorn sculpin are signified by gray bars or gray lines which represent mean SFI and mean %O empty stomach values, respectively. Shorthorn sculpin are signified similarly by dark bars and dark lines. For each analysis, error bars represent ±1 standard error from the mean. Overall summaries of mean SFI and mean %O empty stomach values by species within regions are listed at the top of each figure with their corresponding standard error values. For SFI plots, numbers near the top of a bar represent the mean SFI value for a given size class. For %O empty stomach plots, fractions near points represent the amount of empty stomachs there were in a sample size (numerator) and all stomachs in a sample size (denominator). For both plots, stomach sample sizes used per size class are listed in parentheses underneath the size classes with the number of Arctic staghorn sculpin stomachs listed to the left and shorthorn sculpin stomachs to the right as such (As, Ss).

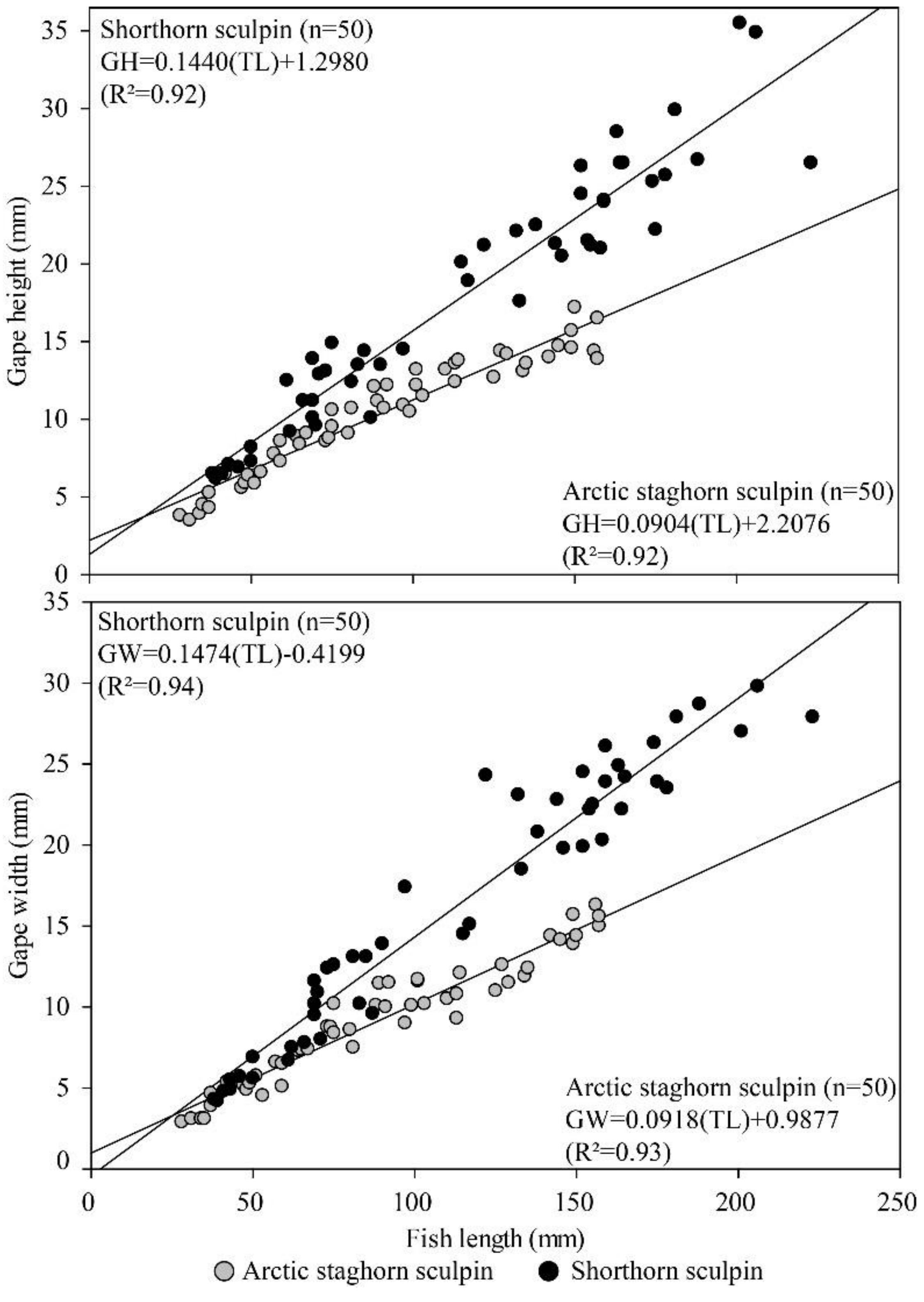

Fig. 7 Gape height (GH) and gape width (GW) regressed against fish total length (TL) for A) Arctic staghorn sculpin and B) shorthorn sculpin.

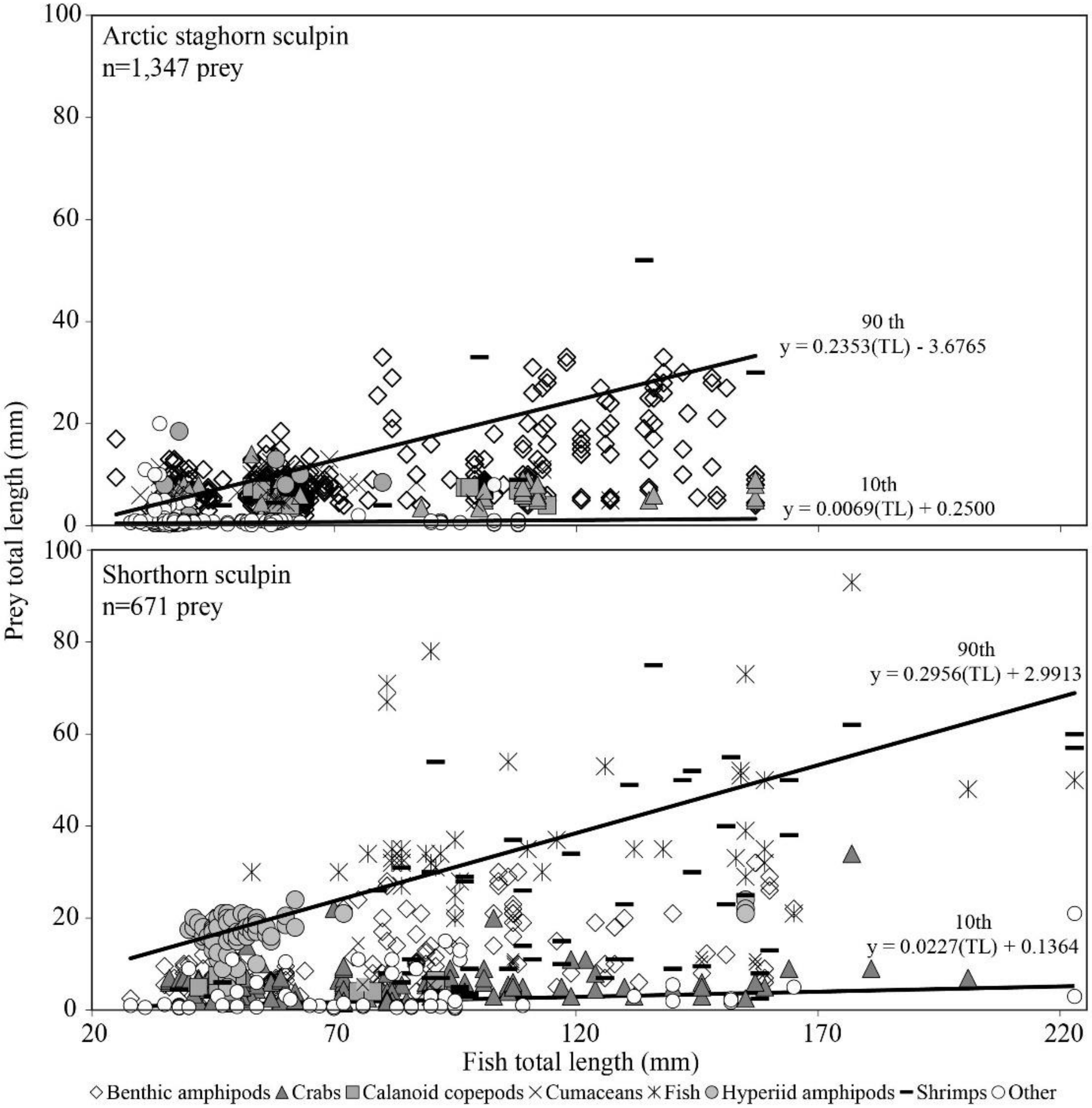

Fig. 8 Regression plots of the 10th and 90th quantiles, highlighting the size ranges of prey consumed by Arctic staghorn sculpin and shorthorn sculpin in the Chukchi and Beaufort Seas at similar total length values.

Table 1. Arctic staghorn sculpin and shorthorn sculpin diets summarized by %$\overline{W}$, %$\overline{N}$, and %O in the south Chukchi (SCS), north Chukchi (NCS), and west Beaufort (WBS) regions. A dash indicates a prey item was not present. Summary information including total stomachs, total prey number, total unique taxa, and regional body size ranges and averages is listed below.

	South Chukchi Sea						North Chukchi Sea						West Beaufort Sea					
	G. tricuspis			M. scorpius			G. tricuspis			M. scorpius			G. tricuspis			M. scorpius		
Prey groups and taxa	%$\overline{W}$	%$\overline{N}$	%O	%$\overline{W}$	%$\overline{N}$	%O	%$\overline{W}$	%$\overline{N}$	%O	%$\overline{W}$	%$\overline{N}$	%O	%$\overline{W}$	%$\overline{N}$	%O	%$\overline{W}$	%$\overline{N}$	%O
Benthic amphipods	**33.3**	**30.1**	**61.5**	**14.1**	**19.0**	**34.2**	**69.5**	**66.7**	**82.7**	**40.5**	**42.5**	**61.5**	**27.7**	**29.1**	**45.3**	**12.4**	**13.2**	**20.0**
Anonyx spp.	1.3	0.2	1.6	0.2	0.1	0.7	2.7	2.2	5.3	0.2	0.1	0.9	1.4	1.4	3.1	–	–	–
Ischyocerus spp.	–	–	–	0.7	0.7	0.7	12.1	12.1	15.0	8.7	7.8	11.1	0.6	0.5	0.6	–	–	–
Melita spp.	4.9	4.6	10.7	5.7	5.5	12.5	4.5	4.2	8.3	2.2	2.2	6.0	5.4	3.7	10.1	3.0	2.4	4.7
Protomedeia spp.	4.3	2.4	7.4	0.7	1.3	2.0	8.1	7.6	17.3	3.5	4.5	8.6	2.5	2.4	4.4	–	–	–
Oedicerotidae	2.5	3.7	8.2	0.8	1.3	3.3	2.2	1.7	5.3	1.4	1.5	3.4	5.5	5.7	10.7	2.9	2.8	4.7
Other benthic amphipods	20.2	19.2	45.9	6.1	10.1	21.7	39.9	38.9	60.9	24.5	26.4	50.4	12.4	15.4	28.3	6.5	8.0	14.1
Calanoid copepods	**1.3**	**1.5**	**8.2**	**0.2**	**0.9**	**2.0**	**0.7**	**0.3**	**0.8**	**0.1**	**1.1**	**2.6**	**1.9**	**2.9**	**3.8**	**2.4**	**2.7**	**5.9**
Crabs	**2.5**	**2.9**	**6.6**	**14.9**	**17.3**	**30.3**	**7.6**	**7.0**	**13.5**	**19.2**	**21.4**	**37.6**	**6.9**	**6.9**	**12.6**	**17.5**	**21.9**	**28.2**
Chionoecetes opilio	–	–	–	1.0	1.5	4.6	–	–	–	2.0	3.0	10.3	–	–	–	–	–	–
Telmessus cheiragonus	1.0	0.8	2.5	3.8	4.5	9.9	0.7	0.4	0.8	1.1	1.5	4.3	–	–	–	–	–	–
Paguridae	0.3	0.7	1.6	5.1	6.6	14.5	2.8	2.4	6.8	5.8	5.3	18.8	5.4	5.2	8.8	14.8	17.7	29.4
Other crabs	1.2	1.4	2.5	5.1	4.8	10.5	4.1	4.2	6.8	10.3	11.5	24.8	1.5	1.8	3.8	2.7	4.2	9.4
Cumacean	**1.6**	**1.7**	**9.0**	**1.0**	**1.8**	**6.6**	**0.8**	**1.0**	**2.3**	**1.0**	**1.4**	**2.6**	**7.2**	**6.0**	**17.0**	**0.1**	**0.1**	**1.2**
Diastylidae	0.3	0.4	1.6	0.2	0.2	0.7	0.7	0.8	0.8	1.0	1.0	1.7	4.7	3.3	10.7	–	–	–
Other cumaceans	1.3	1.3	7.4	0.8	1.6	5.9	0.1	0.2	1.5	<0.1	0.4	0.9	2.5	2.8	8.2	0.1	0.1	1.2
Fish prey	**2.8**	**2.2**	**4.1**	**18.9**	**12.7**	**25.7**	**1.1**	**0.5**	**3.0**	**16.1**	**11.5**	**23.9**	**0.6**	**0.6**	**0.6**	**2.4**	**2.1**	**3.5**
Hyperiid amphipods	**3.0**	**1.5**	**3.3**	**17.8**	**16.6**	**20.4**	**–**	**–**	**–**	**4.9**	**3.8**	**7.7**	**1.5**	**1.6**	**5.7**	**52.2**	**47.1**	**60.0**
Themisto libellula	2.1	0.7	2.5	13.7	12.4	15.1	–	–	–	3.3	2.2	4.3	–	–	–	40.1	32.8	43.5
Other Hyperiid amphipods	0.8	0.8	0.8	4.1	4.2	7.2	–	–	–	1.6	1.6	3.4	1.5	1.6	5.7	12.1	14.3	23.5
Polychaetes	**28.2**	**17.3**	**39.3**	**7.4**	**6.3**	**13.2**	**10.8**	**9.4**	**22.6**	**3.5**	**2.4**	**7.7**	**35.0**	**26.3**	**47.8**	**4.2**	**3.6**	**8.2**
Glyceridae	–	–	–	0.7	0.7	0.7	–	–	–	–	–	–	3.9	2.9	5.7	–	–	–
Polynoidae	3.1	2.1	4.1	0.0	0.2	0.7	3.8	2.6	6.8	0.1	0.1	0.9	1.7	0.8	1.9	<0.1	0.1	1.2
Other polychaetes	25.2	15.3	35.2	6.7	5.5	11.8	6.9	6.8	18.0	3.5	2.3	6.8	29.4	22.6	40.9	4.2	3.5	7.1
Shrimps	**2.4**	**2.0**	**4.1**	**17.8**	**14.5**	**27.0**	**1.6**	**0.6**	**3.0**	**8.4**	**7.9**	**14.5**	**0.2**	**0.1**	**0.6**	**2.7**	**2.6**	**4.7**
Crangonidae	0.9	0.9	1.6	5.3	4.5	10.5	1.2	0.4	1.5	5.1	4.4	8.6	0.2	0.1	0.6	0.1	0.1	1.2
Other shrimps	1.5	1.1	2.5	12.5	10.0	23.0	0.4	0.2	1.5	3.3	3.6	6.8	–	–	–	2.6	2.5	3.5
Other prey	**24.9**	**40.8**	**59.0**	**7.9**	**10.9**	**21.1**	**7.9**	**14.5**	**25.6**	**6.2**	**8.0**	**14.5**	**18.8**	**26.4**	**39.0**	**5.9**	**6.6**	**10.6**
Barnacle cyprids	6.8	14.0	39.3	0.7	1.0	2.0	0.1	1.0	3.0	–	–	–	7.8	10.9	16.4	0.0	0.6	1.2
Harpacticoid cope	7.5	16.6	36.1	0.2	0.8	2.0	1.7	4.0	8.3	–	–	–	3.7	6.2	15.7	1.2	1.2	1.2
Mollusks	5.0	4.2	14.8	1.8	3.9	9.2	2.7	3.6	9.0	1.0	2.0	3.4	1.2	0.9	3.1	<0.1	0.1	1.2
Ostracods	2.8	4.0	18.9	<0.1	0.7	2.0	0.0	0.5	2.3	0.0	0.4	0.9	4.3	7.1	13.8	1.2	1.2	1.2
All other prey	3.0	2.0	12.3	5.3	4.5	9.9	3.4	5.4	8.3	5.2	5.6	10.3	1.7	1.3	2.5	3.5	3.6	5.9
Unidentifiable*	**32.3**	**18.1**	**51.5**	**13.0**	**13.5**	**26.8**	**11.5**	**10.6**	**15.7**	**5.4**	**7.0**	**14.7**	**37.8**	**32.0**	**50.0**	**11.4**	**11.6**	**15.8**
Total stomachs	132			179			160			139			223			104		
Total number of prey	1,016			523			564			465			520			228		
Total unique prey taxa	78			85			78			85			57			36		
Size range-Avg. (mm)	31–157 (58.9)			28–223 (79.6)			30–157 (65.0)			35–175 (74.6)			25–113 (49.9)			31–89 (50.3)		

* Keeping the regional sample sizes constant, the %$\overline{W}$, %$\overline{N}$, and %O of unidentifiable prey was calculated separately so that these values would not deflate the contribution of identifiable prey to sculpin diets.

Supplemental-1 Count of Arctic staghorn sculpin and shorthorn sculpin stomachs used in diet analyses, per station, from the AKMAP 2010 and 2011 cruises. Accompanying spatial and depth information is included for each station.

Cruise	Station	Latitude (deg)	Longitude (deg)	Station depth (m)	Arctic staghorn sculpin	Shorthorn sculpin
AKMAP 10	AKMAP-001	69.8	163.8	26	10	1
	AKMAP-002	69.4	165.4	35	1	0
	AKMAP-003	69.1	164.8	24	0	3
	AKMAP-004	69.0	167.3	49	4	8
	AKMAP-005	69.6	164.7	23	1	6
	AKMAP-006	69.0	165.5	23	1	7
	AKMAP-007	69.2	164.6	25	1	0
	AKMAP-008	69.0	166.6	34	3	0
	AKMAP-009	69.2	165.2	26	2	0
	AKMAP-010	69.7	164.3	28	6	2
	AKMAP-011	70.0	164.6	37	1	10
	AKMAP-012	68.5	167.2	34	6	1
	AKMAP-013	69.3	166.6	40	1	0
	AKMAP-014	69.5	165.1	35	1	1
	AKMAP-015	69.2	166.7	42	2	7
	AKMAP-016	68.7	167.8	49	7	1
	AKMAP-017	69.2	165.7	30	0	6
	AKMAP-018	69.8	163.9	38	11	0
	AKMAP-019	69.5	166.6	44	2	10
	AKMAP-021	69.1	166.3	30	5	2
	AKMAP-022	69.4	166.9	44	8	4
	AKMAP-023	69.0	165.8	22	0	2
	AKMAP-024	68.8	167.1	45	5	2
	AKMAP-025	69.1	164.9	20	0	1
	AKMAP-026	68.8	166.7	44	0	3
	AKMAP-027	69.5	164.5	30	29	7
	AKMAP-029	69.4	164.1	25	0	8
	AKMAP-030	68.4	166.8	25	4	0
	AKMAP-105	69.6	165.5	38	0	7
AKMAP11	AKMAP-032	70.7	160.4	26	13	1
	AKMAP-033	70.8	160.7	52	10	13
	AKMAP-034	70.4	163.1	34	4	10
	AKMAP-035	71.2	158.0	53	10	7
	AKMAP-036	70.7	162.0	42	11	3
	AKMAP-037	70.7	161.1	44	0	2
	AKMAP-038	70.2	163.2	28	7	11
	AKMAP-040	70.6	162.1	39	1	5
	AKMAP-041	70.3	163.7	32	1	2
	AKMAP-042	70.5	162.7	37	4	5
	AKMAP-043	71.2	160.2	53	4	0
	AKMAP-044	71.1	161.0	57	3	0
	AKMAP-045	70.1	163.4	30	3	0
	AKMAP-046	70.5	161.2	26	0	1
	AKMAP-047	71.0	158.1	27	1	1
	AKMAP-048	70.6	160.7	32	9	5
	AKMAP-049	71.0	160.6	53	2	0
	AKMAP-050	70.2	163.7	34	9	1
	AKMAP-051	70.8	160.3	52	0	1
	AKMAP-052	70.2	162.6	17	2	7
	AKMAP-053	71.0	158.8	26	32	20
	AKMAP-054	70.4	162.6	28	0	3
	AKMAP-055	70.7	161.9	39	2	1
	AKMAP-056	70.0	163.0	20	0	7
	AKMAP-058	70.5	161.7	24	1	2
	AKMAP-059	70.9	160.9	53	3	10
	AKMAP-060	70.5	160.9	22	1	3

Supplemental-2 Count of Arctic staghorn sculpin and shorthorn sculpin stomachs used in diet analyses, per station, from the Arctic Eis 2012 cruise. Accompanying spatial and depth information for each station is included here.

Cruise	Station	Latitude (deg)	Longitude (deg)	Station depth (m)	Arctic staghorn sculpin	Shorthorn sculpin
Arctic Eis 12	CH30-F01	68.5	168.5	51	2	4
	CH30-F02	68.5	167.1	34	0	4
	CH30-G01	69.0	168.5	52	2	6
	CH30-G03	69.0	165.7	20	1	3
	CH30-G04	69.0	164.3	30	2	6
	CH30-H01	69.5	168.5	51	1	5
	CH30-H02	69.5	167.1	44	2	12
	CH30-H03	69.5	165.7	35	9	14
	CH30-H04	69.5	164.2	40	2	4
	CH30-I01	70.0	168.5	43	0	8
	CH30-I02	70.0	167.0	45	1	5
	CH30-I03	70.0	165.6	38	0	6
	CH30-I04	70.0	164.1	28	2	4
	CH30-J01	70.5	168.5	39	4	1
	CH30-J03	70.5	165.5	40	1	0
	CH30-J04	70.5	164.0	42	3	4
	CH30-J05	70.5	162.5	32	2	5
	CH30-J06	70.5	161.0	21	1	10
	CH30-L03	71.5	165.4	42	1	0
	CH30-L04	71.5	163.8	44	4	0
	CH30-L05	71.5	162.2	42	2	0
	CH30-L06	71.5	160.6	46	1	0
	CH30-M02	72.0	166.9	47	1	0
	CH30-M05	72.0	162.0	25	2	0
	CH30-M06	72.0	160.4	35	4	0
	CH30-O02	73.0	165.8	58	1	0

Supplemental-3 Count of Arctic staghorn sculpin and shorthorn sculpin stomachs used in diet analyses, per station, from the Beaufish 2011 cruise. Accompanying spatial and depth information for each station is included here.

Cruise	Station	Latitude (deg)	Longitude (deg)	Station depth (m)	Arctic staghorn sculpin	Shorthorn sculpin
Beaufish11	CB01	70.5	147.3	23	4	0
	CB02	70.6	147.7	28	2	0
	CB03	70.6	148.2	23	1	3
	CB04	70.6	148.7	13	2	0
	CB05	70.7	149.2	19	1	0
	CB06	70.7	149.7	19	11	0
	CB07	70.7	150.1	19	3	0
	CB08	70.7	150.5	19	4	2
	CB09	70.8	151.1	18	0	1
	CB11	70.8	147.1	48	3	0
	CB12	70.8	147.5	41	11	0
	CB13	70.8	148.1	43	1	0
	CB16	71.0	149.5	33	0	2
	CB17	71.0	150.0	30	0	3
	CB20	71.1	151.5	20	12	2
	CB26	71.2	149.4	183	1	0
	CB31	70.9	151.8	17	0	1
	CB32	70.8	151.7	16	3	4
	CB33	70.7	150.7	16	10	8
	EB02	70.9	146.7	64	2	0
	EB04	70.4	146.4	35	1	0
	EB06	70.7	146.4	35	2	0
	EB10	70.6	145.2	41	2	0
	EB14	70.5	145.8	39	3	0
	EB16	70.7	145.8	56	2	0
	EB19	70.3	145.4	33	2	0
	EB21	70.6	145.4	52	4	0
	EB23	70.8	145.5	127	1	0
	EB29	70.7	145.1	58	1	0
	WB07	71.7	152.9	183	1	0
	WB10	71.7	153.9	53	5	0
	WB12	71.5	154.0	52	11	5
	WB13	71.4	154.0	43	12	10
	WB14	71.2	153.1	41	2	0
	WB15	71.4	153.0	79	16	0
	WB17	71.2	152.2	24	9	9
	WB18	71.2	152.3	51	1	8
	WB19	71.3	151.9	90	1	1
	WB21	71.6	155.0	48	32	14
	WB22	71.7	154.5	51	11	2
	WB23	71.5	152.8	60	1	0
	WB24	71.6	153.5	53	1	2
	WB25	71.2	154.0	23	2	12
	WB26	71.6	153.8	49	2	1
	WB29	71.5	155.0	15	0	1
	WB30	71.2	155.1	13	16	5
	WB34	71.1	153.2	25	1	6
	WB35	71.1	154.0	18	10	0

Supplemental-4 All prey taxa identified in Arctic staghorn sculpin and Shorthorn sculpin diets throughout the Chukchi and Beaufort Sea study regions. An "x" indicates presence in a species' diet.

	Arctic staghorn sculpin			**Shorthorn sculpin**		
Prey taxonomy list	**S Chukchi**	**N Chukchi**	**W Beaufort**	**S Chukchi**	**N Chukchi**	**W Beaufort**
Benthic amphipods	**x**	**x**	**x**	**x**	**x**	**x**
Ampeliscidae	x	x	x	x	x	
Ampelisca spp.	x			x	x	
Ampelisca eschrichti		x				
Ampelisca macrocephala	x	x			x	
Byblis spp.		x				
Byblis frigidus		x				
Haploops spp.			x			
Ampithoidae		x		x		
Ampithoe spp.		x		x		
Atylidae		x			x	
Atylus collingi		x			x	
Corophiidae	x	x	x	x	x	
Corophium spp.	x					
Pontoporeia spp.		x				
Protomedeia spp.	x	x	x	x	x	
Epimeriidae					x	
Paramphithoe spp.					x	
Eusiridae		x		x	x	
Rhachotropis spp.		x		x	x	
Isaeidae			x			x
Ischyroceridae	x	x	x	x	x	
Ericthonius spp.	x	x		x	x	
Ischyrocerus spp.		x	x	x	x	
Lysianassidae	x	x			x	
Orchomene spp.	x	x			x	
Maeridae		x		x	x	
Maera spp.		x		x	x	
Melitidae	x	x	x	x	x	x
Melita spp.	x	x	x	x	x	x
Oedicerotidae	x	x	x	x	x	x
Acanthostepheia spp.		x	x	x		x
Acanthostepheia behringiensis		x				
Acanthostepheia malmgreni		x				
Aceroides spp.	x	x	x	x	x	
Monoculoides spp.	x		x		x	x
Oediceros spp.	x			x		
Paroediceros spp.		x	x			x
Westwoodilla spp.				x		
Photidae	x	x			x	
Photis spp.	x	x			x	
Phoxocephalidae	x	x			x	
Grandifoxus spp.		x			x	
Harpina spp.	x	x				
Paraphoxus spp.		x			x	
Pleustidae					x	
Pleustes spp.					x	
Pontogeneiidae		x	x			
Pontogeneia spp.		x	x			
Stenothoidae	x			x		
Metopa spp.	x			x		
Synopiidae		x			x	
Syrrhoe spp.		x			x	
Uristidae	x	x	x	x	x	
Anonyx spp.	x	x	x	x	x	
Onisimus spp.	x					
Caprellid amphipod	x	x		x	x	

Supplemental-4 continued Prey consumed by Arctic staghorn sculpin and Shorthorn sculpin.

	Arctic staghorn sculpin			Shorthorn sculpin		
Prey taxonomy list	**S Chukchi**	**N Chukchi**	**W Beaufort**	**S Chukchi**	**N Chukchi**	**W Beaufort**
Calanoid copepods	**x**		**x**	**x**	**x**	**x**
Centropagidae	x					
Centropages abdominalis	x					
Metridinidae	x					
Metridia longa	x					
Euchaetidae						x
Euchaeta spp.						x
Calanidae	x	x		x	x	x
Calanus glacialis	x	x		x	x	x
Calanus hyperboreus			x			x
Neocalanus spp.					x	
Clausocalanidae	x					
Pseudocalanus spp.	x					
Crabs	**x**	**x**	**x**	**x**	**x**	**x**
Decapoda (crab) zoea			x	x	x	x
Decapoda (crab) meg.		x		x	x	x
Cheiragonidae	x	x		x	x	
Telmessus cheiragonus meg.	x			x		
Telmessus cheiragonus juv.	x	x		x	x	
Oregoniidae		x		x	x	x
Chionoecetes opilio zoea				x	x	x
Chionoecetes opilio meg.				x	x	
Chionoecetes opilio juv.				x	x	x
Hyas coarctatus meg.		x		x	x	
Hyas coarctatus juv.		x		x	x	
Lithodidae				x		
Paralithodes spp.				x		
Paguridae	x	x	x	x	x	x
Paguridae zoea			x	x	x	x
Paguridae juvenile	x	x	x	x	x	x
Pagurus spp. juvenile		x				
Labidochirus splendescens					x	
Cumaceans	**x**	**x**	**x**	**x**	**x**	**x**
Diastylidae	x	x	x	x	x	
Diastylis spp.	x	x	x	x	x	
Diastylopsis spp.			x			
Leptostylis spp.			x			
Leuconidae	x		x	x		
Eudorella spp.	x			x		
Eudorellopsis spp.	x					
Leucon nasica			x			
Nannastacidae	x		x	x	x	
Cumella spp.	x		x	x	x	
Euphausiids			**x**	**x**	**x**	**x**
Euphausiidae			x	x	x	x
Thysanoessa raschii			x	x	x	x
Fish prey	**x**	**x**		**x**	**x**	
Agonidae				x		
Aspidophoroides olrikii				x		
Ammodytidae					x	
Ammodytes hexapterus					x	

Supplemental-4 continued Prey consumed by Arctic staghorn sculpin and Shorthorn sculpin.

	Arctic staghorn sculpin			**Shorthorn sculpin**		
Prey taxonomy list	**S Chukchi**	**N Chukchi**	**W Beaufort**	**S Chukchi**	**N Chukchi**	**W Beaufort**
Fish prey	**x**	**x**		**x**	**x**	
Cottidae	x			x	x	
Gymnocanthus tricuspis				x	x	
Gadidae					x	
Boreogadus saida					x	
Liparidae					x	
Liparis spp.					x	
Plueronectidae				x		
Stichaeidae	x			x	x	
Lumpenus fabricii				x		
Zoarcidae					x	
Gymnelus hemifasciatus					x	
Hyperiid amphipods	**x**		**x**	**x**	**x**	**x**
Hyperia spp.			x	x		x
Hyperia galba			x			x
Hyperoche spp.						x
Themisto spp.	x		x	x	x	x
Themisto abyssorum			x			x
Themisto libellula	x		x	x	x	x
Isopods		**x**	**x**	**x**	**x**	**x**
Chaetiliidae			x			
Saduria spp.			x			
Idoteidae		x	x	x	x	
Synidotea spp.		x	x	x	x	
Mollusks	**x**	**x**	**x**	**x**	**x**	**x**
Bivalve	x	x	x	x	x	
Bivalve siphons	x					x
Gastropoda	x		x	x		
Carditidae		x				
Naticidae	x			x		
Lunatia pallida	x					
Nuculana spp.				x		
Pteropoda				x		
Trochidae				x		
Yoldiidae			x			
Polychaetes	**x**	**x**	**x**	**x**	**x**	**x**
Ampharetidae		x				
Flabelligeridae			x			
Glyceridae			x	x		
Glycera spp.			x			
Goniadidae	x					
Glycinde spp.	x					
Lumbrineridae	x	x				
Lumbrineris spp.	x					
Maldanidae		x				
Nephtyidae	x	x				
Nephtys spp.	x	x				
Nuculidae	x					
Ennucula tenuis	x					
Oweniidae	x					
Phyllodocidae		x	x			
Phyllodoce groenlandica			x			
Polynoidae	x	x	x	x	x	x
Arcteobia anticostiensis		x		x		
Gattyana spp.	x	x				
Harmothoe spp.		x		x	x	

Supplemental-4 continued Prey consumed by Arctic staghorn sculpin and Shorthorn sculpin.

	Arctic staghorn sculpin			**Shorthorn sculpin**		
Prey taxonomy list	**S Chukchi**	**N Chukchi**	**W Beaufort**	**S Chukchi**	**N Chukchi**	**W Beaufort**
Polychaetes	**x**	**x**	**x**	**x**	**x**	**x**
Hesperone adventor						**x**
Terebellidae			x			
Shrimps	**x**	**x**	**x**	**x**	**x**	**x**
Crangonidae	x	x	x	x	x	x
Argis spp.	x	x	x	x	x	
Crangon spp.					x	
Sclerocrangon boreas				x		
Hippolytidae				x	x	
Eualus spp.				x	x	
Pandalidae	x			x	x	
Pandalopsis spp.	x					
Pandalus spp.	x			x		
Other prey	**x**	**x**	**x**	**x**	**x**	**x**
Amphipoda frags	x	x	x	x	x	x
Bryozoa		x				
Copepod nauplii	x	x				
Cyclopoid copepod	x					
Cyprid	x	x	x	x		x
Gastropod egg casing	x			x		
Harpacticoid copepod	x	x	x	x		x
Hydrozoa	x				x	
Ophiurodea		x			x	
Ostracoda	x	x	x	x	x	x
Tanaidacea		x		x		
Prey total	**89**	**88**	**69**	**101**	**98**	**46**

Supplemental-5 Results from NPMANOVA model 1, which examined the differences between Arctic staghorn sculpin and shorthorn sculpin diet compositions within the south Chukchi (SCS) and north Chukchi (NCS) regions, over five size classes (≤50 mm, 51–75 mm, 76–100 mm, 101–125 mm, ≥126 mm). The main effects of species, regions, and size classes were included along with their interactions. The two-way interaction between regions and size classes is not listed here because it did not take into account the main effect of species. Multiple comparisons within the significant three-way interaction of species, regions, and size classes were conducted using a separate NPMANOVA model.

Model 1: SCS and NCS (All size classes) Factor(s)	df	SS	MS	Pseudo-F (PERMANOVA) t-value (Multiple comp)	p-value (999 perm)	Partial R^2
Species	1	86328.0	86328.0	35.105	**0.001**	0.052
Regions	1	67210.0	67210.0	27.331	**0.001**	0.040
Size classes	4	78805.0	19701.0	8.012	**0.001**	0.047
Species*Regions	1	5723.1	5723.1	2.327	**0.042**	0.003
Species*Size classes	4	43506.0	10877.0	4.423	**0.001**	0.026
Species*Regions*Size classes	4	23806.0	5951.5	2.420	**0.003**	0.014
Residual	507	1246800.0	2459.1			
Total	522	1661700.0	Tot. R^2=0.250			
Species*Regions*Size classes (Multiple comparisons)						
Arctic staghorn – shorthorn within SCS						
≤50 mm				5.736	**0.001**	–
51–75 mm				1.706	**0.020**	–
76–100 mm				1.730	**0.031**	–
101–125 mm				1.764	**0.021**	–
≥126 mm				2.552	**0.001**	–
Arctic staghorn – shorthorn within NCS						
≤50 mm				1.699	**0.049**	–
51–75 mm				3.395	**0.001**	–
76–100 mm				1.695	**0.036**	–
101-125 mm				1.831	**0.017**	–
≥126 mm				2.560	**0.001**	–

Supplemental-6 Results from NPMANOVA model 2, which examined the differences between Arctic staghorn sculpin and shorthorn sculpin diet compositions within the south Chukchi (SCS), north Chukchi (NCS), and west Beaufort (WBS) regions, over the two smallest size classes (≤50 mm and 51–75 mm). The main effects of species, regions, and size classes were included along with their interactions. The two-way interaction between regions and size classes is not listed here because it did not account for the main effect of species. Multiple comparisons within the significant three-way interaction of species, regions, and size classes were conducted using a separate NPMANOVA model.

Model 2: SCS, NCS, and BS (Small size classes only) Factor(s)	df	SS	MS	Pseudo-F (PERMANOVA); t values (Multiple comparisons)	p-value (999 perm)	Partial R^2
Both seas (small sizes only)						
Species	1	153570.0	153570.0	60.697	**0.001**	0.084
Regions	2	154830.0	77413.0	30.596	**0.001**	0.085
Size classes	1	19821.0	19821.0	7.834	**0.001**	0.011
Species*Regions	2	38467.0	19233.0	7.602	**0.001**	0.021
Species*Size classes	1	18982.0	18982.0	7.502	**0.001**	0.010
Species*Regions*Size classes	2	10870.0	5435.1	2.148	**0.031**	0.006
Residual		1358700.0	2530.1			
Total		1817600.0	Tot. R^2=0.252			
Species*Regions*Size classes (Multiple comparisons)						
Arctic staghorn – shorthorn within SCS						
≤50 mm				5.736	**0.010**	
51–75 mm				1.706	**0.034**	
Arctic staghorn – shorthorn within NCS						
≤50 mm				1.699	**0.049**	
51–75 mm				3.395	**0.001**	
Arctic staghorn – shorthorn within BS						
≤50 mm				5.319	**0.001**	
51–75 mm				5.149	**0.001**	

Appendix K.

Growth dynamics of Saffron cod (*Eleginus gracilis*) and Arctic cod (*Boreogadus saida*) in the Northern Bering and Chukchi Seas

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February 5, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

List of Oral and Poster Presentations

Helser, T.E., Anderl, D. Kastelle, K. Growth dynamics of Saffron cod (*Eleginus gracilis*) and Arctic cod (*Boreogadus saida*) in the Northern Bering and Chukchi Seas. *In* Biophysical Processes at the Arctic–Sub-Arctic Interface. American Geophysical Union Ocean Science Meeting, New Orleans, LA, February 2016.

Proposed Objectives and Study Chronology

As an essential component of the overall Artic Eis research goals, we analyzed the growth dynamics of Arctic cod and saffron cod collected during the 2012 survey operations. Data and otoliths collected from 2013 surface trawls were not used in this study. Specifically our objectives were to 1) develop an age determination procedure for estimating the age of fish from otoliths, 2) characterize the growth dynamics both in terms of population age compositions and estimating growth curves, and 3) examine spatial variation in growth among regions of the Chukchi and Northern Bering Seas. The temporal objective of this study utilized otoliths (and length data) collected during previous 1976-1979 baseline NMFS surveys and were analyzed to provide a comparison of growth separated by 30 years. Further to address objective (1), the annual growth increment periodicity was evaluated for saffron cod using otolith stable oxygen isotope (^{18}O) signatures as a proxy for seasonal water temperature cycles (Helser et al., 2014).

Otoliths used in this study were in part extracted at sea on both the bottom trawl and surface trawl survey operations during the summer and early fall of 2012. Frozen Arctic and saffron cod were also shipped to AFSC in Seattle post surveys and were received between November 2012 and March 2013. Data were transmitted electronically, but not in all cases for the frozen specimens which were included in written data sheets. In some cases in which blocks of frozen specimens were tagged by station individual lengths records were lost. All data, once ageing estimation was complete, were entered into the AGEDATA data base at AFSC.

Age determination criteria for Arctic and saffron cod were developed during the winter of 2013. Micro-milling otoliths for saffron cod followed by mass spectrometry for stable oxygen isotopes to aid in verifying the age determination criteria was performed during the Spring of 2013. Once age readers were full trained in interpreting growth patterns and acceptable precision was achieved, age estimation of Artic and saffron cod otoliths collected from the Arctic Eis was conducted over the course of the following year 2013-2014. During this time otoliths previously collected from 1976-1979 AFSC baseline surveys in Norton Sound and Chukchi sea were also prepared and estimated for age. Modeling the spatio-temporal growth characteristics of Artic and saffron cod was completed during the summer of 2014. A manuscript entitled "Growth dynamics of Saffron cod (*Eleginus gracilis*) and Arctic cod (*Boreogadus saida*) in the Northern Bering and Chukchi Seas" was submitted to Deep Sea Research II during the spring of 2015 and accepted for publication in December 2015. This work was also accepted as a poster presentation at American Geophysical Union Ocean Science Meeting, New Orleans, LA, February 2016.

1. Abstract

Saffron cod (*Eleginus gracilis*) and Arctic cod (*Boreogadus saida*) are two circumpolar gadids that serve as critically important species responsible for energy transfer in Arctic food webs of the northern Bering and Chukchi Seas. To understand the potential effects of sea ice loss and warming temperatures on these species' basic life history, information such as growth is needed. Yet to date, limited effort has been dedicated to the study of their growth dynamics. Based on a large sample of otoliths collected in the first comprehensive ecosystem integrated survey in the northern Bering and Chukchi Seas, procedures were developed to reliably estimate age from otolith growth zones and were used to study the growth dynamics of saffron and Arctic cod. Annual growth zone assignment was validated using oxygen isotope signatures in otoliths and otolith morphology analyzed and compared between species. Saffron cod attained larger asymptotic sizes ($L_\infty = 363$ mm) and achieved their maximum size at a faster rate ($K = 0.378$) than Arctic cod ($L_\infty = 209$ mm; $K = 0.312$). For both species, regional differences in growth were found ($p < 0.01$). Saffron cod grew to a significantly larger size at age in the northern Bering Sea when compared to the Chukchi Sea, particularly at younger ages. Arctic cod grew to smaller asymptotic size but at faster rates in the more northerly central ($L_\infty = 197$ mm; $K = 0.324$) and southern Chukchi Sea ($L_\infty = 221$ mm; $K = 0.297$) when compared to the northern Bering Sea ($L_\infty = 266$ mm; $K = 0.171$), suggesting a possible cline in growth rates with more northerly latitudes. Comparison of growth to two periods separated by 30 years indicate that both species exhibited a decline in maximum size accompanied by higher instantaneous growth rates in more recent years.

2. Introduction

Arctic (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*), two federally managed species in the U.S. zones of the northern Bering, Chukchi, and Beaufort Seas, are considered to be the most abundant fish species in the sub-polar and polar regions (NPFMC, 2009). Both species are essential components of polar food webs and act to transfer energy from plankton to upper trophic levels (Craig et al., 1982; Whitehouse, 2011). While the distribution of these species overlap to some extent, saffron cod are more demersal with a more southerly, nearshore distribution, whereas Arctic cod are more pelagic and are often associated with offshore sea ice with a more northerly residence (Barber et al., 2008). Saffron cod are reported to be a resident species in nearshore areas of the Chukchi and are linked to low salinity conditions (Wong et al., 2013). Nearshore populations of saffron cod have been found as far south as the Gulf of Alaska (Laurel et al., 2007). Arctic cod, in contrast, are principally centered north of the Bering Strait but reportedly extend farther south into the northeast and southeast Bering Sea during years of extended cool pool from more extensive ice (Lauth, 2011). While the exact factors that are responsible for partitioning these species' niches is uncertain, temperature and ice cover probably play a major role. Laurel et al. (2015) demonstrated that juvenile Arctic cod show a cold-water, stenothermic growth response compared to the warmer water, eurythermic growth response of saffron cod under laboratory conditions. Hence, under changing environmental conditions in the Arctic, the physiological response of these species to environmental variability is likely to exert some influence on their distribution, competition for food resource, growth, and survival.

Our ability to manage the living marine resources will be predicated on understanding potential biological responses to environmental variability and in predicting the effects of climate change on individual species, ecosystem processes, and community structure. At the individual species level, growth is a fundamental life history process that is often linked to environmental conditions such as temperature (Jobling, 1981). Understanding population dynamics, bioenergetics, and energy flow through the Chukchi and northern Bering Sea ecosystems will require baseline estimates of growth and its intrinsic spatial variability, which for both species is not well documented in the scientific literature. For instance, phenotypic plasticity in growth of North Atlantic cod (*Gadus morhua*) has been reported on relatively small spatial scales (Olsen et al., 2008), with high-latitude populations growing faster at colder temperatures than populations of the same species at lower latitudes (Hutchings et al., 2007). Furthermore, evidence is emerging that the oceanography of the northern Bering and Chukchi Sea is quite complex with high inter-annual and spatial variability in processes such as temperature, stratification, and ice cover (Danielson et al. this issue). These processes are likely important for structuring different growth phenotypes through mediating metabolism (Purchase and Brown, 2001). Extreme environmental variability in the Arctic may play a similar role in structuring phenotypic growth variability in Arctic cod, in particular, yet limited data have been collected in a comprehensive spatiotemporal way in order to evaluate the extent of growth variation.

The National Marine Fisheries Service, the agency responsible for managing U.S. marine living resources in the Arctic (NPFMC, 2009), has historically conducted periodic but spatially limited assessments of benthic fishes using bottom trawls (Sample and Wolotira, 1985). However, not until 2012 was a fully integrated ecosystem assessment incorporating oceanographic and biological sampling across the entire trophic structure conducted. The 2012 Arctic Ecosystem Integrated Survey (Arctic Eis) was conducted in partnership between the University of Alaska, Fairbanks (UAF), National Marine Fisheries Service (NMFS) and the Bureau of Ocean and Energy Management (BOEM). Biological data including length, weight, and age structures (otoliths) for Arctic cod and saffron cod were collected across a systematic sampling design over an extensive area from the northern Bering Sea, Bering Strait, and Chukchi Sea. As an essential component of the overall Artic Eis research goals, we analyzed the growth dynamics of Arctic cod and saffron cod collected during the 2012 survey operations. Specifically our objectives were to 1) develop an age determination procedure for estimating the age of fish from otoliths, 2) characterize the growth dynamics both in terms of population age compositions and estimating growth curves, and 3) examine spatial variation in growth among regions of the Chukchi and Northern Bering Seas. While the biological data and otoliths collected during the 2012 Eis survey were the focus of this study, otoliths (and length data) collected during previous 1976-1979 baseline NMFS surveys were analyzed to provide a comparison of growth separated by 30 years. Different methods of sample preparation were explored to establish the best age determination procedures, including quality control practices (Kimura and Anderl, 2005) to estimate statistical measures of precision. Furthermore, the annual growth increment periodicity was evaluated for saffron cod using otolith stable oxygen isotope (^{18}O) signatures as a proxy for seasonal water temperature cycles (Helser et al., 2014). Growth curves using the von Bertalanffy (von Bertalanffy, 1938) function were fit to length-at-age data for both species and by regions to explore spatial differences in growth. Because of the paucity of literature on saffron and Arctic cod otolith ageing, otolith growth was estimated using otolith morphometric measurements, including otolith weights, to characterize relative differences in otolith morphometry and growth between the species.

3. Methods

3.1 Sample collection

Otoliths collected for this analysis were sampled as part of the Arctic Eis conducted during the summer and fall of 2012 in the northern Bering and Chukchi Seas. This was the first comprehensive marine resource survey focused on a fully integrated ecosystem data collection program including oceanographic and biological data. Here we provide a brief description of the execution of field sampling as it relates to growth dynamics of Arctic and saffron cod, but greater details can be found in Goddard et al. (2014) and Murphy et al. (2003). During the 2012 Artic Eis survey, biological data for Arctic and saffron cod were collected at sampling stations occupied by two research-purposed industry-chartered vessels spanning 17.5^{o} of latitude (63^{o}N – 72.5^{o}N latitude). Each vessel followed roughly the same standard grid survey sampling framework with sampling stations every 30 miles along E-W transects. The 180 foot FV *Bristol Explorer,* which used surface trawls to target the pelagic fish community, sampled 61 stations over the entire grid from August 1 to September 31. Near-surface hauls were made using a 400/601 Cantrawl[5] with a typical trawl 198 m long with a horizontal and vertical spread of 50 m and 25 m, respectively. Lengths (mm) and weights (g) of Arctic cod and saffron cod were recorded and otoliths extracted at sea or whole fish frozen for later processing in the laboratory. Sex of these fish was not recorded. The 160 foot FV *Alaska Knight* employed 83-112 Eastern bottom trawl to sample the benthic fish community only in the Chukchi Sea, from just north of the Bering Strait (63.1^{o} N latitude) to Barrow Canyon (72^{o}N latitude) covering 71 stations from August 9 to September 24. Hauls were conducted over bottom for 15 minutes at a speed of approximately 3 knots maintained at a constant heading. When possible the tow was conducted

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[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

near the center of a 55.6 × 55.6 km grid cell. As in the surface trawls, catches were sorted by species and subsampled to estimate the total catch in weight and numbers. For both the surface and bottom trawl fish a two-stage random sampling strategy was used to obtain biological data. In the first stage, a simple random sample of length (fork, mm) was taken from the subsampled catch in number. A subsample of otoliths for ageing were then taken from the second stage with a target number or approximately 5 otoliths per 1 cm length class. Fork length was measured to the nearest millimeter and weight to the nearest gram. Sex for both Arctic cod and saffron cod were identified from bottom trawl catches.

Age data for the 1976 and 1979 NMFS baseline survey in the Chukchi and northern Bering Seas were collected during bottom trawling operations on the NOAA ship *Miller Freeman*. Stations during the 1976 survey were sampled in the southeastern Chukchi Sea from the Bering Strait north to Point Hope (68.3°N latitude) and in the northern Bering Sea and Norton Sound from St. Matthews Island (63.1°N latitude) north to the Bering Strait. The 1979 NMFS survey did not conduct trawling operations in the Chukchi Sea, and for the purposes of a retrospective comparison in this study stations sampled in the Northern Bering Sea south of the Bering Strait (including Norton Sound) were combined with the 1976 data and analyzed together. Both the 1976 and 1979 NMFS surveys used 30-minute bottom trawls with a similar 83-112 Eastern net construction as the 2012 Eis bottom trawl survey. A total of 249 and 186 standard bottom trawl stations (in the regular grid) were sampled during the 1976 and 1979 NMFS surveys, respectively. More detail of these baseline surveys can be found in Wolotira et al. (1977) and Sample and Wolotira (1985).

3.2 Age determination

A total of 2,081 Arctic cod and saffron cod otoliths were examined and age estimated from samples collected in the 2012 northern Bering and Chukchi Sea surveys (Table 1), with an additional 1,107 otoliths from the 1976-79 baseline survey. Arctic cod were more commonly collected than saffron cod in the 2012 Arctic Eis survey with 1,460 and 621 otoliths read, respectively. In the laboratory, saffron cod otoliths were in general large enough to use thin section preparation methods. Saffron cod otoliths were embedded in polyester resin using a silicone mold and thin sectioned through the core oriented in the transverse plane to approximately 0.5 mm on an Isomet 5000 high speed saw. Thin sections were then secured to glass slides using Loctite 349 glue and polished to 1200 grit on a Buehler grinding wheel to remove saw marks and enhance the clarity of otolith growth zones. Slides with otoliths were examined with a Leica dissecting stereomicroscope under reflected light to estimate age. Age was determined by counting the number of pairs of translucent (winter growth) and opaque (summer growth) zones in the transverse plane. Because of the larger number, and relatively small size of Arctic cod otoliths, thin sectioning methods would be inefficient and possibly destructive so otoliths were processed using the break and burn (B&B) method (Matta and Kimura, 2012). For this method, whole otoliths were affixed to a clay-mounted chuck in the sagittal plane and cut through the core (transverse cut) using a Buehler saw. One half of the otolith was burned briefly over an ethanol burner or roasted in a toaster oven to enhance the banding pattern. The prepared half-otolith was then examined (with the transverse plane exposed and immersed within water or oil) under a dissecting microscope with reflected light and again age estimated by counting band pairs as before. Greater detail of thin sectioning and B&B ageing methods can be found in Matta and Kimura (2012).

Otolith growth, as inferred through morphometric analysis, was measured from the northern Bering and Chukchi Sea specimens. Whole otolith morphometric measurements, including otolith weights, were obtained to characterize relative differences in otolith morphometry and growth between the species. In the laboratory, individual whole otoliths were cleaned in ethanol followed by ultrasonication, and then weighed on a microbalance to the nearest microgram. Morphometric measurements including otolith area, perimeter, major axis, minor axis, length, and width were measured using ImagePro 9 and a high-resolution digital camera on a dissecting microscope. Otolith weight and area were regressed on body size to characterize otolith growth between the species. Body size and weight (based exclusively on samples taken for ageing) were also used to examine allometric growth following the equation: $W = \alpha L^{\beta}$. Isometric growth (body shape does not change with size) is expected if the parameter β is approximately the cubed power of length (Carlander, 1969; Froese, 2006).

To evaluate quality control roughly 50% of a given sample of otoliths (generally around every batch of 100-120 otoliths) was aged by two independent age readers. Age readers applied the same age determination protocol (processing and reading method) and independently assigned an age based on visual examination of the otolith. To evaluate the quality of ageing, and hence precision, we use a regression analysis, $y = \alpha + \beta x$ where *y* and *x* represent ages of readers 1 and 2, respectively, and tested for $\hat{\alpha} = 0.0$ and $\hat{\beta} = 1.0$ using the functional regression model (Kendall and Stuart, 1973). Percentage agreement, which expresses the percentage of structures (*n*) that are aged the same on two different occasions, was also used to evaluate precision and repeatability, while Bowker's test of symmetry was used to test for between reader relative bias. Greater detail of measures of precision can be found in Kimura and Anderl (2005).

3.3 Oxygen isotope analysis

To assist in the verification of age determination criteria, particularly for the first few annual growth zones, we analyzed three saffron cod otoliths for oxygen isotope signatures to visually identify winter and summer growth zones in the otolith. Helser et al. (2014) applied this technique to Pacific cod by comparing ages determined from visual growth zone counts to ages determined from the seasonal cyclic nature (counts of peaks) of δ^{18}O in otoliths. Saffron cod thin-sectioned otoliths were micro-milled using a Carpenter Systems CM-2 micro-milling instrument. This instrument consisted of a stereo microscope, high resolution digital camera, computer controlled X-Y-Z stage, and a micro drill with a 0.3 mm milling bit. For each thin section, milling software was used to create a sequence of parallel sampling paths from the otolith's core (birth) to the outer edge (capture). The paths were about 30 to 60 µm apart and up to about 1.45 mm in length and followed (exactly paralleling) the laminae of growth zones, reproducing the exact curvature of the otolith. The sequence of samples from core to otolith margin weighed on average approximately 30 to 40 µg with sample resolution approaching about 6-8 samples within the first several annual growth zones, after which the sampling resolution deceased. After milling each sampling path, the aragonite powder was collected, weighed on a microbalance to the nearest microgram, transferred to 3 mm stainless steel cups, and analyzed on a dual-inlet mass spectrometer using a Kiel III carbonate preparation system connected to a MAT 252 mass spectrometer at the Stable Isotope Laboratory at Oregon State University. Results were corrected using a calibrated standard (known ^{13}C and ^{18}O isotopic) and are reported in standard delta notation (δ^{13}C and δ^{18}O) relative to Vienna Pee Dee Belemnite (VPDB). The international standard NBS-19, which was analyzed in each run, yielded isotope values ($\delta^{13}\text{C} = +1.94 \pm 0.02$‰ VPDB and $\delta^{18}\text{O} = -2.21 \pm 0.06$‰ VPDB; n=141) very similar to the expected values of +1.95 and -2.20‰ (δ^{13}C and δ^{18}O, respectively). To confirm the interpretation of otolith annuli the δ^{18}O measurements were directly mapped onto high-resolution digital images of the otolith thin sections which permitted comparison of each identified growth zone interpreted by an age reader to the seasonal δ^{18}O signature. Since δ^{18}O is inversely related to water temperature (Hoie et al., 2004), growth annuli (translucent zones) that corresponded to peaks in the δ^{18}O signature were considered true annual winter growth marks in otolith. Arctic cod otoliths are considerably smaller and were not microsampled for oxygen isotope analysis.

3.4 Statistical analysis

With the limited data recorded for the sex of the animal (bottom trawl survey only) sexual dimorphic growth was explored, however, age data were generally pooled over sex and statistical analysis focused on regional and temporal comparisons. For regional estimation and comparison of Arctic cod and saffron cod, growth data were aggregated in three principal latitudinal ranges: Northern Bering Sea (including the Norton Sound; 63.1°N-65.5°N), Southern Chukchi Sea (65.5°N-68.3°N), and Central Chukchi Sea (68.3°N-72.0°N) (Table 1). The regions correspond to major morphological and oceanographically distinct features partitioned by the Bering Strait in the south and Point Hope in the north (Danielson et al., 2014). Age data were insufficient to develop region specific age compositions so these were generated for each species only from the 2012 Chukchi Sea data. Age compositions were generated using age-length keys which take advantage of both the complete sample of length data as well as the age-length subsample that was aged (Quinn and Deriso, 1999). The unbiased estimator of the age composition, θ_a, from a two-stage random sampling strategy is

$$\hat{\theta}_a = \sum_l \hat{\alpha}_l \hat{\theta}_{la} \equiv \sum_l \gamma_{la}\,, \qquad (1)$$

where $\gamma_{l\alpha}$ is the estimated proportion of fish in length interval *l* and age *a*, and α_l, is the proportion of fish in length interval *l*, and θ_{la}, is the proportion of fish in length interval *l* of age *a (Quinn II and Deriso 1999).* Its variance is provided by two-stage sampling theory and is expressed as:

$$SE^2\left(\hat{\theta}_a\right) = \sum_l \frac{\hat{\alpha}_l^2 \hat{\theta}_{la}\left(1-\hat{\theta}_{la}\right)}{A_l - 1} + \sum_l \frac{\hat{\alpha}_l\left(\hat{\theta}_{la}-\hat{\theta}_a\right)^2}{L} \equiv \sum_l SE^2(\gamma_{la})\,, \qquad (2)$$

where A_l is the number of ages in length interval *l*, and L is the number of lengths.
For growth, the von Bertalanffy growth function (1938), which has been widely used in fisheries

research, was used to estimate the functional relationship between length and age. A number of studies have provided biological interpretations of the parameters (von Bertalanffy, 1957; Pauly, 1981; Moreau, 1987). We assume that Arctic and saffron cod conform to von Bertalanffy growth dynamics. The appropriate statistical form of the nonlinear von Bertalanffy growth equation (von Bertalanffy, 1938) can written as

$$l_{ij} = L_\infty\left(1 - e^{-K(t_i - t_0)}\right) + e_{ij}\,, \qquad (3)$$

where l_{ij} is the fish length in millimeters of the *jth* individual at age t_i (i=1,..., m), L_∞ is the asymptotic maximum length, K is the instantaneous growth constant, t_0 is the age at which length would hypothetically be zero, e_{ij}'s are independent identically distributed additive normal random $N(0, \sigma^2)$ variates. The fitted von Bertalanffy equation can be represented as $l_{ij} = f(\hat{\boldsymbol{\theta}}, t_i) + e_{ij}$, where $\boldsymbol{\theta}$ is the 3×1 vector of parameter estimates for L_∞, K and t_0. The maximum likelihood estimate of $\boldsymbol{\theta}$ is the parameter vector which minimizes the sum of squared residuals

$$S(\theta) = \sum_{ij}^{n}\left[l_{ij} - f(\theta, t_i)\right]^2\,, \qquad (4)$$

where n is the sample size. Assuming that the e_{ij}'s are normally distributed then an estimate of the variance σ^2 for $\boldsymbol{\theta}$ (Rawlings, 1988) is, $s^2 = \frac{1}{n-p}S(\theta)$. Where age-length data were limiting (no observations of age 4+ for northern Bering Sea saffron cod in 2012 and no age-0 observations for Arctic cod from 1976-79) a von Bertalanffy growth parameter (i.e. L_∞) was estimated but shared between regions to obtained better estimates of the remaining parameters. In one case, the parameter t_0 was fixed at the average value in 2012 due to the selectivity of bottom trawls toward 1+ Arctic cod in the population (i.e. no age-0 fish were caught during 1976-1979).

Parameter estimates of the von Bertalanffy growth model were obtained using maximum likelihood (unweighted) from the Marquardt routine in the PROC NLIN procedure in SAS (Statistical Analysis Systems Institute, 1985). In the present study, we used approximate randomization tests (Fisher and Hall, 1990; Manley, 1991), applied to testing growth curve differences (Helser, 1996). Specifically, we were interested in testing for differences between von Bertalanffy growth curves among regions in the northern Bering and Chukchi Seas. A full treatment of the procedure is given in Helser (1996) including power of test simulations and will not be reiterated here, but instead will describe the test statistic and its application. The *F*-ratio statistic was employed in the randomization procedure to test for growth curve differences between a full (separate regions) and reduced model (regions combined), and is given as

$$F = \frac{(SSE_r - SSE_f)/q}{SSE_f/(n-p)} = \frac{(SSE_r - SSE_f)/q}{MSE_f}, \qquad (5)$$

where $SSE_r = \sum_{ij}\left[l_{ij} - f(\theta, t_i)\right]^2$ and $SSE_f = \sum_{ijp}\left[l_{ijp} - f(\varphi_p, t_i)\right]^2$ is the sum of squared error from the observed un-randomized and randomized data, respectively with parameter vectors **θ** and **φ** which minimized the sums of squared residuals from the von Bertalanffy curve fits to the entire data set (reduced model) and separately for two populations (full model). The right side of the equation is written in terms of the mean square error or σ_e^2 which is obtained by dividing by the sample size *n* and number of model parameters *p*. The difference in the number of parameters between the reduced and full model, *q* is the degrees of freedom typically used to find statistical significance. However, the randomization test will instead generate the empirical probability density function (pdf) of the test statistic (under the null hypothesis of no differences in growth curves between regions) for the situation where the length-age pairs have been assigned randomly to two regions. To carry out a single trial, all of the data from the two regions to be compared, say n_1 and n_2, are pooled and then assigned randomly (without replacement) to the two regions, keeping the number of observations per region and for age the same as in the original data. The sum of squared residuals from von Bertalanffy growth equation fits to the entire pooled data set and to the two groups separately is recorded, and the test statistic is computed as

$$F_R = \frac{(SSE_r - SSE_f{}^*)/q}{MSE_f{}^*}, \qquad (6)$$

where $SSE_f = \sum_{ijp}\left[l_{ijp}{}^* - f(\varphi_p{}^*, t_i)\right]^2$ from the randomized data, F_R is the difference in error sum of squares under the null hypothesis of no difference in growth between regions, 2, ***φ*** and *p* are define as above, and * indicates that the estimates are based on random assignment of observations to regions. After repeating this randomization procedure say 5,000 times, the magnitude of the observed test statistic, F_{obs}, was compared to the pdf of F_R. The null hypothesis and its alternative are: $H_o : \theta_{(p=1)} = \theta_{(p=2)}$ and $H_a : \theta_{(p=1)} \neq \theta_{(p=2)}$. H_o is rejected in favor of H_a at significance level α when $\left[F_{obs} > F_{R_\alpha}\right]$, where the critical value, $F_{R(\alpha)}$ is chosen so that $P\left[F_R \geq F_{R_\alpha}\right] \approx \alpha$ calculated under H_o. For all comparisons of growth in this study, we used an α=0.01 level to reject the null hypothesis, to control for the experiment-wise error rate.

4. Results

Saffron cod and Arctic cod otoliths have not previously been examined and studied extensively for age determination in the Chukchi and northern Bering Seas. The preparation methods developed here for these species were largely successful in revealing the otolith growth zones to aid in age estimation. The otolith from the preparation method applied to each species is shown in Figure 1 for selected otoliths; saffron cod (ages 1-8) and Arctic cod (age 1-5). Ages 8 and 5 were the maximum observed for saffron cod and Arctic cod, respectively, from the 2012 sampling efforts. The transverse section image in Figure 1 is superimposed on the whole otolith in the sagittal plane to provide perspective on relative size and shape between the two species. A very notable difference between them is that saffron cod otoliths exhibit a much greater degree of scalloping around the perimeter compared to Arctic cod otoliths. Both species exhibit the distinct annuli, most often interpreted as winter growth zones, the number of which increase with otolith size (and fish length) and were used by the age reader to assign an age. For saffron cod the sequence of contiguous concentric annuli is more distinct compared to Arctic cod possibly due to the fact that transverse thin sections enhance the alternating pattern of summer and winter growth zones. However, among the three different processing methods tested for Arctic cod, the B&B method provided as good or better precision than the thin section method. Precision as evaluated by between reader agreements (+/- 0 ages) was highest from the B&B method (70%) followed by the thin section (68%) and surface (50%) methods. Therefore the larger sample for Arctic cod was processed using the B&B method.

Growth relating body weight to body length (FL) was different between saffron cod and Arctic cod, but did not differ between different regions within species. The parametric relationship for saffron cod and Arctic cod over all regions was $W = 6.075E^{-6} \cdot L^{3.1}$ and $W = 1.30E^{-5} \cdot L^{2.9}$, respectively (Fig. 2). For both species, the estimated value of β is around 3.0 and suggests isometric growth (unchanging body shape over the life time of the fish), while the small value of α is typical of fusiform to eel-like fishes. For Arctic cod, body weight to body size did appear to diverge with lengths greater than 200 mm, however this could not be confirmed due to the paucity of Chukchi Sea observations in that size range. Saffron cod otoliths were considerably larger, had larger mass (measured as weight), and exhibited higher otolith accretion rates than Arctic cod otoliths as a function of body size (Fig. 2). For both species, otolith size in length (major axis) grew as a linear function of body size (fork length): saffron cod OL = 1.345 + 0.047 FL (r^2 = 0.97); Arctic cod OL = 0.279 + 0.039 FL (r^2 = 0.95). Otolith mass also grew as a power of body size in both species: OM = 2.0E-07 $FL^{2.467}$ (r^2 = 0.97); Arctic cod OM = 1.0E-07 $FL^{2.388}$ (r^2 = 0.95). This result suggests that otolith accretion rates leading to mass and size increase as a function of body size is substantially greater in saffron cod.

Efforts to establish an age determination criteria that produce consistent, reproducible age estimates were successful for both saffron cod and Arctic cod. Ageing precision as measured by between age reader agreement (+/- 0 years) was approximately 90% and 70% for saffron and Arctic cod, respectively, for the aggregate of all samples (Fig. 3). These values are better than typically found for other gadid species in the North Pacific such as walleye pollock or Pacific cod. For each species, a minimum of three independent trials of approximately 100 samples each were conducted to measure between age reader agreement and were consistent with the overall average. Reader agreement plots (Fig. 3) also illustrate age determination precision which shows that for the majority of the sample independent age readers assigned the same age, although a smaller fraction of the sample ages were inconsistently assigned an age by 1 or 2 years between reading trials. For both Arctic cod and saffron cod the functional regression resulted in both the $\hat{\alpha}$ and $\hat{\beta}$ parameters not significantly different than 0 and 1.0, respectively, at $p = 0.05$. Bowker's test of symmetry, which measures between reader relative bias, was not significant ($|z| < 1.96$) for saffron cod, but did show a slight bias toward older ages for Arctic cod ($|z| = 2.54$), although this test is sensitive to small sample sizes.   In general, these results suggest that for each trial (and for the aggregate sample) each of the two age readers were applying the age determination criteria in a consistent manor.

Oxygen isotope ratios measured in saffron cod otoliths confirmed the identification and placement of the first two or three annuli consistent with age determination protocol. In general, microsampling resolution was sufficient to obtain at least discrete bi-monthly $\delta^{18}O$

measurements as a proxy for seasonal variation in water temperature (Fig. 4). In each case, the first several peaks in the δ^{18}O signature corresponded to the visual interpretation of the translucent zones. Water temperature and δ^{18}O are inversely related, so the translucent zones can be interpreted as winter growth during the season when ambient ocean temperatures are low. While these results do not verify the absolute age of the saffron cod and they are based on a relatively small sample, they do suggest that the age determination is correctly interpreting the first few translucent marks, up to an age of about 4 years, as true annual cycles in the growth of the otolith. Beyond age 4 the oxygen isotope signature becomes less informative due to the dense spacing of growth zones. Also of note is the observation that δ^{18}O steadily declines with each subsequent age and may suggest that saffron cod exhibit an ontogenetic migration pattern to warmer water (or less saline) after their juvenile stage of life.

Age compositions estimated from samples taken during the 2012 survey suggest predominant age classes of Arctic cod were age 2 or less, while for saffron cod ages 0 and 1 were the most dominant (Fig. 5). Ages from the survey, as measured by comparing lengths from otolith samples to overall length samples taken for saffron cod, seemed to be taken in relative proportion indicating the sample was fairly representative (Fig. 5). For Arctic cod, otoliths were taken in relative proportion in the bottom trawls, however they were over-represented among lengths greater than 100 mm in the surface trawls. Based on observed size at age (age 1 < 60 mm, age 2 > 100 mm), this may have led to a greater proportion of age 1- and 2-year old fish in the population than expected. The maximum age attained was 8 and 5 years old for saffron cod and Arctic cod, respectively, while ages less than 4 years old were more common. This suggests that longevity for these polar species is quite short, implying high rates of natural mortality.

Saffron cod attain larger asymptotic sizes and achieve their maximum size at generally a faster rate than Arctic cod (Table 2, Fig. 6). For saffron cod, asymptotic size was on average 150 mm ($L_\infty = 363$ mm, $K = 0.378$) greater than for Arctic cod ($L_\infty = 209$ mm, $K = 0.312$) with slightly higher instantaneous rates of growth. There was evidence of sexually dimorphic growth in both species. Female saffron cod, from data collected during the 1976-1979 bottom trawl survey, showed greater asymptotic sizes ($L_\infty = 410$ mm, $K = 0.224$) than males ($L_\infty = 320$ mm, $K = 0.351$). Arctic cod from the same survey showed a similar sexually dimorphic pattern of growth (females: $L_\infty = 286$ mm, $K = 0.185$) than males ($L_\infty = 232$ mm, $K = 0.298$). For both sexes the sex ratio of samples collected were nearly equal.

For both time periods studied, saffron cod and Arctic cod growth curves were statistically different (H_o was rejected) among regions (Table 3, Figs. 6 & 7). For saffron cod, significant differences in growth curves between the Chukchi and northern Bering seas were found in both 1976-79 ($p < 0.01$) and 2012 ($p < 0.0001$) which were principally due to differences in the initial size at younger ages (age 0 – age 1). This indicates that size at age, especially at younger ages, is larger in the northern Bering Sea compared to the Chukchi Sea (Fig. 6). Due to the paucity of age 4+ saffron cod captured during the 2012 survey the parameter L_∞ was shared for both regions. For Arctic cod, regional differences in growth were found among the two areas of the Chukchi Sea ($p < 0.005$) and Northern Bering Sea ($p < 0.01$) (Tables 2 & 3). Arctic cod grew to smaller asymptotic size but at faster rates in the more northerly central ($L_\infty = 197$ mm, $K = 0.324$) and southern ($L_\infty = 221$ mm, $K = 0.297$) Chukchi Sea than compared to the northern Bering Sea ($L_\infty = 266$ mm, $K = 0.171$). These results seem to suggest a possible cline in growth with more northerly latitudes exhibiting faster rates of growth in polar water more suitable to Arctic cod. This supports the notion that stenothermic, high-latitude fish such as Arctic cod grow faster at colder temperatures than fish of the same species at lower latitudes.

Both species appeared to exhibit temporal variation in growth. Saffron cod showed an overall reduction in the asymptotic size accompanied by higher instantaneous rates of growth from the late 1970s ($L_\infty = 560$ mm, $K = 0.121$) to 2012 ($L_\infty = 363$ mm, $K = 0.378$) (Table 2; Fig. 6). Arctic cod appeared to exhibit a similar decline in overall asymptotic size along with an increase in growth rates in both the southern Chukchi Sea ($L_\infty = 263$ mm to 221 mm, $K = 0.204$ to 0.297) and northern Bering Sea ($L_\infty = 300$ mm to 266 mm, $K = 0.208$ to 0.171) compared to the same regions 30 years later in 2012 (Table 2; Figs. 6 & 7). The early baseline surveys (1976-79) did not sample stations north of Point Hope which precluded comparisons between the Central Chukchi and regions to the south. It should be noted that the parameter t_0 was fixed at the average value in 2012 due to the selectivity of bottom trawls toward older Arctic cod in the population (no age-0 Arctic cod were caught during 1976-79). In general, size at age for both species was highly variable over time, even when region-specific growth curves were fit to that data. An examination of residuals in size from the regionally predicted growth curves did not show any patterns with regard to latitude, bottom depth, or bottom temperature.

5. Discussion

Two important and often overlooked elements of developing a reliable age determination criteria are quantifying ageing imprecision and verifying (or validating) the annual nature of the growth increments used to assign age (Campana, 2001). Age reading error has been recognized for many decades, and it is a well-known problem associated with the process of assigning age based on scales and other hard structures such as fish otoliths, spines, and vertebrae (Van Oosten, 1941; Beamish and McFarlane, 1983). Imprecision occurs at random between independent trials of age assignment (by two age readers), whereas bias occurs when there is a systematic difference between the estimated age and true age. In practice, both types of error occur during the age determination process. In this study, the imprecision of age estimation was quantified, and the age determination criteria validated, at least for saffron cod. Between-age reader agreement (+/- 0 years) for saffron cod and Arctic cod was 90% and 70%, respectively, which is generally better than for other gadids, such as walleye pollock and Pacific cod, in the North Pacific Ocean (Kimura and Andrel, 2005). It is uncertain how these ageing precision estimates compare with saffron cod and Arctic cod in other polar seas since they are rarely reported.

For saffron cod, the visual interpretation of annual growth zones in the otolith used to assign age was verified using oxygen isotope signatures. This procedure exploited the established inverse relationship between fractionation of δ^{18}O in otoliths and water temperature (Thorrold et al., 1997; Hoie et al., 2004) which have been used to identify seasonality in otolith growth or accretion rates. Indeed, chemical analysis of oxygen isotopes has been applied to assess the accuracy of otolith growth zone counts for other gadids; Atlantic cod, *Gadus morhua* in the Northeast Atlantic Ocean (Weidman and Millner, 2000) and Pacific cod, *Gadus macrocephalus* in the North Pacific Ocean (Helser et al., 2014). Helser et al. (2014) documented the expected temperature-driven variation in δ^{18}O in Bering Sea Pacific cod otolith aragonite of 0.2‰ δ^{18}O/^{o}C (r^2=0.74, p<0.01), which is surprisingly consistent with North Atlantic waters (Grossman and Ku, 1986; Thorrold et al., 1997). In this study, the peaks in δ^{18}O of saffron cod otoliths coincided with translucent growth zones (interpreted as annual growth) which is what would be expected based on the aforementioned relationship. Interestingly, the downward trend in otolith δ^{18}O signatures of these 4-5 year old fish suggests the animal experienced warmer water at older ages of growth. Whether this temperature “signal” in the otoliths of these fish suggests a general warming trend in the Chukchi Sea (2008-2012) or possible preferential migration to warmer water masses with age warrants further study. This explanation would be consistent with lab-based studies showing a significantly positive growth response in juvenile saffron cod to warmer water (Laurel et al., 2015). Saffron cod are considered eurythermic (wide thermal tolerance) and are able to take advantage of high water temperatures (Golovanov, 1996; Laurel et al. 2015), and possibly preferentially seek areas of more thermally favorable habitat.

Owing to their lack of commercial importance, life history studies of saffron cod and Arctic cod in the Arctic seas of the Pacific have been limited compared to other gadids such as Pacific cod and walleye pollock. Wolotira et al. (1977) and Gillespie et al. (1997) reported on early efforts by NMFS to characterize benthic distributions of fish and shellfish in the Chukchi Sea, which included growth of Arctic cod relating size at age based on otolith collections. As others have suggested, Arctic cod have a very short life span compared to other gadids (Gillispie et al. 1997; Craig et al., 1982). The oldest reported ages have been 7 years (Bradstreet et al., 1986) or 8 years (Gillispie et al., 1997). In this study of a sample of over 1800 otoliths spanning thirty years the oldest Arctic cod encountered were 8 and 7 years of age captured in the northern Bering Sea-Norton Sound and southern Chukchi Sea region, respectively, in 1976-79. Saffron cod also appear to exhibit a very short life span as the oldest saffron cod encountered from otoliths taken during the 2012 survey was 8 years of age, which is consistent with the 9 years of age reported by Wolotira et al. (1997) from the Chukchi Sea. By far, the most abundant ages for both species are less than 2-3 years of age, with individuals exceeding age 5 years being very rare, suggesting high rates of natural mortality (Welch et al., 1993; Hop et al., 1997). A number of authors suggest that Arctic cod is an r-selected species (Craig et al., 1982; Mikhail, 1985) with characteristics consistent with small bodies, short life span, and early maturity, although the relatively slow growth rates found in this study does not conform to that pattern (Adams, 1980).

Estimates of size at age, maximum size, and growth rates of Arctic cod from this study are, in general, consistent with other studies from the Chukchi and Beaufort Seas. In 2012, Arctic cod maximum size ranged between 170 mm to 280 mm at age 5 (oldest age) which is comparable to 160 mm to 230 mm (ages 5+) reported for the Chukchi Sea from the 1990-1991 study (Gillispie et al., 1997), and a range of 198 mm to 257 mm (ages 5+) from the Beaufort Sea (Craig et al., 1982). Craig et al. (1982) summarized a half dozen studies from both the Chukchi and Beaufort Seas, reporting size at age-5 ranging from 180 mm to 300 mm. Although it is not clear if this range represents an average or maximum observed size at age-5, Arctic cod from this study (over years and regions, 175 mm to 210 mm) were clearly within, if not slightly on the lower range, for the species.

Environmental conditions have been suggested to play a role in the spatial and temporal variation in Arctic cod growth. Craig et al. (1982) observed that Arctic cod in the nearshore waters of the Beaufort Sea attained a larger average size at all ages when compared to fish sampled in deeper offshore waters (Lowry and Frost, 1981), and suggested that warmer coastal water may be more favorable for growth. In the Chukchi Sea, Gillispie et al. (1997) also reported significantly larger sizes of age 3+ Arctic cod in nearshore stations compared to offshore waters. These authors suggest more nutrient-rich, warmer coastal current water plays a role in growth variability. Gillispie et al. (1997) also found larger average size at age in Arctic cod collected between 1990 and 1991 suggesting that overall warmer conditions in the Chukchi Sea may have been more favorable for growth and survival. While we found strong growth variation in saffron cod and Arctic cod at somewhat larger regional scales in the northern Bering and Chukchi Seas than have been reported, it is unclear what the direct role temperature plays in this life history characteristic. Arctic cod was found to vary among regions in the northern Bering, southern Chukchi, and central Chukchi Sea showing a systematic larger body size at age with generally warmer southerly water influenced by the Alaska Coastal Current (Sigler et al. DSR II this issue). Higher instantaneous rates of growth were found in Arctic cod in higher latitude regions such as the central and southern Chukchi Sea which supports the notion that stenothermic, high-latitude fish such as Arctic cod grow faster at colder temperatures than fish of the same species at lower latitudes. This could also represent countergradient growth variation (CGV) which has been reported for other species (Conover et al. 1997; Rypel, 2012) suggesting that populations at higher latitudes grow at faster rates to compensate for the shorter seasonal opportunity. Unlike the studies mentioned above, smaller scale differences in station temperature or depth did not explain any additional variation in growth residuals once regional scale growth was accounted for. This might be a fruitful area of investigation, particularly by examining growth increment widths and body condition of field caught juveniles during their first year of life in relation to spatial variation in temperature. This would validate laboratory studies showing temperature-dependent growth of both Arctic cod and saffron cod (Laurel et al., 2015). Similar to Gillispie et al. (1997), temporal variation in growth of Arctic cod was observed in this study as well. Arctic cod growth (size at age) by region (S. Chukchi and northern Bering-Norton Sound) and overall all regions was greater in 1976-79 compared to 2012. However, it is again unclear if temperature plays a role, if any, on these temporal differences in Arctic cod growth since during the late 1970s, ice cover was more expansive and temperatures cooler than recent years in the northern Bering and Chukchi Sea (Danielson et al., 2011).

In this study, we quantified spatial and temporal variability in saffron cod and Arctic cod growth and found relatively high variation over regional and decadal scales in the northern Bering and Chukchi Seas. We did not directly model temperature as a covariate, and while it would be speculative to say that temperature plays a significant role in this variation, there is substantive evidence from the scientific literature that temperature is, at least in part, a key factor regulating growth (Jobling, 1981). For instance, temperature is widely accepted as a principal factor underlying gadid growth variability, particularly in the well-studied Atlantic cod (Brander, 1994). Temperature has also been shown to affect growth rates of North Pacific juvenile gadids such as saffron cod and Arctic cod (Laurel et al., In press), as well as sub-arctic Pacific cod (Hurst et al., 2010), but observational field data demonstrating temperature-dependent growth of adult gadids are sparse. Beyond growth, temperature is also thought to be responsible for structuring spatial distributions in coldwater ecosystems (Perry et al., 2005; Mueter and Litzow, 2008; Kotwicki and Lauth, 2008). Projected scenarios of warming and reductions in sea ice are expected such that the summer Arctic may be nearly sea-ice free as early as 2040, according to climate model projections (IPCC, 2007; Overland and Wang, 2013). Such effects could have profound consequences on these species and the ecosystem as a whole, including temperature-induced changes in optimal thermal-growth windows resulting in shifts in life history reaction norms. Mixing among sub-arctic eurythermic and cold-adapted Arctic species may also lead to compression of suitable habitat and increased inter-species interactions altering predation and morality rates. Understanding potential biological responses to environmental variability may aid in predicting the effects of climate change on individual species, ecosystem processes, and community structure. However, it is important to recognize that these effects may not necessarily be felt uniformly across a species' range due to geographical differences in factors such as bathymetry, oceanography, and species interactions. Therefore, understanding both the intrinsic (phenotypic and genetic) and extrinsic (environmental) factors affecting life history responses such as growth will be critical for managing these key species in the northern Bering Sea and Chukchi Sea ecosystems. Future studies should strive to more fully characterize both temporal and spatial variability in growth and other life history responses throughout the species range, and test the importance of environmental factors. Further, temperature-dependent growth from laboratory studies (Laurel et al., 2015) should be experimentally extrapolated to field studies to confirm whether the underlying thermal growth response is conserved under more varied environmental conditions, both at the juvenile and adult life stages. Finally, this study serves as a baseline for future investigations on the effects of climate change on fish growth and ecosystem process in the Arctic.

6. Acknowledgements

We thank Stan Kotwicki and Andy Whitehouse of the Alaska Fisheries Science Center, and the three anonymous reviewers for comments that improved the quality of this manuscript. This study was funded [in part] by the U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM) through Cooperative Agreement M12PG00018 between BOEM, Alaska Outer Continental Shelf Region and University of Alaska Fairbanks / Alaska Fisheries Science Center.

The findings and conclusions in the paper of those of the author(s) and do not necessarily represent the views of the National Marine Fisheries Service. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Table 1. Summary of Saffron cod and Arctic cod otolith samples used for age determination and growth curve estimation by region and year. Samples in 2012 were taken by bottom trawl (BT) and surface trawl (ST) during the 2012 Arctic Ecosystem Integrated Survey and in 1976-1979 in the NMFS base-line survey. Regions are separated in central and southern Chukchi Sea and northern Bering Sea.

Region	Year	Gear	Latitude Range	Average Latitude	Number Saffron cod	Number Arctic cod
S. Chukchi Sea	1976-79	BT	65.5 - 68.3	67.1	250	108
N. Bering Sea	1976-79	BT	63.1 - 65.5	64.2	433	316
C. Chukchi Sea	2012	BT, ST	68.3 - 72.0	69.9	150	605
S. Chukchi Sea	2012	BT, ST	65.5 - 68.3	66.9	170	622
N. Bering Sea	2012	ST,	63.1 - 65.5	63.6	301	233

Table 2. Growth parameters (von Bertalanffy) for saffron cod and Arctic cod by region and survey year. Samples in 2012 were taken by bottom trawl (BT) and surface trawl (ST) during the 2012 Arctic

Ecosystem Integrated Survey and in 1976-1979 in the NMFS base-line survey. Regions are defined in Table 1.

Region	n	Parameter estimate (ASE)			r^2	s^2
		L_∞	K	t_0		
			Saffron Cod			
1976-79						
Chukchi Sea	250	556	0.141	-0.947	0.86	530
		(410 – 701)	(0.090 – 0.202)	(-1.235 – -0.660)		
Northern Bering Sea	433	514	0.131	-1.612	0.87	505
		(398 – 675)	(0.088 – 0.180)	(-1.918 – -1.311)		
All regions		**560**	**0.121**	**-1.465**	0.86	546
		(446 – 396)	(0.081 – 0.159)	(-0.563 – -0.420)		
2012						
Chukchi Sea[1]	320	438[2]	0.262	-0.398	0.91	646
		(385 – 501)	(0.200 – 0.313)	(-0.470 – -0.333)		
Northern Bering Sea	301	438[2]	0.250	-0.944	0.73	704
		(385 – 501)	(0.172 – 0.483)	(-1.05 – -0.652)		
All regions		**363**	**0.378**	**-0.492**	0.86	675
		(330 – 396)	(0.312 – 0.444)	(-0.563 – -0.420)		
1976-79			**Arctic Cod**			
Southern Chukchi Sea	108	263	0.204	NE[3]	0.65	375
		(213 – 311)	(0.139 – 0.270)			
Northern Bering Sea	316	300	0.208	NE	0.75	418
		(262 – 335)	(0.169 – 0.247)			
All regions		**244**	**0.276**	NE	0.73	489
		(225 – 262)	(0.237 – 0.314)			
2012						
Central Chukchi Sea	605	197	0.324	-1.065	0.57	330
		(166 – 289)	(0.610 – 0.443)	(-1.371 – - 0.759)		
Southern Chukchi Sea	622	221	0.297	-0.895	0.71	346
		(189 – 253)	(0.212 – 0.381)	(-1.077 – -0.715)		
Northern Bering Sea	233	266	0.171	-1.174	0.73	361
		(182 – 450)	(0.051 – 0.393)	(-3.031 – -0.531)		
All regions		**209**	**0.312**	**-0.959**	0.71	351
		(187 – 226)	(0.251 – 0.382)	(-1.113 – -0.807)		

[1] Age data for central and southern Chukchi Sea combined.

[2] Parameter estimate L_∞ is shared between regions due to lack of data for ages 4+

[3] NE = Not estimated. Parameter t_0 set equal to 2012 for all regions due to lack of age 0 data in 1976-79.

Table 3. Approximate randomization tests comparing von Bertalanffy growth curves fit separately to each region for saffron cod and Arctic cod in the Chukchi (C = central Chukchi, S = southern Chukchi) and northern Bering Seas. Regions are defined in Table 1.

		Test statistic[1]		
Year	Regional comparison	Observed: F_{obs}	Under null: $F_R(\alpha) = 0.01$[2]	*Probability* $P[F(x) \geq F_{\text{obs}}]$
		Saffron Cod		
1976-79	Chukchi Sea – N. Bering Sea	5.65	2.62	< 0.01
2012	Chukchi Sea[3] – Northern Bering Sea	36.4	5.23	< 0.0001
		Arctic Cod		
1976-79	Chukchi Sea – N. Bering Sea	26.9	5.76	< 0.0001
2012	C. Chukchi Sea - S. Chukchi Sea	4.50	1.90	< 0.005
	C. Chukchi Sea – N. Bering Sea	3.31	2.20	< 0.01
	S. Chukchi Sea N. Bering Sea	2.40	1.70	< 0.01

[1] $F = \frac{(SSE_r - SSE_f)/q}{SSE_f/(n-p)} = \frac{(SSE_r - SSE_f)/q}{MSE_f}$, subscripts *obs* and *R* refer to observed and randomized test statistics, respectively. The test statistic, *F*, is the difference in the residual sums of squares between the fit of the von Bertalanffy growth model to the pooled data set minus the residual sums of squares from the region-specific model. Hypothesis tests are constructed by comparing the observed test statistic, F_{obs}, to the empirical probability density function (pdf) of F_R generated under the null hypothesis by repeated randomization of the data to regions. Test outcomes are reported in terms of the probability, assuming the null hypothesis is true, that the test statistic would have been as large or larger than F_{obs}, i.e., $P[F(x) \geq F_{\text{obs}}]$.

[2] Comparison-wise error rate

[3] Central and southern Chukchi Sea age data combined.

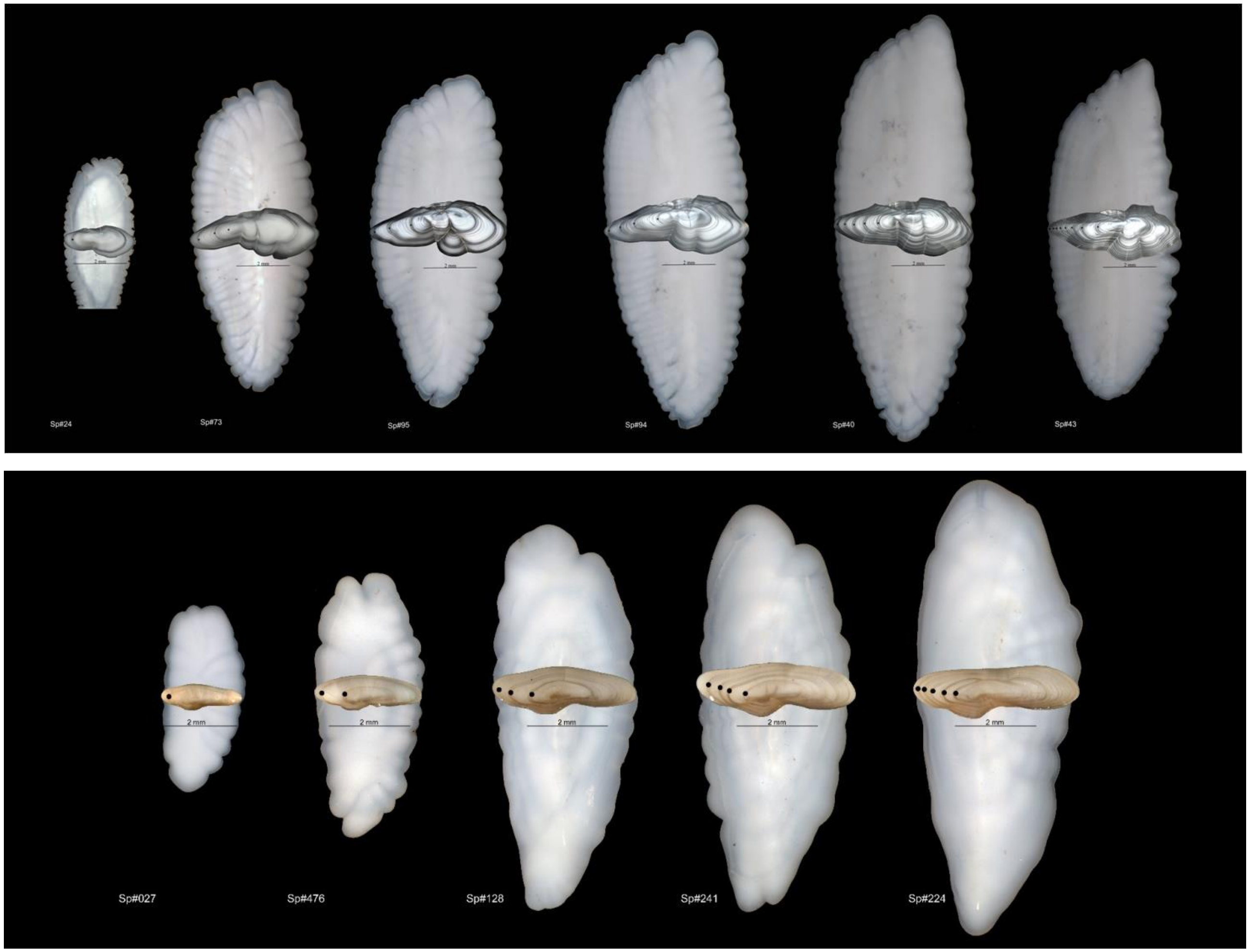

Figure 1. Whole and sectioned otoliths (superimposed over the whole otolith) from saffron cod and Arctic cod for a range of ages (1 to 8 years) collected during the 2012 Arctic Ecosystem Integrated Survey. Saffron cod otoliths were prepared using thin sectioning while Arctic cod were prepared using break and burn.

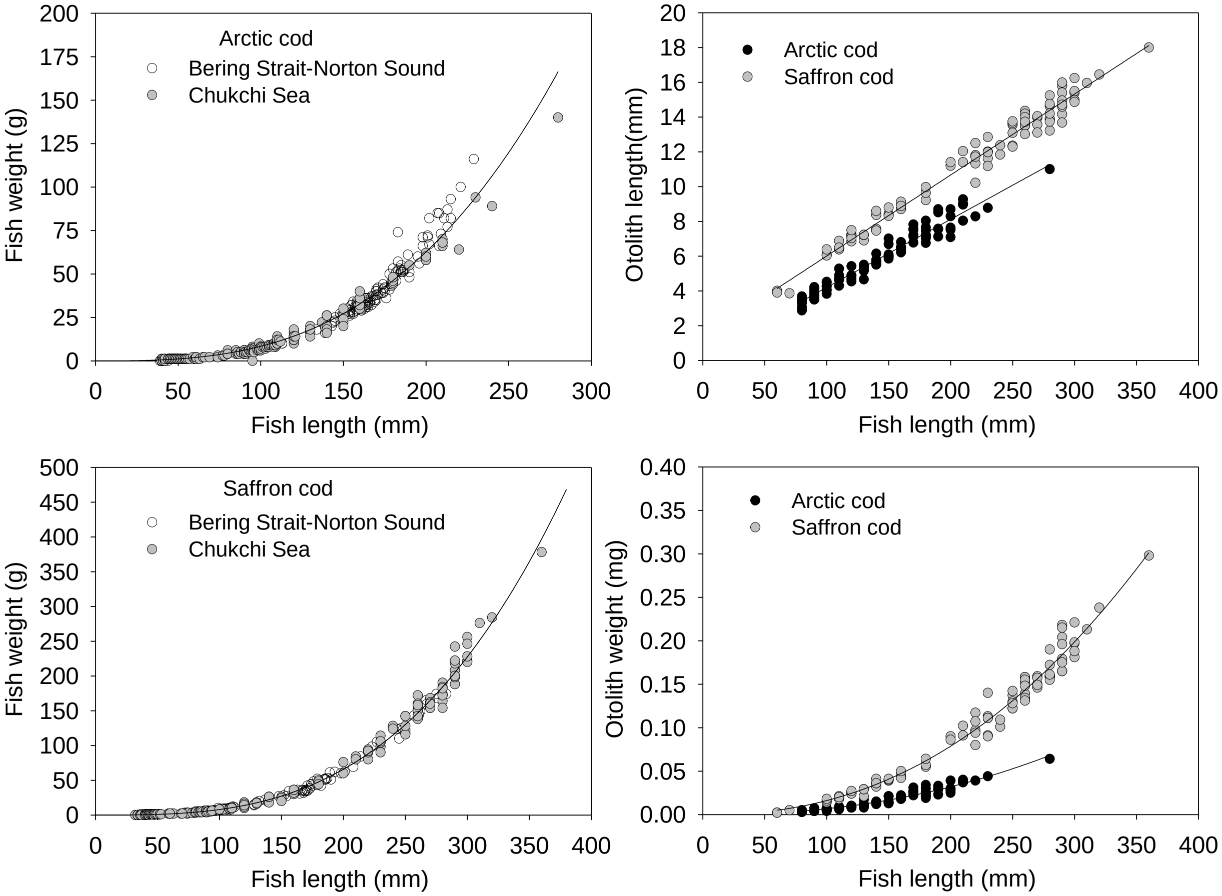

Figure 2. Saffron cod and Arctic cod body weight-body length, otolith mass-body length, and otolith area-body length relationships from specimens collected during the 2012 Arctic Ecosystem Integrated Survey in the Chukchi Sea.

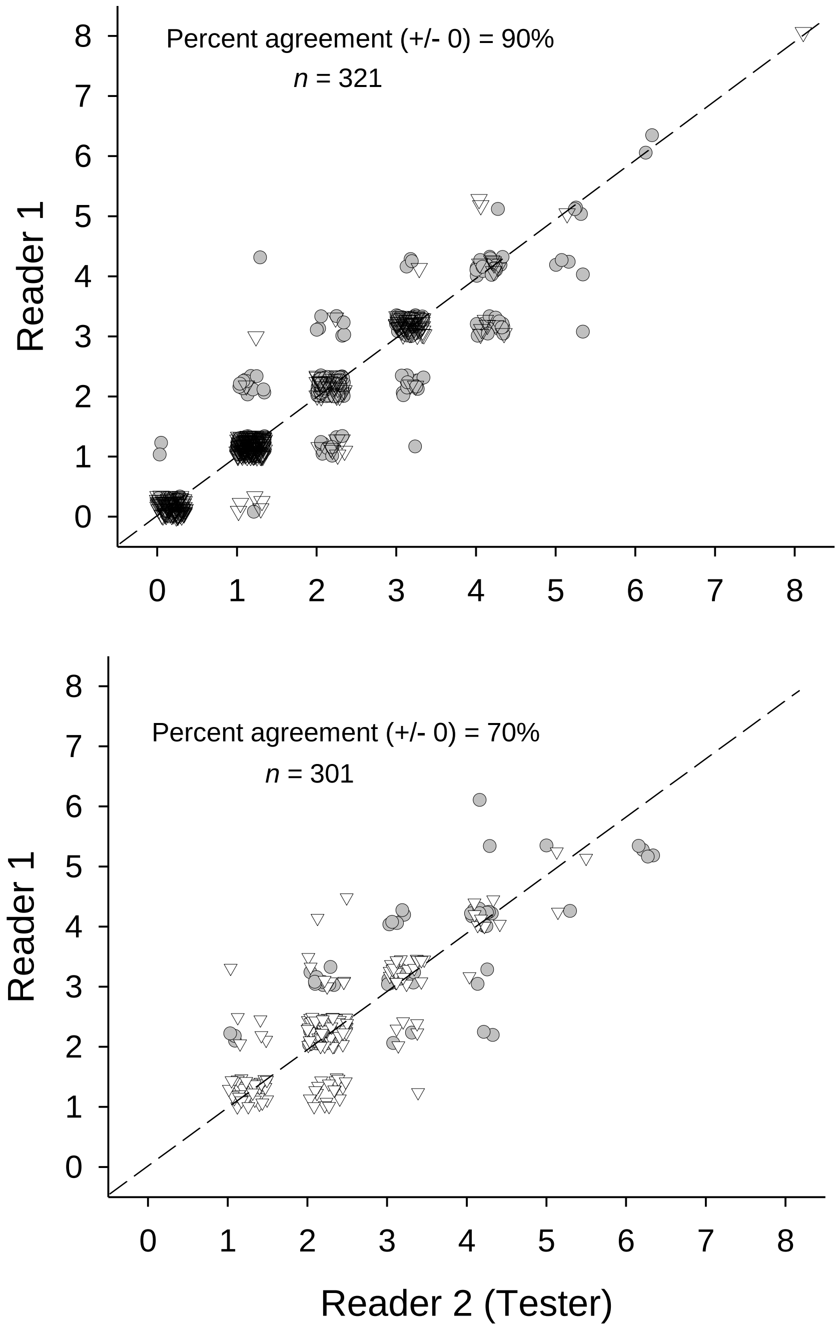

Figure 3. Saffron cod and Arctic cod age estimation precision from plots showing the age assignment agreement between two independent readers for saffron and Arctic cod from fish collected in the northern Bering and Chukchi Seas. Between reader agreement (+/- 0 years) was 90% and 70% for saffron cod and Arctic cod, respectively, overall from specimens collected during the 1976-1979 AFSC base-line survey (down tringle) and 2012 Arctic Ecosystem Integrated Survey (gray circles).

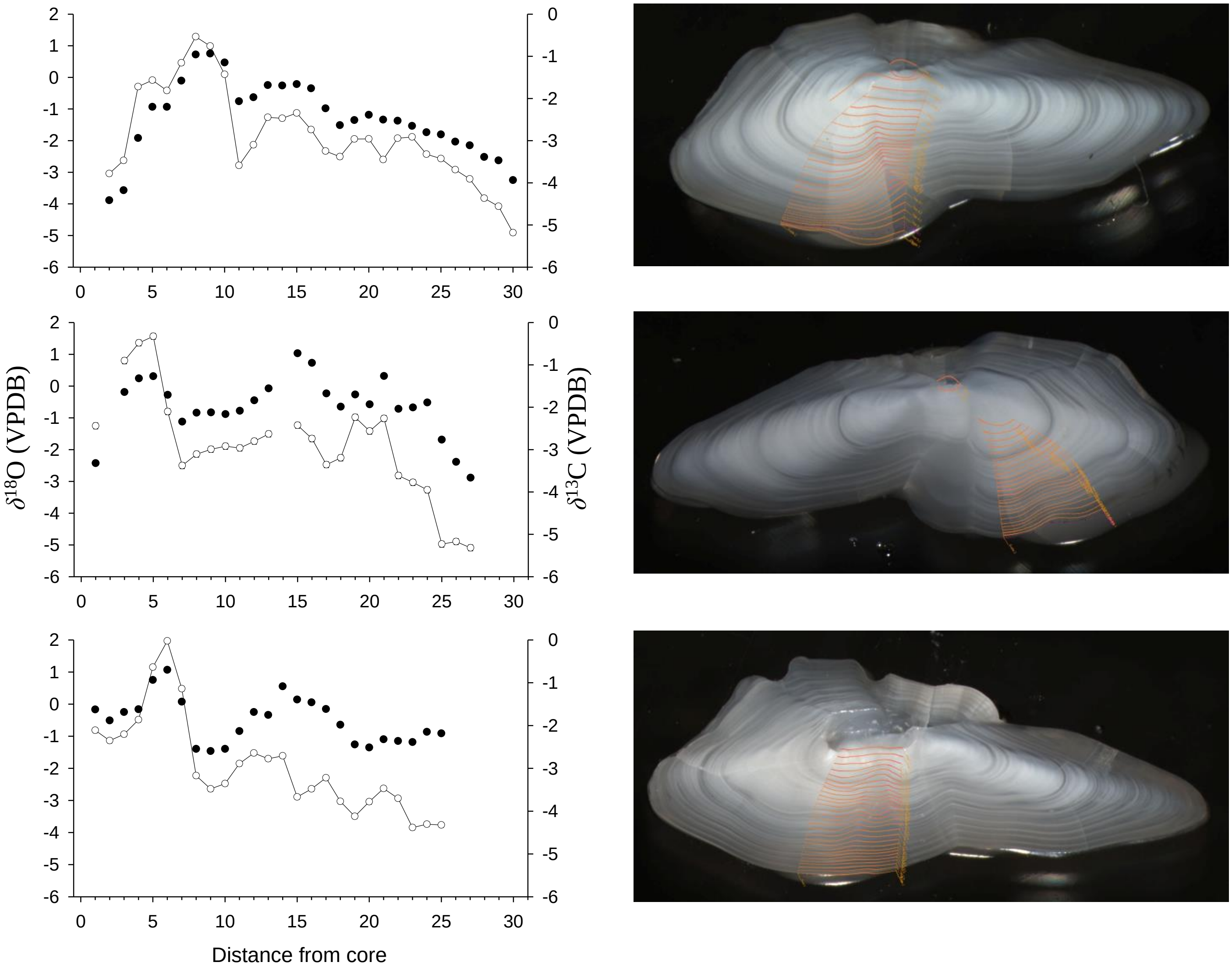

Figure 4. Left) Sequence of sub-annual stable oxygen (δ^{18}O; open dots) and carbon (δ^{13}C; black dots) isotopes measured from 3 saffron cod taken from the otolith core to margin. The δ^{18}O signature on these otoliths show that translucent growth zones (annuli) coincide with δ^{18}O maxima indicating annuli form during winter months when water is cold. Right) Saffron cod otolith cross section, estimated to be 4 to 5 years old, showing sample paths (n=25) from otolith core to edge that were micro sampled using the Carpenter Systems CM-2 computer-aided micromill. Each path (microsample) on the right from core to margin corresponds to a δ^{18}O measurement on the left plotted as a function of distance from the core.

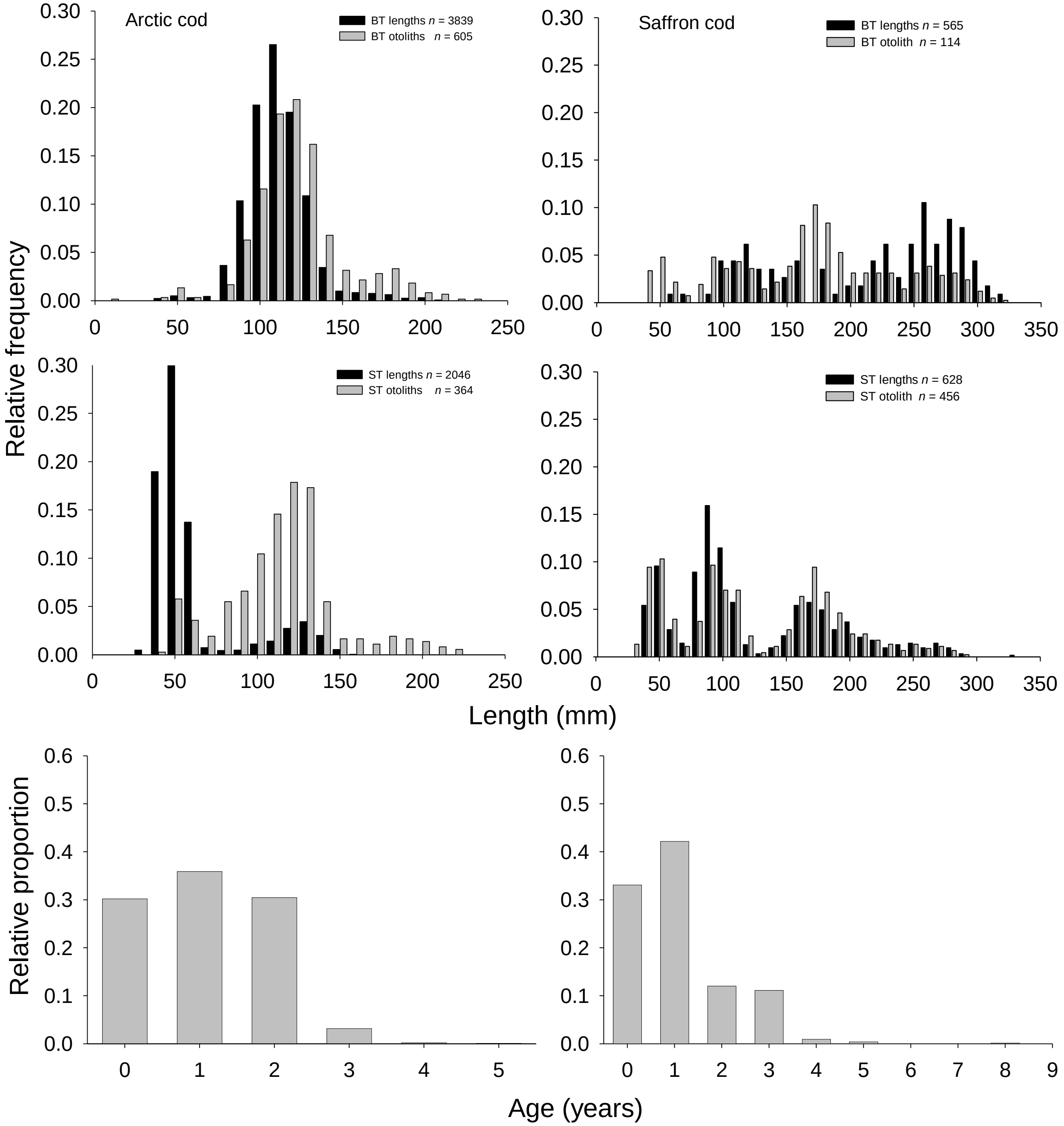

Figure 5. Saffron cod (right column) and Arctic cod (left column) bottom trawl (BT; top row) and surface trawl (ST; middle row) length frequencies showing consistency between samples taken for lengths and those taken for ages in the 2012 Arctic Ecosystem Integrated Survey. Saffron cod (right column) and Arctic cod (left column) age compositions (bottom row) estimated by applying all lengths sampled to age-length keys.

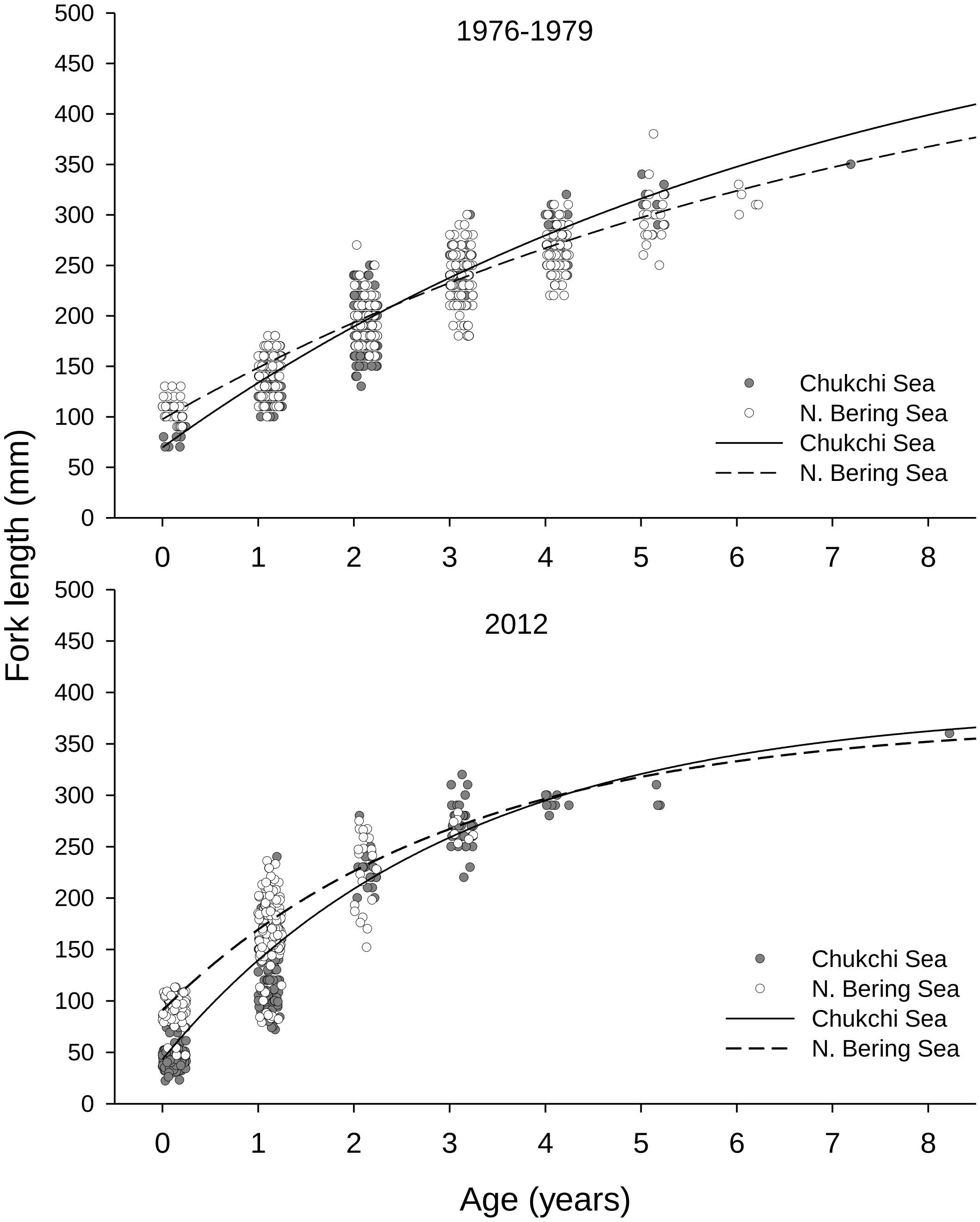

Figure 6. Saffron cod length (fork length, mm) at age (estimated by otoliths) and fitted von Bertalanffy growth curves by region in the northern Bering and Chukchi Seas from data collected during the 1976-1979 AFSC base-line and 2012 Arctic Ecosystem Integrated Surveys. Regions correspond northern Bering Sea (including the Norton Sound; 63.1^{o}N-65.5^{o}N), southern Chukchi Sea (65.5^{o}N-68.3^{o}N), and central Chukchi Sea (68.3^{o}N-72.0^{o}N). No data were collected in the central Chukchi Sea during the 1976-1979 AFSC base-line survey and 2012 was aggregated as Chukchi Sea.

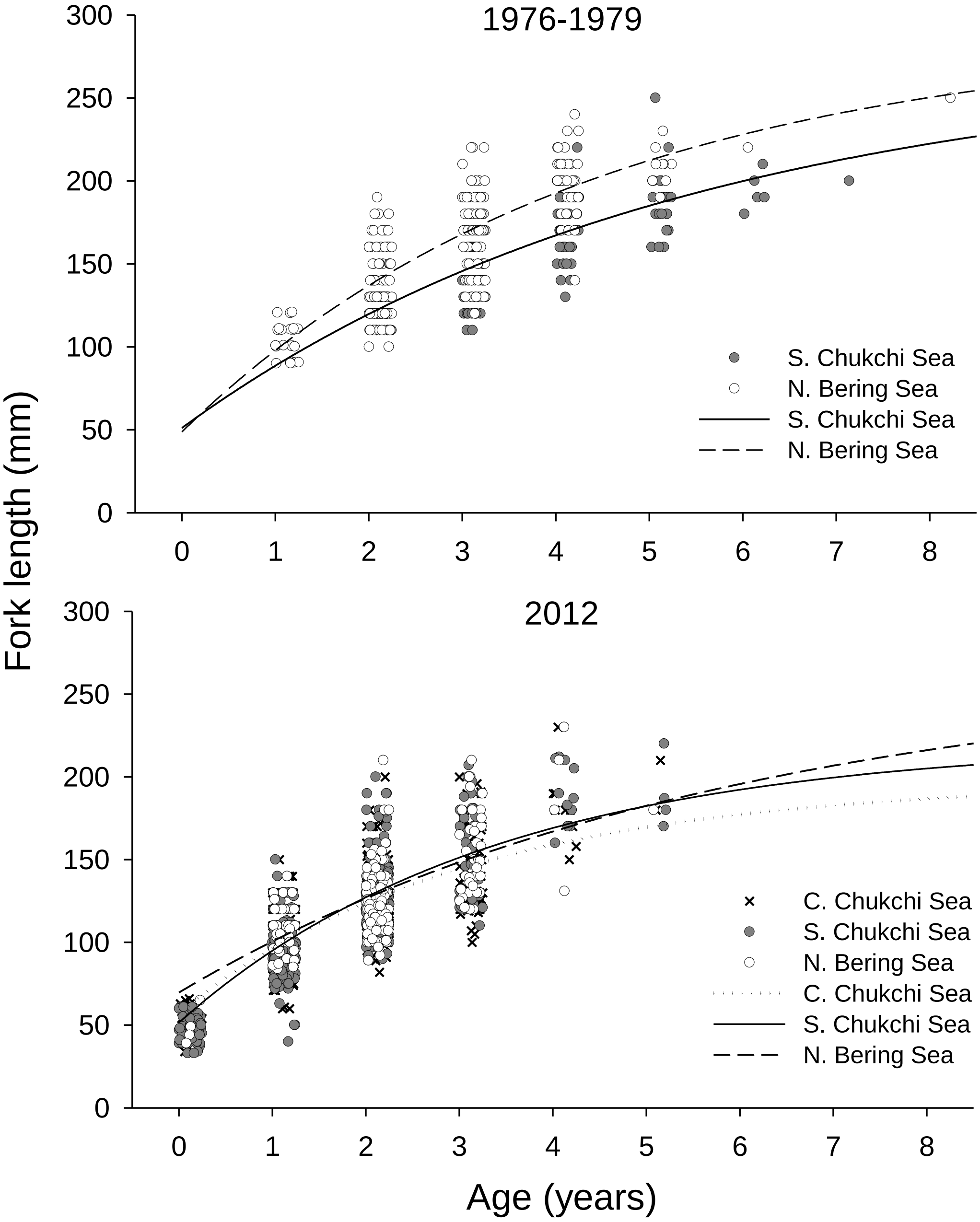

Figure 7. Arctic cod length (fork length, mm) at age (estimated by otoliths) and fitted von Bertalanffy growth curves by region in the northern Bering and Chukchi Seas from data collected during the 1976-1979 AFSC base-line and 2012 Arctic Ecosystem Integrated Surveys. Regions correspond northern Bering Sea (including the Norton Sound; 63.1^{o}N-65.5^{o}N), southern Chukchi Sea (65.5^{o}N-68.3^{o}N), and central Chukchi Sea (68.3^{o}N-72.0^{o}N). No data were collected in the central Chukchi Sea during the 1976-1979 AFSC base-line survey.

Appendix L.

Stock Composition Analysis of Juvenile Chum and Chinook Salmon Captured on the 2012 and 2013 Bering Sea and Chukchi Sea Surface Trawl Surveys

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June 19, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
SNP	single nucleotide polymorphism
BASIS	Bering-Aleutian Salmon International Survey
DFO	Fisheries and Oceans Canada
NMFS	National Marine Fisheries Service
ABL	Auke Bay Laboratories
NPAFC	North Pacific Anadromous Fish Commission

List of Oral and Poster Presentations

None

Proposed Objectives and Study Chronology

The Arctic Eis project provided a comprehensive assessment of the data-poor northeastern Bering Sea and Chukchi Sea ecosystems from the physical environment through the primary and secondary producers that support Arctic marine food webs to the numerous fish species inhabiting the area. The study objectives were to provide baseline datasets useful for understanding the structure and function of ecosystems and the ecology of important fish species, and for assessing the potential effects of future development and climate changes on fisheries resources and the marine environment in the Arctic region. Fish species of interest included juvenile Pacific salmon (*Oncorhynchus* spp.) that provide links between freshwater, estuarine, coastal, and offshore marine habitats. The distribution of juvenile chum (*O. keta*) and Chinook (*O. tshawytscha)* salmon stocks in this region was estimated by genetic stock identification analysis of samples collected during this study and is one of the measurable outcomes of the first two proposed project goals (pertinent words underlined):

1. Collect baseline fisheries and oceanographic data to enable resource managers to better predict effects of climate and human impacts on ocean productivity and on the ecology of marine and anadromous fish species within the northeastern Bering Sea and Chukchi Sea.
2. Assess the distribution, relative abundance, diet, energy density, size, and potential predators of juvenile salmon, other commercial fish, and forage fish within the northeastern Bering Sea and Chukchi Sea.

The genetic analyses of juvenile salmon samples collected by surface trawl in 2012 and 2013 estimated the proportion of stocks present in the northeastern Bering Sea and Chukchi Sea during late summer/early fall. Stock estimates of chum and Chinook salmon collected during their early marine life can be compared to stock proportions in future years.

Juvenile chum and Chinook salmon collected in surface trawls were frozen onboard and shipped to the Auke Bay Laboratories (ABL) for further processing. At ABL, tissues were subsampled from the juvenile salmon samples and stored individually in 2 mL vials with 95-100% ethanol. In the ABL Genetics Lab, DNA was extracted from approximately 20 mg of each sample and stored frozen. Each sample was analyzed at a set of genetic markers, either microsatellites or SNPs, through an amplification protocol, collection of raw genetic data via instrumentation, and determination of genotypes. One minor problem encountered was species misidentification of a few juvenile salmon in the field. Nine fish with unusual genetic (microsatellite) patterns, initially identified as chum salmon, were analyzed with a genetic (single nucleotide polymorphism=SNP) species identification assay and determined to be pink salmon. The chum and Chinook salmon genotypes were used in Bayesian genetic stock identification analyses by species and year to estimate the contribution of coastwide regions to each set of samples. Results were published in two NPAFC documents (Chapters 1 and 2, below). The genotypes are in an Excel spreadsheets and Progeny database housed at ABL and are available upon request to: Chris Kondzela (907-789-6084, chris.kondzela@noaa.gov), Chuck Guthrie (907-789-6093, chuck.guthrie@noaa.gov), or Jeff Guyon (907-789-6079, jeff.guyon@noaa.gov).

Data will also be made publicly available through the AOOS Arctic Portal and NODC by January 2017.

Chapter 1

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Stock Composition Analysis of Juvenile Chum and Chinook Salmon Captured on the 2012 Bering Sea and Chukchi Sea Research Surveys

by

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Submitted to the

NORTH PACIFIC ANADROMOUS FISH COMMISSION

by

United States

April 2014

THIS PAPER MAY BE CITED IN THE FOLLOWING MANNER:
Kondzela, C.M., C.M. Guthrie III, C.T. Marvin, J. A. Whittle, H.T. Nguyen, C. Ramsower, and J.R. Guyon. 2014. Stock composition analysis of juvenile chum and Chinook salmon captured on the 2012 Bering Sea and Chukchi Sea research surveys. NPAFC Doc. 1521. 13 pp. Auke Bay Laboratories, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 17109 Pt. Lena Loop Road, Juneau, AK 99801, USA. (Available at http://www.npafc.org).

Stock Composition Analysis of Juvenile Chum and Chinook Salmon Captured on the 2012 Bering Sea and Chukchi Sea Research Surveys

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Keywords: Juvenile salmon, chum, Chinook, Bering Sea, 2012

Abstract

Juvenile chum (*Oncorhynchus keta*) and Chinook salmon (*O. tshawytscha*) were collected in the Bering and Chukchi seas as part of the 2012 U.S. BASIS/Arctic Ecosystem Integrated Survey (Arctic EIS) cruises. Juvenile chum salmon were more commonly encountered on the survey and 1,222 juveniles were genotyped for 11 microsatellite markers to determine their stock of origin. The most northern sample set was relatively small; juvenile chum salmon collected in the Chukchi Sea were predominantly from the Kotzebue Sound stock group. Juvenile chum salmon collected in the northern Bering Sea near Norton Sound were predominantly of Norton Sound origin. Yukon River chum salmon were present in both survey areas of the Bering Sea, but were more prevalent between lat. 60-63°N. Juvenile Chinook salmon were not encountered in the Chukchi Sea, but a small sample of 81 juveniles from the Bering Sea was genotyped for 43 single nucleotide polymorphism (SNP) markers. Most of the Chinook salmon were from the Upper Yukon, Coastal Western Alaska, and Middle Yukon stock groups. This study determined the freshwater origin of juvenile chum and Chinook salmon from the northern Bering and Chukchi seas during late-summer/fall based on genetic data and may be used to help guide future surveys of juvenile salmon abundance in western Alaska.

Introduction

Both Chinook (*Oncorhynchus tshawytscha*) and chum (*O. keta*) salmon are high priority species whose management has significant allocation, conservation, and management implications. Over the last couple of decades, declines in both chum and Chinook salmon returns in some western Alaska drainages prompted various disaster declarations by the Governor of Alaska and federal agencies (Nelson, 2011). It is unclear why salmon returns have declined recently. There is some speculation that a significant source of mortality exists during the transition when juvenile salmon migrate out of fresh water as fry and smolts into salt water (Healey, 1982). Understanding the migration dynamics of juvenile salmon stocks and their relative abundance at sea may help determine the stresses that salmon undergo during this transition and could possibly lead to future models of estimating adult returns.

Juvenile chum and Chinook salmon were collected as part of annual U.S. BASIS cruises in the eastern Bering Sea since 2002. Juvenile chum salmon collected in 2002 and a subset in 2007 were genetically analyzed (Farley et al. 2004; Kondzela et al. 2009); samples from other years remained unanalyzed until recently (Kondzela et al., in preparation). The 2002 sample set was collected in the eastern Bering Sea between lat. 58-63°N, in an area from west of the Kuskokwim River to west of the Yukon River mouth. The 2002 sample set was genotyped for allozyme markers; mixed-stock analysis of samples from five areas showed that most of the fish were from coastal western Alaska and fall-run Yukon River stocks. The fall-run Yukon fish were found predominantly west and south of the Yukon River mouth, but not in the area west of the Kuskokwim River mouth. Contribution from northern Russian stocks was observed in the most northern and western stations. The 2007 samples from just south of the Bering Strait were predominately from northern Russian stocks, but the samples from the Chukchi Sea were from Kotzebue and Norton Sounds.

Chinook salmon are the least abundant of the Pacific salmon species in Alaska (Healey 1991). Not surprisingly, the number of juvenile Chinook salmon collected from the 2012 eastern Bering Sea survey was smaller than that of chum salmon. Genetic stock composition estimates for the 2002-2006 juvenile Chinook salmon samples from the eastern Bering Sea were completed by the Alaska Department of Fish and Game (ADF&G; Murphy et al. 2009), and the 2009-2011 samples have recently been analyzed by the National Marine Fisheries Service (Murphy et al., in preparation). Juvenile Chinook salmon from those two multi-year datasets were primarily from Coastal Western Alaska, Middle Yukon, and Upper Yukon stock groups.

Our study reports the sample locations and genetic stock composition estimates for juvenile Chinook and chum salmon collected from the Bering Sea and Chukchi Sea on the 2012 U.S. BASIS/Arctic Ecosystem Integrated Survey (Arctic EIS) research cruises. These results will help elucidate the migrations of juvenile salmon in western Alaska as they emigrate from freshwater to marine environments, and are expected to complement the mixed-stock analyses of the juvenile salmon samples collected from the eastern Bering Sea and Chukchi Sea in other years.

Materials and Methods

Sample Collection and DNA Extraction

Juvenile salmon samples were collected in the Bering Sea and Chukchi Sea as part of the 2012 U.S. BASIS/Arctic EIS surveys, following the methods described in Farley et al. (2005). DNA was extracted from the tails or opercles of the juvenile salmon with a DNeasy® Blood and Tissue Kit (Qiagen, Inc., Germantown, Maryland)[6] or Corbett reagents (Corbett Robotics Pty. Ltd., Australia), and processed with a X-Tractor Gene™ CAS-1820 robot as described by the manufacturer (Corbett Robotics). Extracted DNA was stored in 96-well DNA plates at -20ºC.

Genetic Baselines

Allele frequencies of the 381-population Pacific Rim chum salmon microsatellite baseline (Beacham et al. 2009) were downloaded from the Fisheries and Oceans Canada (DFO) Molecular Genetics web page (http://www-sci.pac.dfo-mpo.gc.ca/mgl/data_e.htm). Baseline files were created with Excel (Microsoft, Inc.) for 11 of the 14 markers that we routinely use in our laboratory for mixed-stock analyses (McCraney et al. 2012). The species-wide Chinook salmon baseline provided by the ADF&G (Templin et al. 2011) contains a set of 43 single nucleotide polymorphism (SNP) markers all of which were used in the stock composition analyses of our report. The SNP baseline contains genetic information for 172 populations of Chinook salmon grouped into 11 geographic regions.

Genotyping – Chum Salmon

The juvenile chum salmon samples were assayed for 11 microsatellite loci (Beacham et al. 2009)–*Oki100*(Beacham et al. 2008)(Beacham et al. 2008)(Beacham et al. 2008)(Beacham et al. 2008)(Beacham et al. 2008)(Beacham et al. 2008), *Omm1070*, *Omy1011*, *One101*, *One102*, *One104*, *One114*, *Ots103*, *Ots3*, *Otsg68*, and *Ssa419*–with a Qiagen® Multiplex PCR Kit following the manufacturer's protocols. Thermal cycling for the amplification of DNA fragments with the polymerase chain reaction (PCR) was performed on a dual 384-well GeneAmp® PCR System 9700 (Applied Biosystems, Foster City, California). Samples from the PCR reactions were diluted into 96-well plates for analysis by a 16-capillary, 36 cm array on the ABI 3130*xl* Genetic Analyzer (Applied Biosystems).

Genotypes were double-scored with GeneMapper® software, Version 4.0 (Applied Biosystems) and exported to Excel spreadsheets for further analysis. Of the 1,412 samples analyzed, 1,222 were genotyped for 8 or more of the markers (average 10.8 markers). The

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[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

remaining 188 samples were deleted either due to a lower number of successfully genotyped markers or an excess of homozygosity; the data from one sample from each of two pairs of duplicates were deleted. Most of the loss of genotype data was associated with samples collected early in the survey. Quality control of sample handling and genotyping was examined by plating DNA from 12.5% of the successfully genotyped samples that were then re-processed for genotyping as described above. Overall, the genotyping error rate was <1%.

Microsatellite allele designations were converted to match those in the DFO chum salmon microsatellite baseline (Beacham et al. 2009) from a conversion table that was developed by genotyping samples shared between the laboratories. Converted genotypes were then formatted into mixture files that were compatible with BAYES software.

Genotyping – Chinook salmon

The juvenile Chinook salmon samples were genotyped for the 43 SNP DNA markers represented in the Chinook salmon baseline with a "Matrix-assisted laser desorption/ionization - time of flight" (MALDI-TOF) method performed by using a Sequenom MassARRAY iPLEX platform (Gabriel et al. 2009). In addition to internal MALDI-TOF chip controls, ten previously genotyped samples were included on each chip during the analyses and resulting genotypes were compared to those from ADF&G, which used TaqMan® chemistries (Applied Biosystems). Concordance rates of 99.9% between the two chemistries confirmed the compatibility of both genotyping methods. Of the 90 samples analyzed, 81 samples were successfully genotyped for 35 or more of the 43 SNP markers (average of 41 SNPs).

Stock Composition Analysis

Stock composition estimates were determined with a Bayesian (BAYES; Pella and Masuda 2001) approach by comparing mixture genotypes with allele frequencies from reference baseline populations. For each BAYES analysis, Monte Carlo chains starting at disparate values of stock proportions for each region were configured such that 95% of the stocks came from one designated region with weights equally distributed among the stocks of that region. The remaining 5% was equally distributed among remaining stocks from all other regions. For all estimates, a flat prior was used for all baseline populations. The stock composition analyses were completed for a chain length of 10,000 with the first 5,000 discarded as burn-in and convergence of the chains to posterior distributions of stock proportions was determined with Gelman and Rubin (1992) shrink factors.

Baseline evaluation

The chum salmon baseline data were examined to determine major regional stock groupings of populations that would then be used for mixed-stock analyses of the chum salmon samples. Larger regional stock groupings can increase estimation accuracy and provide a means to compare similar studies. Population genetic structure was examined in two ways. First, structure was examined in the software NT-SYS (Applied Biostatistics, Inc.) with a principal coordinate analyses of chord distances (Cavelli-Sforza and Edwards, 1967) that were calculated from the allele frequencies of the baseline populations. Second, baseline simulation analyses were performed with SPAM software (Version 3.7; ADF&G, 2003) to evaluate the effectiveness of the baseline to allocate stocks to the correct regions. Hypothetical mixtures of 400 fish from single stock groupings were compared with the baseline to determine the percentage that reallocated back to the correct stock group. Simulations were done with baseline population resampling, a conservative method that incorporates the sensitivity of the baseline to small changes in allele frequency differences.

Results

Sample collection and distribution

Between August 6 and September 26, 2012, stations along the eastern Bering Sea and Chukchi Sea shelf from longitudinal meridians 159-168°W and from lat. 60-69°N were sampled for juvenile chum and Chinook salmon. The sampling locations for the successfully genotyped juvenile chum and Chinook salmon are shown in Figures 1A and 1B, respectively.

Chum salmon - stock composition

The number of successfully genotyped juvenile chum salmon samples from each of the three areas depicted in Figure 1A is shown in Table 1. Stock composition estimates were made for the total 1,222 sample set and for each sample set from the three areas. When six large regional baseline stock groupings were used in the stock composition analyses, most of the juvenile chum salmon samples were estimated to be from the Coastal Western Alaska stock group. A smaller proportion from the Upper/Middle Yukon stock group was present in the Bering Sea, but absent in the Chukchi Sea (Figure 2A).

To determine the relative contribution of more local stocks, the coastwide baseline was refined to 58 western Alaska/Arctic populations–from northern Bristol Bay to the Peel River in the Arctic–in five temporal-spatial stock groupings. The middle Yukon, including the Koyukuk and Tanana rivers, has both a summer and fall run of chum salmon. Some of the middle Yukon River populations were included with the Yukon Fall (upper river) stock group based on principle coordinate analysis of the baseline (not shown). The simulation results identify the difficulty of separating the coastal western Alaska chum salmon populations (Table 2); however, a stock composition analysis can provide at least a relative measure of contribution. Stock composition estimates made with this smaller baseline showed that samples collected between lat. 60-63°N were predominantly of Yukon River origin (Summer and Fall stock groups). About half the fish collected between lat. 64-66°N were from the Yukon River and most of the remainder from the Norton Sound stock group, whereas 94% of the Chukchi Sea collection was from the Kotzebue Sound stock group (Table 2B).

Chinook salmon - stock composition

After SNP genotyping, the 81 juvenile Chinook salmon samples were analyzed as a single dataset due to the small number of samples available (Table 1). Based on the coastwide Chinook salmon baseline aggregated into 11 large regions, the juvenile Chinook samples allocated primarily to the Coastal Western Alaska, Middle Yukon, and Upper Yukon stock groups (Figure 3A). The genetic variance for those estimates was relatively large, a result of the small sample set. To minimize potential cumulative effects from the misassignment of low stock estimates, the baseline was refined to the five most proximal Bering Sea stock groups and the mixed stock analysis was repeated. With a localized baseline, all samples allocated to the Coastal Western Alaska and Yukon stock groups in proportions nearly identical to those estimated with the full baseline (Figure 3B).

Discussion

Juvenile chum and Chinook salmon samples were collected in late-summer/fall 2012 from U.S. BASIS/Arctic EIS research surveys in the Bering Sea and Chukchi Sea. Genetic stock composition analyses show that juvenile salmon from multiple stock groups in western Alaska had migrated into the Bering and Chukchi seas at the time of the surveys. Due to the large spatial pooling of samples used in these analyses, the extent of population mixing on the continental shelf during the first summer at sea is not known. The stock estimates support an essentially westward (offshore) and southern migration of juvenile Chinook and chum salmon from the Yukon River.

The stock composition estimates for chum salmon show that the Yukon River stocks were most common between 60-63°N, an area located just south of the river mouth. Given the genetic similarity between lower Yukon and Kuskokwim stocks, it is possible that some Kuskokwim fish could have misallocated to the Summer Yukon stock group (Table 2). However, the relatively minor contribution of the Kuskokwim/Northeastern Bristol Bay stock group to the 60-63°N collection suggests that these southern Bering Sea stocks were not large contributors. The 2012 juvenile chum salmon samples from the Chukchi Sea were caught nearshore in mid-August above Cape Lisburne, where sea surface temperatures in August-September were relatively warm (Lisa Eisner, unpublished data; https://web.sfos.uaf.edu/wordpress/arcticeis/?page_id=209, accessed 3/26/14). Results from our study corroborate those of a previous analysis in which Kotzebue stocks dominated the juvenile chum salmon samples collected in early September 2007 from nearly the same location in the Chukchi Sea (Kondzela et al. 2009). We speculate that survival of juvenile chum salmon in the Chukchi Sea requires migration southward before sea ice formation to overwinter in the southern Bering Sea. In 2012, chum salmon from the Kotzebue Sound region were not present in samples collected in the eastern Bering Sea, off the Yukon River more than a month after they were detected in the Chukchi Sea. Kotzebue region chum salmon are genetically distinct and the 2011 parent abundance was high (Menard et al. 2012), so if the juveniles migrated south into the Bering Sea, perhaps they moved farther offshore than the area surveyed, or migrated south later in the season. The possibility of a later migration time is supported by the record low sea ice cover minimum in the Arctic Ocean in September 2012 (Perovich et al. 2013).

Stock composition estimates for the 2012 juvenile Chinook salmon were similar to those from previous years (Murphy et al. 2009) with the Upper Yukon stock group having the highest contribution, followed closely by the Coastal Western Alaska and Middle Yukon stock groups. The Coastal Western Alaska stock group includes many populations south of the Yukon River (Templin et al. 2011). Because juvenile Chinook from the Yukon River are thought to migrate offshore in a southwesterly direction (Farley et al. 2005), the Coastal Western Alaska portion of Chinook captured in the 2012 survey is likely to be from the lower Yukon River.

The genetic data generated from our study will support ongoing investigations of Yukon River juvenile salmon migration, abundance, and the inter-annual variation of proportions of summer and fall-run chum salmon. The samples from 60-63°N contained the largest number of Yukon River chum and Chinook salmon, and given the wide interest in the salmon resources of the Yukon River drainage, supports future survey effort in that area of the eastern Bering Sea.

Acknowledgements

Genotyping for our study was funded by the National Marine Fisheries Service (NMFS) and the Coastal Impact Assistance Program (CIAP) through an award to the NMFS. Chris Kondzela (ABL), Colby Marvin (ABL), and Jackie Whittle (ABL) genotyped the chum salmon samples for the 11 microsatellite markers used in this report. Charles Guthrie (ABL), Colleen Ramsower (UAriz), and Jeff Guyon (ABL) genotyped the Chinook salmon samples for the 43 SNP markers used in this report. Sample DNA was purified by Hanhvan Nguyen (ABL).

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Table 1. Number of genotyped juvenile chum and Chinook salmon collected between August 6 and September 26, 2012 from the Bering Sea and Chukchi Sea research surveys.

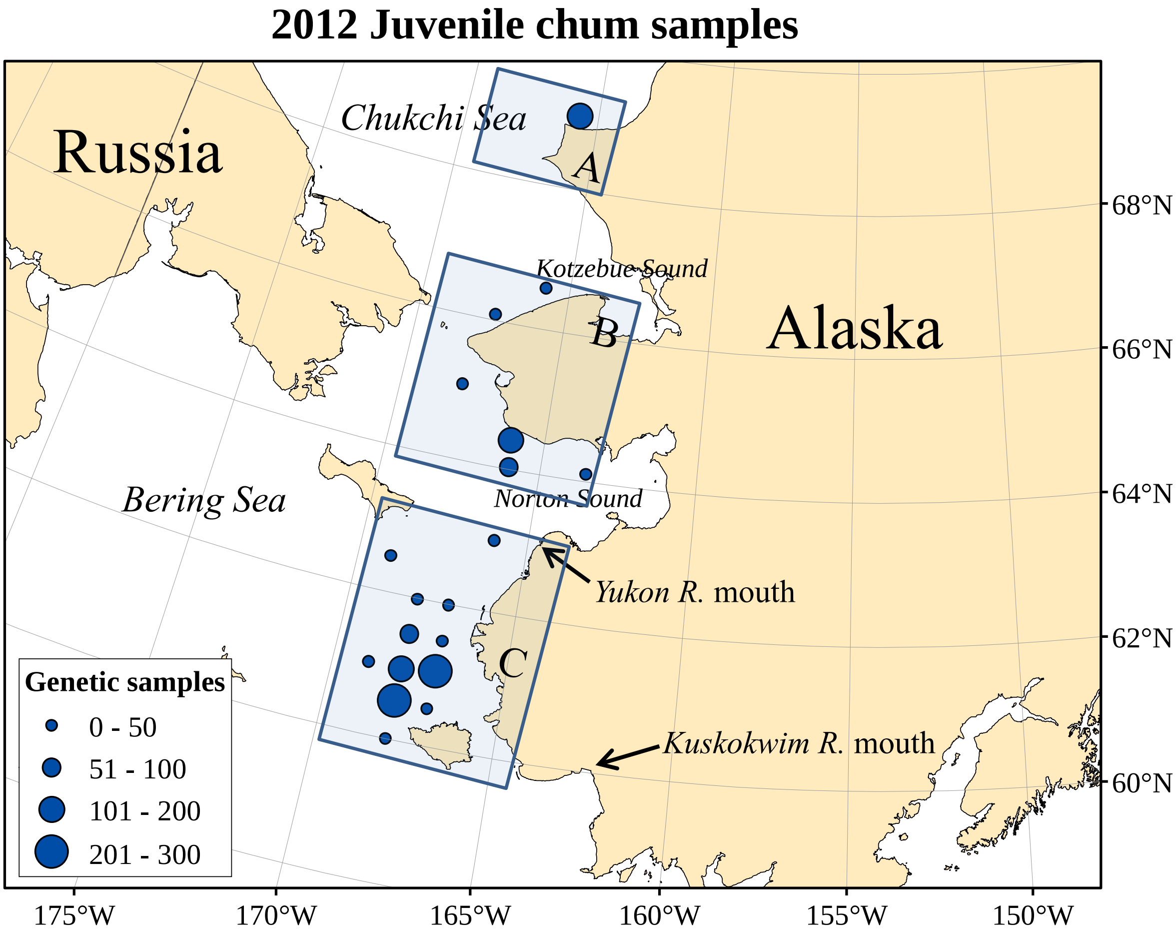
Location	Date of chum collections	Number of chum samples	Number of Chinook samples
60 to 63°N	Sep 18-25	880	64
64 to 66°N	Aug 8, Sep 12-17	228	17
69°N	Aug 8	114	0
Total		**1,222**	**81**

Table 2. Chum salmon baseline simulation analysis – 100% simulations for 5 western Alaska regions with 11 microsatellite loci. NEBB = northeastern Bristol Bay.

Region	Yukon Summer	Yukon Fall	Norton Sound	Kuskokwim-NEBB	Kotzebue
Yukon Summer	**0.799**	0.047	0.070	0.217	0.019
Yukon Fall	0.022	**0.935**	0.006	0.007	0.005
Norton Sound	0.129	0.009	**0.883**	0.239	0.273
Kuskokwim-NEBB	0.040	0.004	0.023	**0.522**	0.009
Kotzebue Sound	0.005	0.001	0.014	0.003	**0.666**

Figure 1. Sampling locations from the 2012 Bering Sea and Chukchi Sea research surveys: juvenile chum salmon in Panel A, and juvenile Chinook salmon in Panel B. Relative sample sizes are indicated by the size of the blue dots. Areas A, B, and C in Panel A at lat. 69°N, 64-66°N, and 60-63°N, respectively, encompass the three chum salmon sample sets used for stock composition analyses.

A.


2012 Juvenile chum samples
Chukchi Sea
Russia
A
Kotzebue Sound
B
Alaska
Bering Sea
Norton Sound
Yukon R. mouth
C
Kuskokwim R. mouth
Genetic samples
0 - 50
51 - 100
101 - 200
201 - 300
68°N
66°N
64°N
62°N
60°N
175°W
170°W
165°W
160°W
155°W
150°W

B.

2012 Juvenile Chinook samples

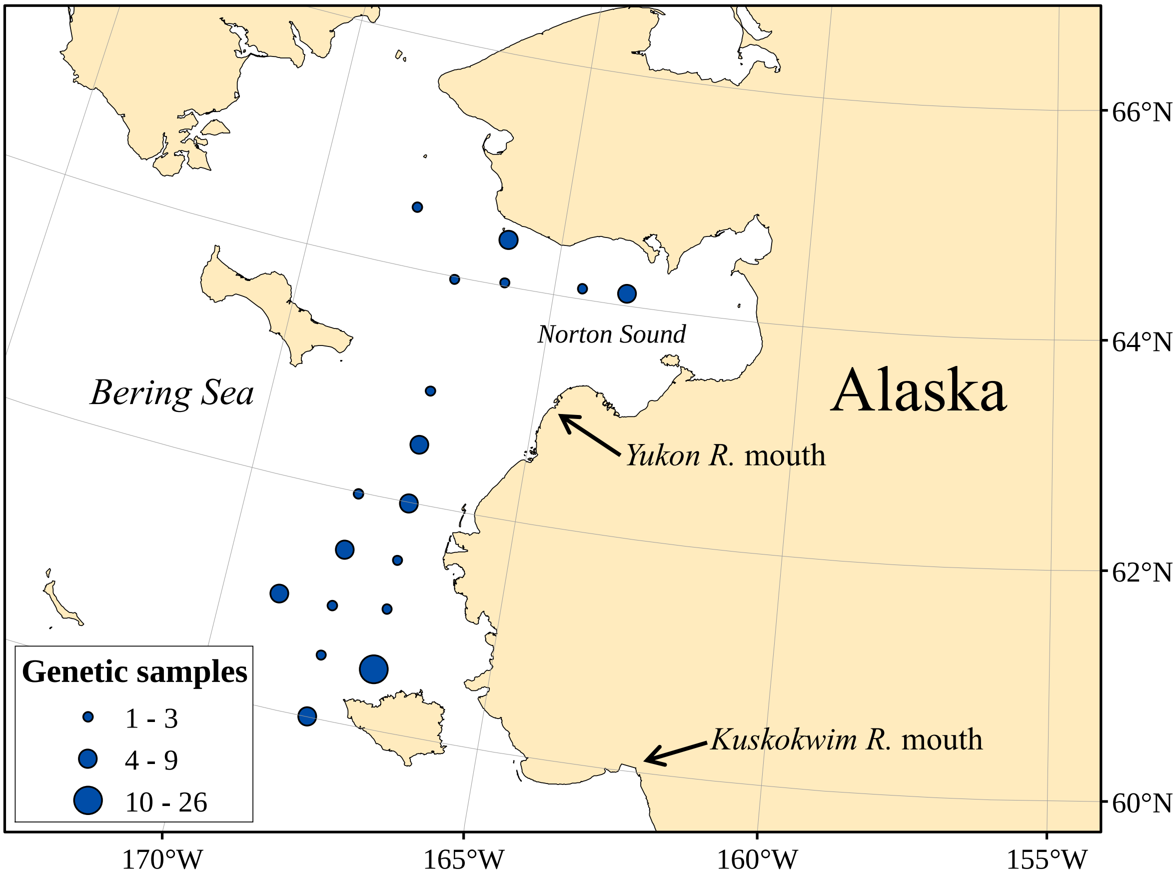
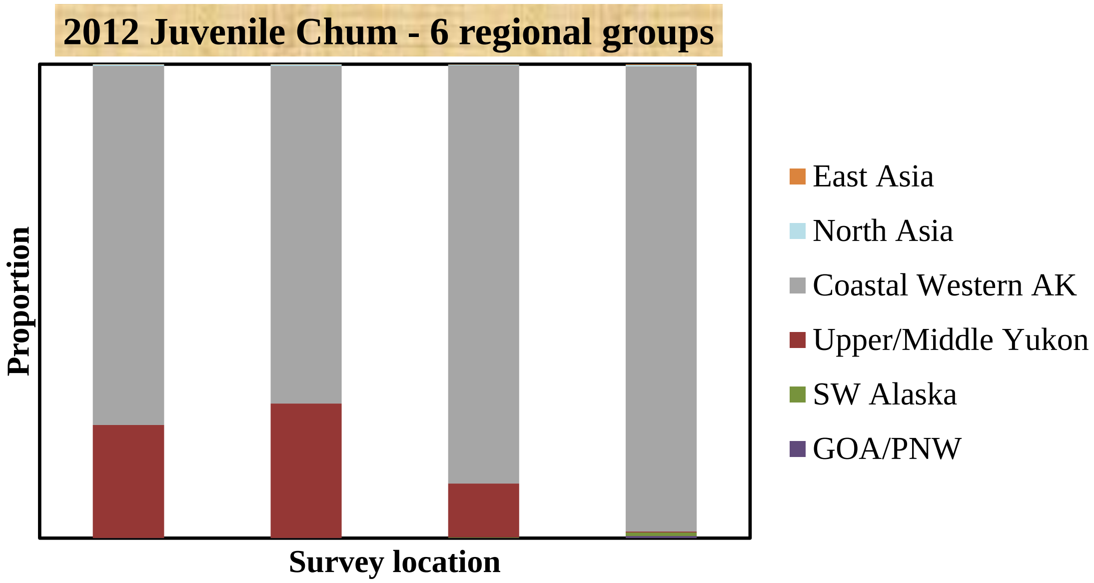


Figure 2. BAYES stock composition estimates for juvenile chum salmon samples from the 2012 Bering Sea and Chukchi Sea research surveys. Estimates from analyses that used a coastwide baseline (panel A), and a more localized western Alaska baseline (panel B). GOA = Gulf of Alaska, PNW = Pacific Northwest, NEBB = northeastern Bristol Bay

A.



B.

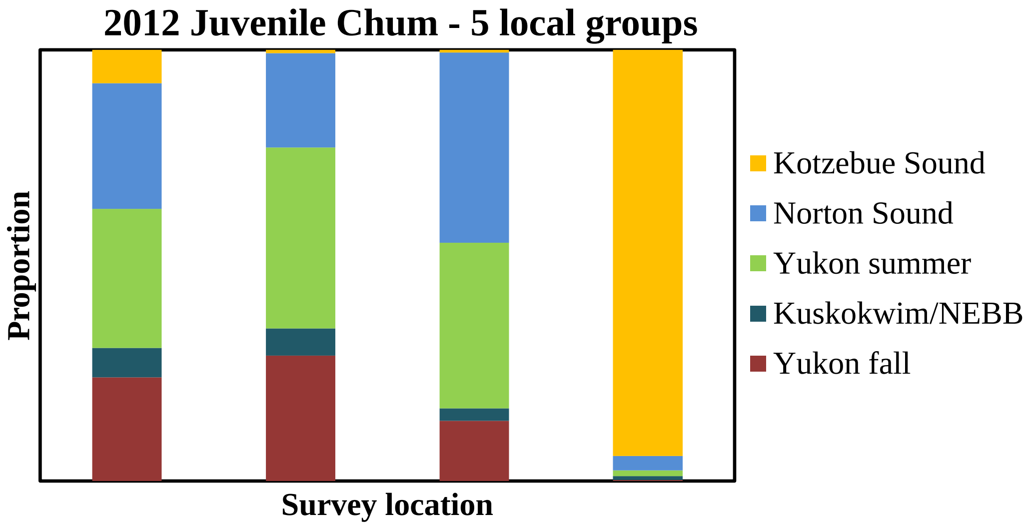
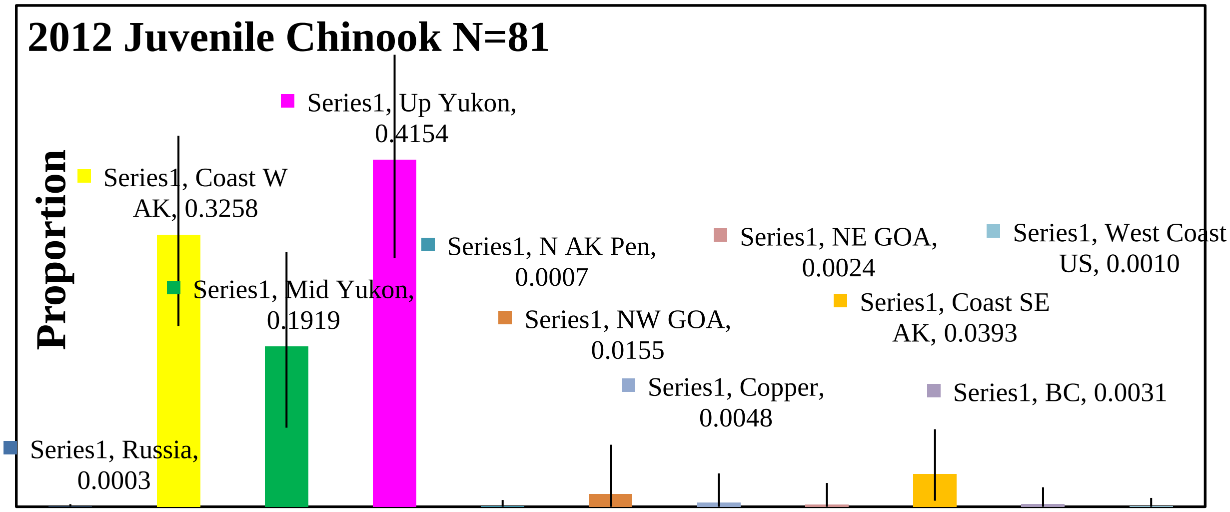
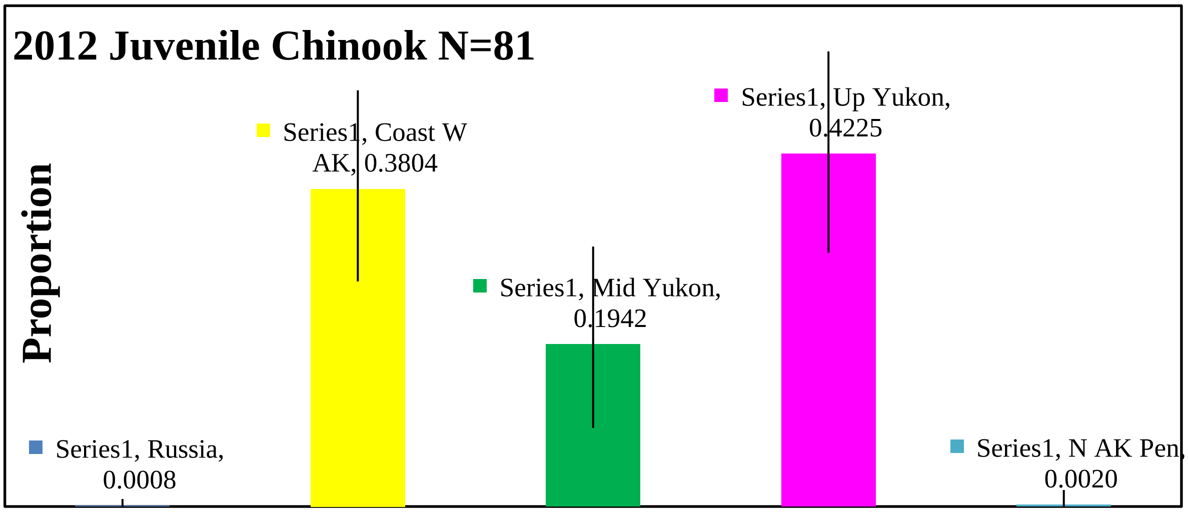


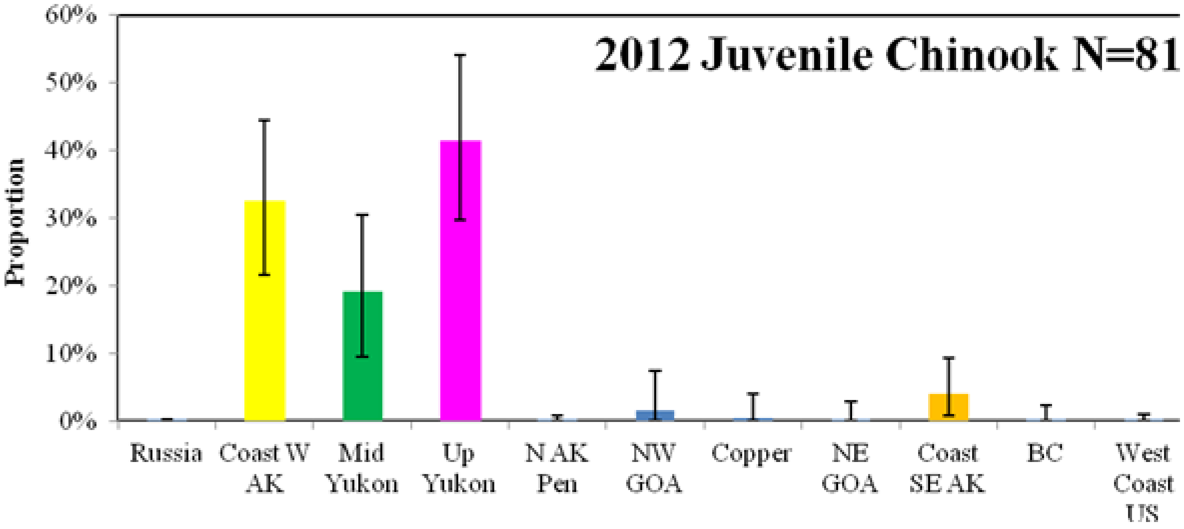
Figure 3. BAYES stock composition estimates (± credible intervals) for juvenile Chinook salmon from the 2012 Bering Sea research survey. Estimates from analyses that used a coastwide baseline (panel A), and a more localized western Alaska baseline (panel B).

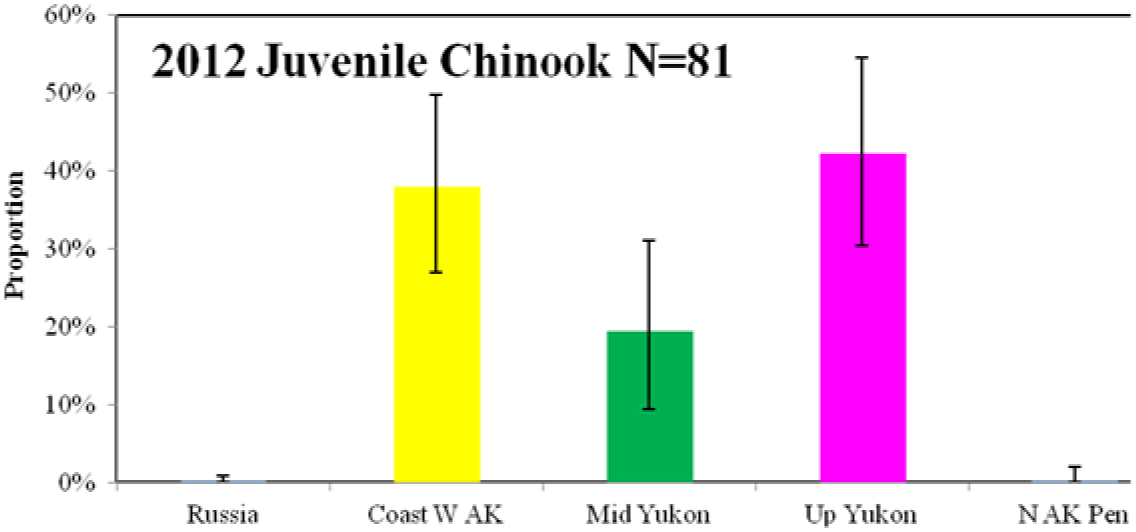
A.



B.




2012 Juvenile Chinook N=81
Proportion
60%
50%
40%
30%
20%
10%
0%
Russia
Coast W AK
Mid Yukon
Up Yukon
N AK Pen
NW GOA
Copper
NE GOA
Coast SE AK
BC
West Coast US


2012 Juvenile Chinook N=81
Proportion
60%
50%
40%
30%
20%
10%
0%
Russia
Coast W AK
Mid Yukon
Up Yukon
N AK Pen

Chapter 2

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Stock Estimates of Juvenile Chum Salmon Captured on the 2013 Bering Sea and Chukchi Sea Research Survey

by

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Submitted to the

NORTH PACIFIC ANADROMOUS FISH COMMISSION

by

United States of America

April 2016

THIS PAPER MAY BE CITED IN THE FOLLOWING MANNER:
Kondzela, C.M., J.A. Whittle, C.M. Guthrie III, and J.R. Guyon. 2016. Stock estimates of juvenile chum salmon captured on the 2013 Bering Sea and Chukchi Sea research survey. NPAFC Doc. 1633. 8 pp. Auke Bay Laboratories, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration (Available at http://www.npafc.org).

Stock Estimates of Juvenile Chum Salmon Captured on the 2013 Bering Sea and Chukchi Sea Research Survey

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99801, USA

Keywords: Juvenile chum salmon, Chukchi Sea, genetic stock identification

Abstract

Juvenile chum salmon (*Oncorhynchus keta*) were collected during late-summer/fall in the northern Bering and southeastern Chukchi seas as part of the 2013 U.S. BASIS/Arctic Ecosystem Integrated Survey (Arctic Eis) cruises. A small number of genetic samples were collected, most from the Chukchi Sea, and genotyped for 11 microsatellite markers to determine freshwater origin. All of the juvenile chum salmon samples were from western Alaska populations: about half from the Yukon River, one-quarter from Kotzebue Sound, and the remainder from Norton Sound and Kuskokwim/northeastern Bristol Bay. About two-thirds of the fish that originated from the Yukon River were from fall-run populations in the middle and upper reaches of the river. This study adds to a growing body of information about the early marine distribution of juvenile chum salmon from western Alaska.

Introduction

Chum salmon (*Oncorhynchus keta*) are an important resource throughout the North Pacific region. Over the last couple of decades, the abundance of chum salmon returns in some western Alaska drainages has fluctuated widely (JTC 2014), the causes of which remain unknown. There is some speculation that a significant source of mortality exists during the transition when juvenile salmon migrate out of fresh water as fry and smolts into salt water (Healey 1982). Understanding the migration dynamics of juvenile salmon stocks and their relative abundance at sea may help determine the stresses that salmon undergo during this transition and could possibly lead to future models of estimating adult returns.

Since 2002, juvenile chum salmon have been collected during annual U.S. BASIS cruises in the eastern Bering Sea. In 2012, juvenile chum salmon were also collected in the northern Bering and Chukchi seas during the first Arctic Ecosystem Integrated Survey (Arctic Eis) survey (Andrews 2012). Genetic stock identification of juvenile chum salmon from these surveys is providing insight into their migration routes during the first summer in the marine environment (Farley et al. 2004; Kondzela et al. accepted; Kondzela et al. 2014, 2009). Juvenile chum salmon collected in the eastern Bering Sea in an area west of the Kuskokwim and Yukon rivers were from coastal western Alaska and fall-run Yukon River stocks. Northern Russian stocks were present in more northerly Bering Sea stations, but samples from the Chukchi Sea were from primarily from Kotzebue and Norton sounds.

Our study reports the genetic stock composition estimates for available samples of juvenile chum salmon collected from the Bering Sea and Chukchi Sea on the 2013 U.S. BASIS/Arctic Eis research cruises (Anonymous 2014). These results add to our understanding of migration processes of juvenile salmon in western Alaska as they emigrate from freshwater to marine environments.

Materials and Methods

Sample Collection and DNA Extraction

Juvenile chum salmon samples were collected in the northern Bering Sea and southeastern Chukchi Sea as part of the 2013 U.S. BASIS/Arctic Eis surveys, following the methods described in Farley et al. (2005). DNA was extracted from the tails or opercles of the juvenile salmon with a DNeasy® Blood and Tissue Kit (Qiagen, Inc., Germantown, Maryland)[7] and a QIAcube HT® instrument as described by the manufacturer (Qiagen). Extracted DNA was stored in 96-well DNA plates at -20ºC.

Genetic Baseline

Allele frequencies of the 381-population Pacific Rim chum salmon microsatellite baseline (Beacham et al. 2009) were downloaded from the Fisheries and Oceans Canada (DFO) Molecular Genetics web page (http://www-sci.pac.dfo-mpo.gc.ca/mgl/data_e.htm). Baseline files were created with Excel (Microsoft, Inc.) for 11 of the 14 markers that we routinely use in our laboratory for mixed-stock analyses (e.g., McCraney et al. 2012, Kondzela et al. accepted).

Genotyping

The juvenile chum salmon samples were assayed for 11 microsatellite loci (Beacham et al. 2009)–*Oki100*, *Omm1070*, *Omy1011*, *One101*, *One102*, *One104*, *One114*, *Ots103*, *Ots3*, *Otsg68*, and *Ssa419*–with a Qiagen® Multiplex PCR Kit following the manufacturer's protocols. Thermal cycling for the amplification of DNA fragments with the polymerase chain reaction (PCR) was performed on a dual 384-well GeneAmp® PCR System 9700 (Applied Biosystems, Foster City, California). Samples from the PCR reactions were diluted into 96-well plates for analysis on the 16- and 48-capillary, 36 cm arrays on the ABI 3130*xl* and 3730*xl* Genetic Analyzers (Applied Biosystems).

Genotypes were double-scored with GeneMapper® software, Version 5.0 (Applied Biosystems) and exported to Excel spreadsheets for further analysis. Quality control of sample

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[7] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

handling and genotyping was examined by comparing genotypes from the two DNA Genetic Analyzers. Microsatellite allele designations were converted to match those in the DFO chum salmon microsatellite baseline (Beacham et al. 2009) from a conversion table that was developed by genotyping samples shared between laboratories. Converted genotypes were then formatted into mixture files that were compatible with BAYES software.

Stock Composition Analysis

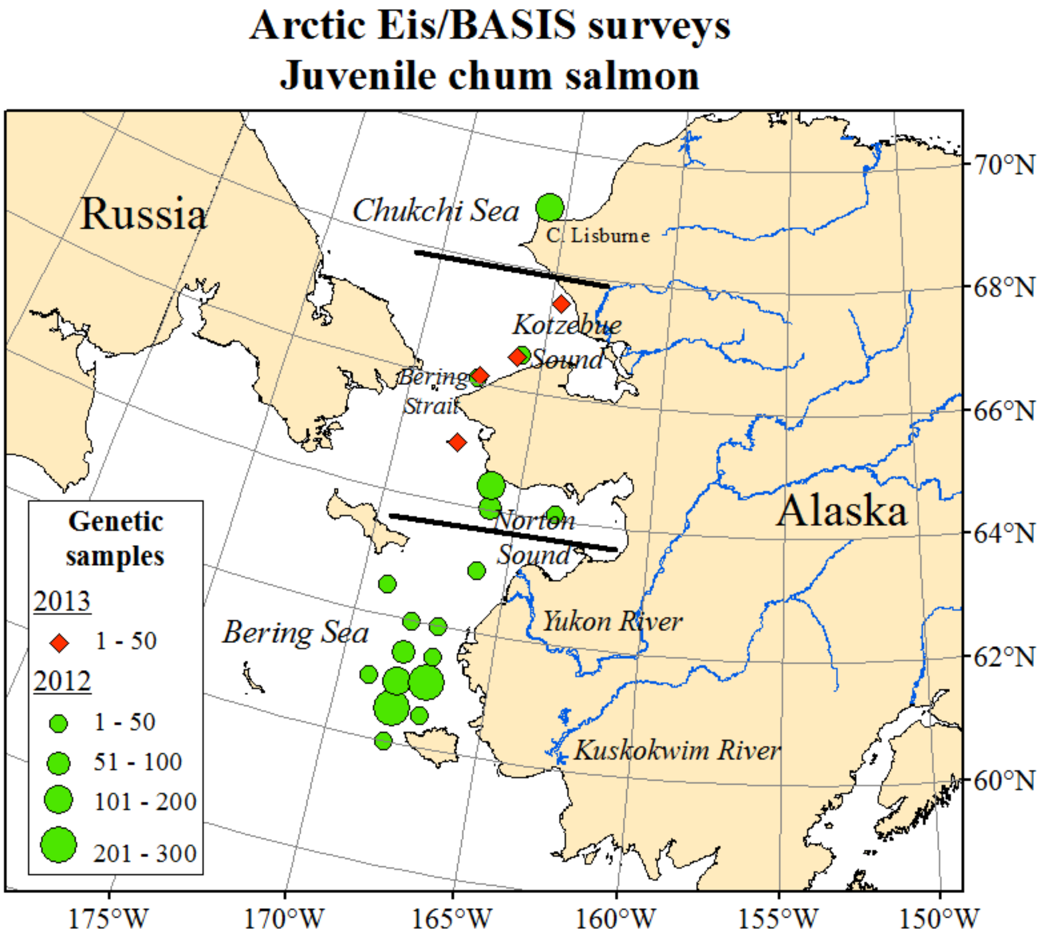
Stock composition estimates were determined with a Bayesian (BAYES; Pella and Masuda 2001) approach by comparing mixture genotypes with allele frequencies from reference baseline populations. For all estimates, the Dirichlet prior parameters for the stock proportions were defined by reporting group to be $1/(GC_g)$, where C_g is the number of baseline populations in reporting group g, and G is the number of reporting groups. For each BAYES analysis, Monte Carlo chains starting at disparate values of stock proportions for each reporting group were configured such that 95% of the stocks came from one reporting group with weights equally distributed among the stocks of that reporting group. The remaining 5% was equally distributed among remaining stocks from all other reporting groups. The stock composition analyses were completed for a chain length of 50,000 or 100,000 MCMC with the first half discarded as burn-in and convergence of the chains to posterior distributions of stock proportions was assessed with Gelman and Rubin (1992) shrink factors. As was done with the 2012 Arctic Eis juvenile chum salmon samples (Kondzela et al. 2014), stock composition analyses were run for six large regional groups with the 381-population coastwide baseline, and for five finer-scale temporal-spatial stock groups with the subset of 58 western Alaska populations.

Results

Sample collection and distribution

Between 8 August and 11 September 2013, stations along the northern Bering Sea (60-65.5°N) and Chukchi Sea shelf (65.5-72.5°N) were sampled for juvenile chum salmon. Most of the samples collected from the northern Bering Sea during 2013 were lost at sea (Mueter et al. 2014). Of the 105 available samples, 96 were successfully genotyped for 8 or more of the markers (average 10.8 markers), the sampling locations of which are shown in Figure 1. The remaining 9 samples were deleted from the project due to a low number of successfully genotyped markers in five fish, four of which were subsequently determined to be pink salmon; two samples that contained DNA from more than one individual; and two pairs of duplicates–the data from one sample from each of two pairs of duplicates were deleted. The 87 samples from the Chukchi Sea were collected during 8-11 August. Nine samples were collected southeast of the Bering Strait on 11 September, a month after the Chukchi samples were collected. Quality control testing of sample handling and genotyping indicated that the genotyping error rate was < 1%.

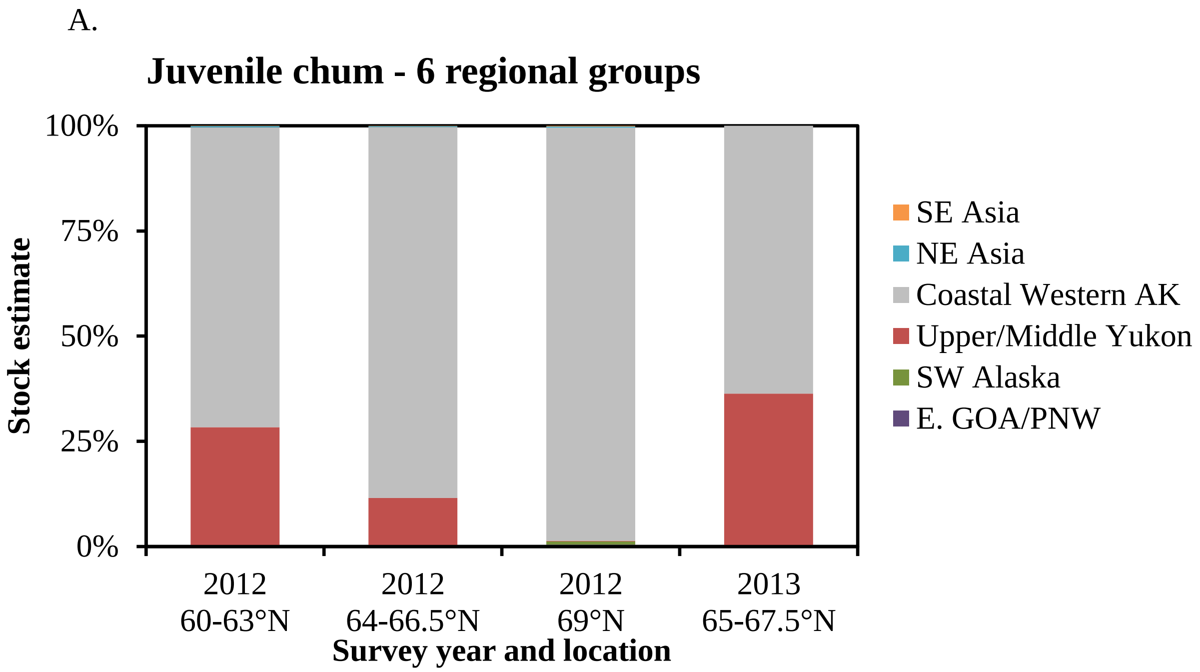
Figure 1. Sampling locations of juvenile chum salmon samples genotyped from the 2012 (green circles) and 2013 (red diamonds) U.S. BASIS/Arctic Eis research surveys. Black lines separate the three aggregated sample sets from 2012 used to estimate stock compositions. Relative sample sizes are indicated by the size of the markers.

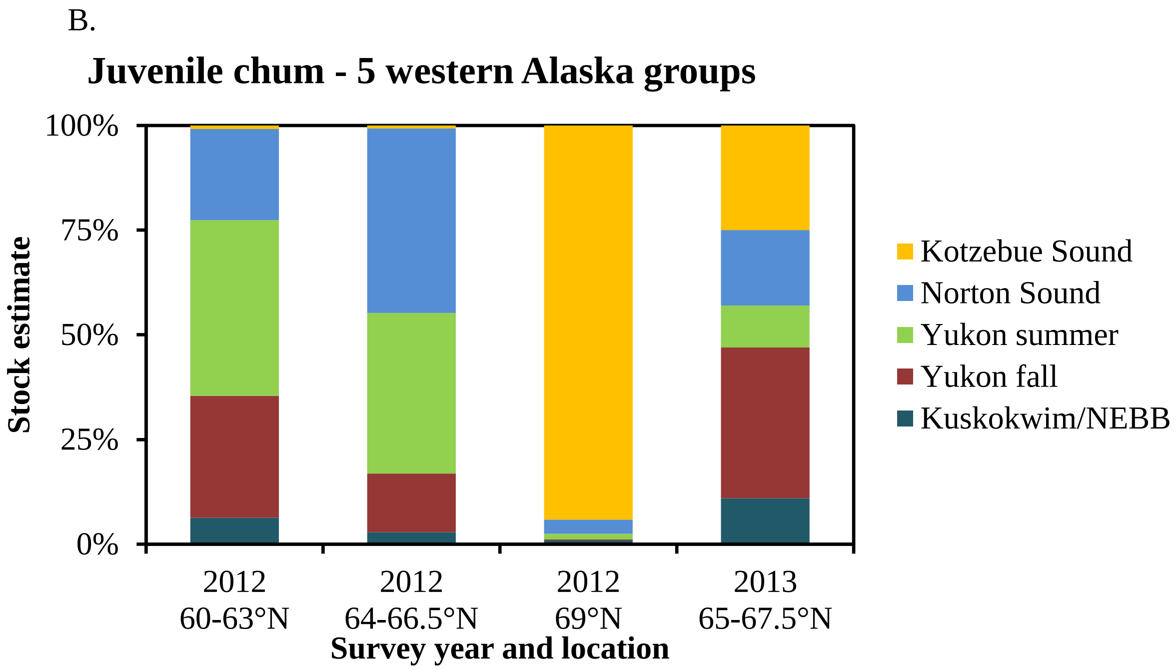


Stock composition

When six large regional baseline stock groupings were used in the stock composition analyses, about two-thirds of the 96 juvenile chum salmon samples were estimated to be from the Coastal Western Alaska stock group and one-third from the Upper/Middle Yukon stock group (Figure 2A). Stock composition estimates made with the smaller western Alaska baseline (Figure 2B) showed that a portion of the samples were from northern Alaska stocks in Kotzebue Sound (25%) and Norton Sound (18%). Nearly half of the samples were from the Yukon River stocks, with about one-third of those from summer-run Yukon (11%) and two-thirds of those from fall-run Yukon (36%) stocks. Kuskokwim/NE Bristol Bay (10%) stocks made up the remainder.

Figure 2. Stock composition estimates for juvenile chum salmon samples from the 2013 U.S. BASIS/Arctic Eis research survey. Estimates from the 2012 survey are included for comparison. Estimates from analyses that used a coastwide baseline (panel A), and a more localized western Alaska baseline (panel B). GOA = Gulf of Alaska, PNW = Pacific Northwest, NEBB = northeastern Bristol Bay





Discussion

Juvenile chum salmon samples were collected in late-summer/fall 2013 from U.S. BASIS/Arctic Eis research cruises in the northern Bering Sea and southeastern Chukchi Sea. As in 2012, genetic stock composition analysis showed that juvenile chum salmon were from western Alaska stocks. However, with the finer-scale baseline of western Alaska populations, stock proportions differed between the two years. In 2013, a higher proportion of the juvenile chum samples were from fall-run Yukon River stocks and a lower proportion from Kotzebue Sound stocks. Because the stations in the northern Bering Sea and southeastern Chukchi Sea were sampled at nearly the same locations and dates each year, temporal variation can be ruled out. What did differ between years was the quantity and spatial distribution of the samples. First, the sample set from 2013 was very small (96 total) in comparison to the 2012 sample sets (1,222 total) (Kondzela et al. 2014) due to the loss of northern Bering Sea samples during a flooding event at sea (Mueter et al. 2014). Second, most of the 2013 samples were collected in waters between the two northernmost sample sets in 2012 (Figure 1).

Stock estimates from 2013 indicate that some portion of the juvenile chum salmon from western Alaska stocks migrate northward through the Bering Strait in the same direction as the Alaska Coastal Current (ACC), the prevailing surface current (Danielson et al. 2015). Whether juvenile chum salmon north of the Bering Strait survive or migrate southward before winter sea-ice formation in the Chukchi and Bering seas is unknown.

The distributions of marine species assemblages are influenced by atmospheric and oceanographic conditions in this region (Sigler et al. 2016). Although the same nearshore stations were trawled at virtually the same time of year during the two years of sampling, no juvenile chum salmon were caught north of Cape Lisburne in 2013. The dominant northward transport of water around the shore of northwestern Alaska via the ACC was reduced during August-September in 2013 and the westward spread of the Alaska Coastal Water mass in the northern Bering Sea increased in 2013 (Danielson et al. 2015), and we speculate that these conditions may have restricted the northern extent of juvenile chum salmon distribution in 2013.

Acknowledgements

Genotyping for our study was funded by the National Marine Fisheries Service (NMFS) and the Coastal Impact Assistance Program (CIAP) through an award to the NMFS. We thank Ed Farley and Alex Andrews for supporting field collections and Emily Fergusson and Sarah Ballard for coordinating sample processing.

The findings and conclusions are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service.

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Appendix M.

Environmental and biological influences on the distribution and population dynamics of Arctic cod (*Boreogadus saida*) in the US Chukchi Sea

Authors
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Date
September 12, 2017

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

Table of Contents

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

C	Carbon
N	Nitrogen
ACW	Alaska Coastal Water
BCSW	Bering Chukchi Summer Water
MW	Melt Water
CWW	Chukchi Winter Water
SIA	Stable Isotope Analysis

List of Oral and Poster Presentations

Marsh JM, Mueter FJ, Quinn TQ II (Jan. 2017) Estimated abundance and reproductive potential of Arctic cod (*Boreogadus saida*) in the US Chukchi Sea. Alaska Marine Science Symposium (AMSS), Anchorage, AK.

Marsh JM, Mueter FJ, Quinn TQ II, Iken K, Danielson S (February 25, 2016) Population dynamics, distribution and diet of Arctic cod (*Boreogadus saida*) in the eastern Chukchi Sea Ocean Sciences Meeting, New Orleans LA

Marsh JM, Mueter FJ, Farley EV, Jr. (Nov. 2015) Environmental and biological influences on the distribution of Arctic cod (*Boreogadus saida*) in the US Chukchi Sea. Alaska Chapter American Fisheries Society (AFS) Meeting, Homer, AK.

Marsh JM, Mueter FJ, Quinn, TQ, II (Aug. 2015) Population dynamics of Arctic cod in the US Chukchi Sea. Annual AFS Meeting, Portland. OR. (Poster)

Marsh JM, Mueter FJ, Quinn, TQ, II (May 2015) Population dynamics of Arctic cod in the US Chukchi Sea. 30th Lowell Wakefield Symposium, Anchorage, AK. (Poster)

Marsh JM (April 25, 2015) A cold-adapted fish in a warming sea. Cod chronicles and salmon stories. Community outreach event, Juneau, AK.

Marsh JM, Mueter FJ, Gray B, De Robertis A (Apr. 2014) Distribution and trophodynamics of Arctic cod (*Boreogadus saida*) in the eastern Chukchi and northeastern Bering Seas. Ecosystem Studies of the Sub-Arctic Seas (ESSAS) Annual Science Meeting, Copenhagen, Denmark.

Proposed Objectives and Study Chronology

Arctic cod, *Boreogadus* saida, is a widely distributed and abundant fish species throughout the Arctic Ocean and its marginal seas and provides a key link between lower and upper trophic levels in these areas (Craig et al. 1982, Bluhm and Gradinger 2008, Marsh et al. 2017, Whitehouse et al. 2017). As such, studies of Arctic cod are of critical importance to understand potential effects of human activities including oil and gas exploration and CO_2 emissions on the Chukchi Sea and other Arctic marine ecosystems. Arctic cod has also been identified as one of three potential target species for a commercial fishery in Alaska's Arctic (NPFMC 2009). In spite of this potential and their ecological importance, the life history, abundance and dynamics of Arctic cod off Alaska remain poorly understood. Therefore, the objectives of this component of the Arctic Eis project were to (1) provide estimates of some key biological parameters for Arctic cod in the US portion of the Chukchi Sea and (2) assess the abundance and population dynamics of Arctic cod in the US portion of the Chukchi Sea. Abundances of age-0 Arctic cod in the water column were estimated from acoustic trawl surveys conducted during the 2012 and 2013 Arctic Eis cruises. Spatially resolved abundance estimates for this report were provided by Alex de Robertis (NOAA AFSC, Seattle) and the data and methods are summarized in de Robertis et al. (2017b). Catch-per-unit-effort of demersal Arctic cod and their length compositions at stations sampled during the 2012 bottom trawl survey were provided by Robert Lauth (NOAA AFSC, Seattle) and are summarized in Goddard et al (2014). All data used in this study have been uploaded to the AOOS Arctic Eis Ocean Workspace and will be made available to the public. Key biological parameters for Arctic cod were obtained from the literature on Arctic cod from other regions or were estimated from the available data for the Chukchi Sea. This report is being prepared for submission as a manuscript and will be part of Ph.D. student Jennifer Marsh's dissertation.

Abstract

As the most abundant and widespread forage fish in the Chukchi Sea, Arctic cod (*Boreogadus saida*) is considered a keystone species. In addition to their integral role in the ecosystem, Arctic cod was identified as one of three potential target species in the 2009 North Pacific Fishery Management Council Arctic Fisheries Management Plan. Currently, commercial fishing is prohibited in the US Arctic due to insufficient data to assess the sustainability of potential fisheries. To address this need, comprehensive fisheries oceanography surveys took place throughout the US Chukchi Sea during the late summers of 2012 and 2013. High densities of age-0 Arctic cod were observed in the northeast Chukchi Sea during both years, while older Arctic cod (age-1+) were more widely distributed throughout the survey area. Our objectives were to improve our understanding of the factors driving variations in the distribution and abundance of Arctic cod and to assess the current status and dynamics of Arctic cod in the Chukchi Sea. We estimated age-structure, abundance, biomass, and reproductive potential using data from the recent surveys combined with available estimates of biological parameters found in the literature. Results indicate that temperature is an important driver in the distribution of both age-0 and age 1+ Arctic cod with age-0 cod less likely to be present in warmer temperatures. Estimates of egg production and early survival suggest that the number of mature Arctic cod present in the summer are unlikely to produce the observed high abundances of age-0 Arctic cod in the US Chukchi Sea. This could imply that either mature Arctic cod migrate from surrounding regionst to the Chukchi Sea to spawn in the winter, that the age-0s are advected from outside the study area, or that we are underestimating adult Arctic cod abundance. Continued systematic surveys and further research is needed on the origins of age-0 Arctic cod and their early life survival to assess changes in this ecologically important forage fish.

1. Introduction

Arctic cod (*Boreogadus saida*) are the most abundant and widely distributed forage fish in the Arctic Ocean and surrounding seas (Lowry and Frost 1981; Barber et al. 1997; Gillispie et al. 1997). They are adapted to low light conditions (Jonsson et al. 2014) and cold temperatures (sub-zero) through the production of anti-freeze glycoproteins (Osuga and Feeney 1978). They play a central role in Arctic food webs, linking upper and lower trophic levels and transferring energy between benthic and pelagic realms (Welch et al. 1992). Because of their high abundance and energy density (Harter et al. 2013) they are an important prey resource for many migrating seabirds (Matley et al. 2012) and marine mammals (Laidre and Heide-Jørgensen 2005, Loseto et al. 2009). Although their commercial potential has been recognized (e.g. NPFMC 2009), there have been few historical or current fisheries for Arctic cod. In the Barents Sea there is a longstanding pelagic trawl fishery targeting concentrations of Arctic cod in late autumn during southward spawning migrations. The fishery began in the 1950s with participants mainly from Russia and Norway. Catches peaked at over 348,000 metric tons (mt) in 1971 (Gjøsæter 1995) and continue at much reduced levels with 19,600 mt harvested by Russia in 2011 (ICES 2012). Off the coast of Alaska, small amounts of Arctic cod are caught in subsistence fisheries in the Beaufort and Chukchi seas (Magdanz et al. 2010). Past fisheries have found commercial uses for Arctic cod, but due to their integral role in the ecosystem, there are concerns over commercial removals. Currently, commercial fishing is prohibited in the US Arctic due to insufficient data to assess the sustainability of a potential fishery (NPFMC 2009).

To address this need, comprehensive fisheries oceanography surveys took place throughout the US Chukchi Sea during the late summers of 2012 and 2013 (Mueter et al. 2017). High densities of age-0 Arctic cod were observed in the northeast Chukchi Sea during both years (De Robertis et al. 2017b), either in the surface mixed layer or throughout the water column. In contrast, older Arctic cod (age-1+) were more widely distributed throughout the Chukchi Sea during bottom trawl surveys conducted in 2012 (Goddard et al. 2014).

The objectives of this study are (1) to improve our understanding of the factors driving variations in the distribution and abundance of Arctic cod in the US Chukchi Sea and (2) to assess the current status and dynamics of Arctic cod in the Chukchi Sea. To meet these objectives, we used new survey data combined with available estimates of biological parameters for Arctic cod from other regions. First, we modeled survey catch per unit effort (CPUE) of age-0 and age-1+ Arctic cod relative to physical (temperature, salinity) and biological (productivity, competitors, prey) factors. Second, we compiled and updated life history information on Arctic cod to estimate their age-structure, abundance, biomass, and reproductive potential in the Chukchi Sea. Finally, we used a Leslie Matrix model with updated life history parameters and recent survey data to simulate and better understand the population dynamics of Arctic cod.

2. Methods

2.1 Survey and data collection

In August and September of 2012 and 2013, comprehensive fishery oceanography surveys were conducted in the northeastern Bering Sea and eastern Chukchi Sea bounded by the U.S.-Russia Maritime Boundary to the west and by the 10 m isobath along the Alaskan coast to the east. Main trawling stations were spaced every 55.6 km (Fig. 1a & 1b; 61 stations in 2012 and 39 in 2013) on a standardized grid. At each main station, pelagic fishes and invertebrates were collected with a 400/601 Cantrawl (122 m headrope, 162 to 1.2 cm mesh) from the upper 25 m of the water column, oceanographic data were gathered with a conductivity, temperature and depth meter (CTD) throughout the water column (SBE 9-11 plus or FastCat CTD, Sea-Bird Electronics, Inc, Bellevue, WA) and zooplankton were collected in paired oblique bongo tows (505 µm and 153 µm cod-end mesh) aboard the F/V Bristol Explorer. Acoustic data were gathered while in transit between stations using a split-beam SimRad ES60 echosounder with backscatter at 38 and 120 kHz (details in De Robertis et al. 2017a). Midwater trawls were deployed opportunistically when acoustic signals were strong using the same 400/601 Cantrawl, as well as a modified Marinovich trawl (2013 only; 2 m headrope, 6.4 to 0.3 cm mesh). In 2012 only, a concurrent bottom trawl survey was conducted aboard the F/V Alaska Knight at 71 stations (Fig. 2a) using two gear types to sample epibenthic fishes and invertebrates. The 83-112 Eastern bottom trawl (EBT; 25.3 m headrope, 34.1 m footrope and 32 mm mesh cod-end liner) was towed at all 71 stations, while a 3 m plumb-staff beam trawl (PSBT; 4.1 m headrope, 5.1 m footrope and a 4 mm mesh cod-end liner) was deployed at 39 stations. Temperatures were recorded with a Sea-Bird SBE-39 datalogger attached to the head rope of the EBT. More details can be found in Goddard et al. (2014). Subsamples of fishes collected during the bottom trawl survey were measured to the nearest cm, while fishes sampled in the surface and midwater trawls were measured to the nearest mm and weighed to the nearest g.

2.2. Analysis of environmental and biological influences on Arctic cod distribution

2.2.1 Data processing

Due to poor net selectivity of the surface trawl (De Robertis et al. 2017a) and because age-0 Arctic cod often occurred below the sampling depth of the surface trawl net (Alex De Robertis, NOAA, Seattle, pers. comm.), we used acoustic estimates to calculate station-specific age-0 Arctic cod densities (#/km^2). We extracted the mean age-0 Arctic cod (<7.5 cm), and capelin (*Mallotus villosus*) density estimates from the acoustic transects (De Robertis et al. 2017b) within a 2.5 nautical mile radius of each surface trawl main station in 2012 and 2013 (Fig.1) using ArcGIS version 10.3. To estimate densities of older (age 1+) Arctic cod on the bottom (Fig. 2), we adjusted station-specific CPUE (#/km^2) estimates from the bottom trawl survey to exclude age-0 Arctic cod (≤ 7.0 cm) and to account for gear selectivity (for methods of gear selectivity adjusted CPUE see *biomass, abundance and egg production* section). The 7 cm cutoff was selected based on the overall length-frequency distribution of all Arctic cod sampled, in which the two smallest size modes were separated at approximately 7 cm.

We examined if physical (temperature, salinity) and biological (productivity, competitors, prey) factors may be driving the distribution of age 0 and age 1+ Arctic cod using a statistical modeling approach. Potential explanatory variables included in models for age-0 Arctic cod were sea surface temperature (°C), integrated water column chlorophyll *a* (mg/m^2, Danielson et a1. 2017) as a proxy for productivity, *Calanus* spp. densities (#/m^3; Pinchuk and Eisner 2017) as an indicator of available prey (Gray et al. 2016), capelin CPUE as a likely competitor (Hop and Gjoseater 2013, McNicholl et al. 2016), and lion's mane jellyfish (*Cyanea capillata*) CPUE (#/km$^{2;}$ area swept estimates from the surface trawl catch) as a likely predator (Crawford 2016). Potential explanatory variables used to model age 1+ Arctic cod CPUE were bottom temperature (°C), bottom salinity, integrated water column chlorophyll *a*, and *Calanus* spp. density. For simplicity, we refer to both acoustic density estimates and trawl survey density estimates as CPUE. Prior to model fitting, CPUE estimates were log-transformed to achieve approximate normality of model residuals.

2.2.2 Statistical analyses

To address objective 1, we examined the effects of environmental and biological variables on Arctic cod using a generalized modeling approach. The abundances of age-0 Arctic cod in the water column and age-1 Arctic cod on the bottom were modeled separately. Age-0 Arctic cod CPUE had a disproportionate amount of zeros and the combined 2012 and 2013 data were modeled using a 2-stage approach. In the first stage, the presence or absence of age-0 cod was modeled as a binomial response using a logistic regression with a logit link. In the second stage, log-transformed abundances (CPUE) at those stations where age-0 cod were present were modeled using a generalized additive model (GAM) with a Gaussian response.

We first fit full models at each stage that included all of the hypothesized explanatory variables, but no interactions. In the first stage, the logit of the probability of age-0 Arctic cod being present in sample *i* (p_i) is modeled as a linear function of the predictor variables as follows:

$$\log\left(\frac{p_i}{1-p_i}\right) = \alpha_t + \beta_1(SST_i) + \beta_2(Chla_i) + \beta_3(Cal_i) + \beta_4(Cape_i) + \beta_5(Lion_i) + \varepsilon_i \quad (1)$$

where α_t is the intercept for year *t*, β_1- β_5 are coefficients (slopes) for sea surface temperature (*SST*), Chlorophyll a (*Chla*), *Calanus* spp. density (*Cal*), capelin CPUE (*Cape*), and lions mane jellyfish CPUE (*Lion*), and ε_i is the residual for sample *i*.

To model variability in age-0 Arctic cod CPUE-where-present (log transformed to approximate normality) we used Generalized Additive Models (GAMs) to allow for potential non-linearities in the relationships between CPUE and explanatory variables. The full-model equation was as follows:

$$\log(Bsa_i) = \alpha_t + f_1(SST_i) + f_2(Chla_i) + f_3(Cal_i) + f_4(Cape_i) + f_5(Lion_i) + \varepsilon_i \quad (2)$$

where log(*Bsa*$_i$) is the log$_e$-transformed CPUE of age-0 Arctic cod, α_t is the year-specific intercept for year *t, f_1- f_5* are non-parametric smooth functions for each explanatory variable, and the residuals, ε_i, are assumed to follow a normal distribution with mean 0 and variance σ_ε^2.

To examine variability in Age-1+ Arctic cod, which were present at 70 out of 71 bottom trawl stations, we modeled log-transformed CPUE as a function of selected explanatory variables. The full model equation was as follows:

$$\log(Bsa_i) = \alpha_t + f_1(BT_i) + f_2(Sal_i) + f_3(Chla_i) + f_4(Cal_i) + \varepsilon_i \quad (3)$$

where α_t is an intercept for each year *t, f_1-f_4* are separate smoothing functions for bottom temperature (*BT*), bottom salinity (*Sal*), Chlorophyll a (*Chla*), and *Calanus* spp. CPUE (*Cal*), and the residuals, ε_i are assumed to follow a normal distribution with mean 0 and variance σ_ε^2.

To identify which environmental or biological variables are most likely to influence Arctic cod presence and abundance, we compared each of the full models to reduced models using a step-wise parameter selection (removing the term with the highest p-value) and selected the best-fit model using Akaike's Information Criterion (AIC; Akaike, 1974). When the difference in AIC values was < 2, the more parsimonious model (fewer parameters) was selected. Results from the best-fit models were plotted to visualize the estimated relationships between biological or environmental factors and Arctic cod presence or CPUE. All regression analyses were performed in the statistical program R (version 3.1.2; R Core Team 2014) and GAMs were fit using the R package mgcv (Wood and Augustin 2002). The explanatory variables *Chla* and *Cal* were only available for a reduced dataset. If these variables were not present in the best-fit models for the reduced dataset, the model was re-fit using the complete dataset.

2.3 Abundance, biomass and egg production estimates

2.3.1 Gear selectivity

To account for known under-sampling of smaller sized fish in the EBT hauls, we used CPUE estimates from the paired PSBT and EBT hauls to estimate gear selectivity for Arctic cod at different lengths. Paired trawls with both the EBT and the PSBT gear types were conducted at 39 of the 71 bottom trawl stations. Paired trawls were typically deployed on the same day, but at 4 stations the two gear types were used 30-35 days apart. These stations were not included in the selectivity analysis. An additional paired trawl was excluded, in which 3 Arctic cod were caught in the EBT but no associated lengths were recorded. The PSBT has smaller meshes and is effective for sampling juvenile and small adult fishes (e.g. Abookire and Rose 2005), while the EBT has relatively large meshes, which retain larger fishes, but allow for some escapement of smaller fishes like age-0 gadids (e.g. Somerton et al. 2011). Using area-swept (tow distance x net width), we estimated CPUE (#/km^2) within 1cm size bins for each station and gear type. First, station and gear-specific length frequency distributions were constructed for all Arctic cod captured in a haul or for a random subsamples of the catch. Length-frequencies from subsamples were extrapolated to the entire haul, and CPUE was calculated by length bin for each gear type and station combination. Arctic cod length-binned CPUEs from the 34 paired hauls were averaged across hauls for each gear type. To estimate selectivity of the two gear types, we made the following assumptions: (1) the selectivity of each gear can be described by a logistic curve, (2) selectivity of the PSBT is close to one for small fishes and decreases with length, and (3) selectivity of the EBT increases with length and approaches one for large fishes. Selectivity of gear type *j* in length bin *l* (y_{jl}) was modeled using the following logistic equation:

$$y_{jl} = \frac{1}{1+e^{b_j(x_l-a_j)}} \quad (4)$$

where x_l is the mid-point of length bin *l*, parameter a_j corresponds to size at 50% selectivity for gear type *j* (PSBT or EBT) and b_j corresponds to the slope of the curve for gear type *j*. For the PSBT the slope was constrained to be positive ($b \geq 0$), corresponding to decreasing selectivity with length, while for the EBT we assumed $b \leq 0$. We estimated the parameters using a least-squares approach that minimized a weighted sum of squared differences between the predicted length-binned CPUEs for the two gear types. The squared differences for each length bin were weighted by the inverse of the total number of fish in a given length bin. To reduce variability in the weights across length bins and avoid problems with zeros in some length bins, the number of fish per length bin was smoothed using a running average over 3 consecutive length bins prior to weighting.

2.3.2 Abundance

We used the area-swept method to estimate Arctic cod overall abundance and abundance by length across the survey region. It was assumed that the measured sub-sample from each haul was representative of the length frequency of the entire sample. We calculated the selectivity adjusted EBT CPUE (#/km^2) by length bin for each haul, by dividing EBT CPUE estimates by selectivity-at-length ($y_{L,EBT}$). The sampling design was on a standardized grid, with each station representing an area equal to (55.6 km)^2, except stations close to land which were assumed to be representative of all waters within a grid cell that were deeper than 5 m (based on ETOPO1 Global Relief Model; Amante and Eakins 2009). Those stations represented areas ranging from (40.3 km)^2 to (55.4 km)^2. We estimated total abundance at length (N_L) across the survey area using the following equation:

$$N_L = \sum_{S=1}^{71} CPUE_{L,S}/y_{L,EBT} \times Area_S \quad (5)$$

where $CPUE_{L,S}$ is the area swept CPUE of Arctic cod in length bin *L* at station *S* (1-71). The total abundance of age 1+ Arctic cod was then estimated by summing abundances across all length bins ≥ 8cm, assuming that smaller Arctic cod were age-0. We used unadjusted CPUE estimates (the sum of station area x unadjusted station CPUE) for comparison with abundance estimates from 1990-91 surveys that were not adjusted for net selectivity and used very similar sampling gear.

2.3.3 Biomass

To estimate the biomass of Arctic cod in the eastern Chukchi Sea at the time of the survey, lengths were converted to weights using the length-weight relationship from Helser et al. (2016):

$$W = 1.30E^{-5} \times L^{2.9} \quad (6)$$

where *W* is the weight of fish in g and *L* is length in mm. Selectivity-adjusted abundance estimates from each length bin (≥ 8 cm) were multiplied by the corresponding weight and summed to calculate the Arctic cod age 1+ biomass. The survey area biomass was converted to metric tons (mt). We compared this new biomass estimate with the estimate in the Arctic FMP (NPFMC 2009) and updated estimates of maximum sustainable yield for the Chukchi Sea provided in the Arctic FMP (NPFMC 2009).

2.3.4 Egg production

We calculated potential egg production by Arctic cod sampled in the Chukchi Sea survey area based on the abundance-at-length estimates and maturity and fecundity estimates at length. No data on Arctic cod maturity or fecundity at length are available from the Pacific Arctic region, so we used literature values from Atlantic and Arctic domains around Svalbard (Nahrgang et al. 2014). Assuming that Arctic cod in the Chukchi Sea have a 1:1 sex ratio and spawn every year after reaching maturity (Sakurai et al. 1998), we estimated egg production (*E*) using the following equation:

$$E_D = \sum_{L=8}^{25} \frac{N_L m_{LD} f_{LD}}{2} \quad (7)$$

where N_L is the abundance-at-length *L* (8 – 25 cm), m_{LD} is the proportion of females that are mature-at-length *L* based on estimates from domain *D* (Arctic or Atlantic) and f_{LD} is fecundity-at-length *L* for domain *D*.

2.3.5 Uncertainty

To evaluate uncertainty in selectivity parameters, abundance-at-length estimates, biomass and egg production we used a bootstrap approach. First, the length-binned CPUE values from 34 paired trawls were resampled with replacement to obtain a new bootstrap sample of size 34. The selectivity parameters for the EBT (a and b in Eq. 1) were estimated from this bootstrap sample using the methods described in the gear selectivity section above and the resulting selectivity vector was saved. Next, the length-binned CPUE estimates for the remaining 36 unpaired EBT trawls were resampled with replacement. Finally, using the saved selectivity vector and the combined bootstrap sample of 70 (34+36) CPUE at length vectors, we estimated selectivity adjusted abundance at length, biomass and egg production as for the original sample. This procedure was repeated 10,000 times to obtain approximate 95% confidence intervals and standard errors for abundance at length, biomass and egg production. Basic bootstrap confidence intervals were constructed based on percentiles of the bootstrap distribution of each quantity of interest (Davison and Hinkley 1997).

2.3.6 Estimates of Natural Mortality

Natural mortality (*M*) is a key parameter in population dynamics models and we used three alternative approaches to estimating mortality. First, we assumed a longevity dependent constant natural mortality (Hoenig 1983) with maximum age set at 8 years (Gillispie et al. 1997):

$$\log(M) = 1.46 - 1.01\log(t_{max}) \quad (8)$$

where t_{max} is the maximum age. Second, we used catch curve analysis to estimate a constant mortality (Quinn and Deriso 1999). For this method, we assumed that the estimated age distributions from the 2012 bottom trawl survey represent the stable age distribution of the population.

$$N_a = N_0 e^{-Ma}$$

$$\log(N_a) = \log(N_0) - Ma \quad (9)$$

where N_a is abundance-at-age *a*. We converted estimated abundance-at-length (N_L) to abundance-at-age (N_a) for age 1+ Arctic cod in the survey area using the selectivity adjusted abundance-at-length data from the EBT and von Bertalanffy growth parameters (Helser et al. 2017). Arctic cod exhibited different growth dynamics north (L_∞ = 197, k = 0.324, t_0 =-1.065) and south (L_∞ = 221, k = 0.297, t_0 =-0.895) of 68.3°N with fish in the north growing at a faster rate, while achieving a smaller asymptotic size (Helser et al. 2017). Because of these regional differences, we estimated the abundance-at-age for each region separately from the selectivity adjusted abundance-at-length data for hauls in each region. Ages were estimated using cohort slicing, which deterministically predicts age from length using the inverse of the Von Bertalanffy growth curve (e.g., Ailloud et al. 2014). For this calculation we used the age_slicing function in the R package ALKr (Loff et al. 2014). The minimum and maximum ages were constrained to 0 and 6. Arctic cod have a maximum observed age of 8, but fish older than 5 are rarely observed. Finally, we estimated weight-varying mortality (M_w) for marine fishes (Lorenzen 1996):

$$M_w = 3.69W^{-0.305} \quad (10)$$

where *W* is the mean weight at age (Table 2).

2.3.7 Leslie Matrix Model

We evaluated the estimates of M in the context of a simple population model, which requires estimates of fecundity-at-age (f_a), survival-at-age (S_a) and abundance-at-age. The Leslie Matrix model is an age-structured population model that can be used to predict population growth or estimate life-history parameters under the assumption that the population is in equilibrium. For a population with three age groups, the model has the form:

$$\begin{bmatrix} N_{1,\,t+1} \\ N_{2,\,t+1} \\ N_{3^+,\,t+1} \end{bmatrix} = \begin{bmatrix} S_0 f_1 & S_0 f_2 & S_0 f_{3^+} \\ S_1 & 0 & 0 \\ 0 & S_2 & S_{3^+} \end{bmatrix} \begin{bmatrix} N_{1,\,t} \\ N_{2,\,t} \\ N_{3^+,t} \end{bmatrix} \quad (11)$$

where $N_{a,t}$ is the number of females at age a at time t, S is the fraction surviving from age a to age $a+1$, and f_a is the net fecundity at age a (see below). Using the estimated abundances at age (ages1 through 6+), three different scenarios for survival and two fecundity scenarios, we calculated the population rate of increase over 50 years to determine which values of M may result in a stable population.

Survival (S_a) at age a (1+) was calculated as follows (Quinn and Deriso 1999):

$$S_a = e^{-M_a} \quad (12)$$

where M_a is natural mortality at age a. Survival was calculated for each of the three natural mortality methods in the previous section.

We estimated two separate fecundity-at-age vectors based on maturity and fecundity at length values from the Arctic and Atlantic domains D, respectively, to bracket likely values for the Chukchi Sea, whose temperatures overlap with the temperature ranges of both domains (Nahrgang et al. 2014). Fecundity-at-age (f_{aD}) was calculated for each age class a (1 through 6+) using the following equation:

$$f_{aD} = \frac{\sum N_{aLR} f_{LD} m_{LD}}{N_a} \quad (13)$$

where N_{aLR} is the abundance at age a, in length class L and in region R (North and South; see Table 2 for age length key by region), m_{LD} is the proportion of females that are mature at length L based on estimates from domain D (Arctic or Atlantic), f_{LD} is gross fecundity (number of eggs produced per mature female) at length L for domain D, N_a is the abundance estimate at age a (1 through 6+; equation 9), and the summation is over all length classes.

For our final Leslie Matrix Model input, we estimated survival from spawning to age-1 (S_0) using the equation:

$$S_0 = \frac{N_1{}'}{E} \quad (14)$$

where $N_1{}'$ is the abundance estimate of age-1 cod from the bottom trawl survey and E is the estimated total egg production (eqn. 7).

2.4 Reconciling age-0 and age 1+ abundances

There is an apparent discrepancy between the estimated age-1+ abundances from the bottom trawl survey and the densities of age-0 Arctic cod in the Chukchi Sea estimated from the acoustic survey. While the latter were very high (comparable to age-0 walleye pollock densities in the southeastern Bering Sea; De Robertis et al. 2017b), adult abundances over the shelf were very low. Hence, we explored whether the adult fish that were present in the study area at the time of sampling could have produced the observed number of age-0 fish in late summer. We predicted a range of abundances of late summer age-0 Arctic cod based on the potential egg production of survey estimatedArctic cod, early life history survival, and egg and larval stage durations. The predicted range of abundances was compared to abundance estimates of age-0 Arctic cod from the 2013 acoustic survey (De Robertis et al. 2017b).

In order to predict the expected number of age-0 fish in late summer, we made assumptions about four aspects of early life history: spawning time, hatch time, egg mortality and larval mortality. In general, early life survival of Arctic cod is poorly understood and very little is known about the life history of Arctic cod in the Chukchi Sea, so we used values from the literature and borrowed from other north Pacific gadids. The predicted abundance of age-0 Arctic cod (N_0) at the time of the survey (mean sampling date) was estimated using the following equation:

$$N_0 = (E \times e^{-M_E t_E}) \times e^{-M_L t_L} \quad (15)$$

where E is egg production (see *egg production* section for calculation, equation 7), M_E is egg daily instantaneous mortality rate, t_E is time to hatch (egg stage duration) in days, M_l is larval daily instantaneous mortality rate, and t_L is time spent as larvae (hatch time to mean sampling date).

Due to considerable uncertainty in these early life history parameter estimates, we estimated the distribution of or assumed a range based on available literature for each of the input parameters to get a lower, upper and mean estimate for N_0. For egg production we used Arctic domain values for maturity and fecundity to estimate mean egg production and the bootstrapped 95% confidence intervals for the upper (97.5%) and lower (2.5%) bounds. Egg mortality rates were unavailable for Arctic cod, so we used literature values for walleye pollock (*Gadus chalcogrammus*), which also have pelagic eggs that are comparable in size. To keep the estimates conservative we used the lowest estimated daily instantaneous mortality rate, which was 0.091 in the Gulf of Alaska (Kim 1989). To examine sensitivity of result to variations in egg mortality, we decreased and increased the assumed mortality rate by 50%. Egg stage duration values were obtained from the literature. Arctic cod eggs hatch between 28 and 90 days after spawning (Rass 1968; Aronovich et al. 1975; Graham and Hop 1995; Ponomarenko 2000; Kent et al. 2016) and spawning occurs between late fall and early winter (Craig et al. 1982), so we used a range of spawn times that allowed for hatch times within the range described in the literature. For the mean estimate N_0, a mean egg duration of 56 days was used. Ninety days was used as an upper bound for egg duration and 28 days as a lower-bound, to estimate lower and upper bounds, respectively, for N_0. To estimate larval duration, first we estimated the approximate hatch date by back-calculating from the average length of age-0s observed in August (35 mm; De Robertis et al. 2017b) using the regression of length on hatch date in Bouchard and Fortier (2011). In the current study, Age-0 Arctic cod were observed between August 7 and September 8, so we chose a mean date of August 23 (day 235) as our observation day and subtracted the hatch date corresponding to mean length to get the time that an average fish spent in the larval stage. The length distribution observed from the acoustic survey was used to estimate variability in larval duration and construct a 95% confidence interval for larval duration. Finally, we used the estimated range of larval daily instantaneous mortality rates (0.037 – 0.046 day^{-1}) from Bouchard et al. (2014) as lower and upper bounds for larval mortality and assumed that the midpoint corresponds to the mean mortality rate (Table 3).

3. Results

3.1 Environmental and biological influences on Arctic cod distribution

Warm surface temperatures of the Alaska Coastal Current extended further North in 2012 than in 2013 (Fig. 1). In 2012, bottom temperatures and lower bottom salinities also extended along the coast to Barrow Canyon, similar to surface conditions (Fig. 2). Age-0 fish were largely confined to the northern Chukchi Sea (Fig. 1a, b), while age-1+ fish were caught in the bottom trawl throughout the study area.

The best-fit model for probability of occurrence of age-0 Arctic cod included terms for year, sea-surface temperature, the abundance of capelin, and the abundance of *Calanus* copepods, but only the sea surface temperature term was highly significant (Table 1a). Probability of occurrence decreased from close to 100% at the lowest temperatures to less than 20% or 40% at the highest observed temperatures in 2012 and 2013, respectively (Figure 1 c,d), when all other variables were held constant at their means. Probability of occurrence slightly increased with capelin abundance and decreased with *Calanus* abundance (not shown).

Based on the best fit model for CPUE-where-present of age-0 Arctic cod, their abundance was significantly related to SST and Chlorophyll *a* and differed significantly between 2012 and 2013 (Table 1b). CPUE was significantly higher in 2013 compared with 2012 (Figure 1e, f) CPUE was lower at the coldest temperatures, increased to a maximum at ~ 6.5 °C and then decreased sharply at higher temperatures (Figure 1e, f). CPUE was fairly constant at log(*Chla*) values <4 and then decreased with increasing *Chla* values. However, it should be noted that the relationship was only slightly significant (p-value = 0.03) and there were only 3 observations of log(*Chla*) > 4: one in 2012 and two in 2013, hence the effect of *Chla* is weak at best.

The best model of Age-1 CPUE, based on 57 stations with complete data for all potential explanatory variables, included only bottom salinity as independent variable, while integrated *Chla*, and zooplankton collected during the surface trawl were not significant (Table 1c). Therefore, we re-fit the model using the full dataset from the bottom trawl survey (71 stations; Table 1d). While the best-fit model included both bottom temperature and bottom salinity (Table 1d), these variables are strongly confounded (Spearman rank correlation = -0.93, p<0.0001) and their effects are difficult to separate. Therefore, we chose to also examine the effects of bottom temperature and salinity on CPUE separately (Figure 2b,d). While age 1+ Arctic cod occur at all temperatures, CPUE was relatively high at low temperatures, increased to a peak around 6 °C, and declined sharply at higher temperatures (Figure 2b). CPUE increased near linearly with increasing salinities to a maximum at 31 psu (Figure 2d). The lowest abundances of age-1+ Arctic cod occurred in low-salinity, warm Alaska Coastal Water. Because salinity and temperature are highly correlated, it is difficult to separate their relative effects on the distribution of age-1+ Arctic cod, although temperature resulted in a much better fit (ΔAIC = 14.3) and was estimated to have a stronger effect than salinity in the best model (Table 1d).

3.2 Abundance, biomass and egg production estimates

The selectivity of the EBT was reasonably well estimated under the assumption that it follows a logistic curve (Figure 3). Size at 50% selectivity (*a* in Eq. 4) was estimated to be 97.7 mm (95% confidence interval: 74.2 mm – 108.0 mm) and the estimated slope (b) was -0.072 (-0.16 – -0.05). For the PSBT model, the corresponding parameter estimates were a = 125.7 mm (95% confidence interval: 117.0 mm – 148.1 mm) and b = 0.088 (95% confidence interval: 0.06 – 0.93).

The estimated selectivity-adjusted total abundance of age 1+ Arctic cod was approximately 3.9 billion (95% confidence interval: 2.1 – 6.2 billion) with a reproductive potential of 5.9 trillion eggs (95% confidence interval: 3.7 – 8.9 trillion eggs) and 5.8 trillion eggs (95% confidence interval: 3.6 – 8.7 trillion eggs), assuming that maturity is similar to that in the Arctic or Atlantic domains around Svalbard

(Nahrgang et al. 2014), respectively. The estimated total adult biomass within the 207,975 km^2 survey area was approximately 44,500 mt (95% confidence interval: 26,583 – 66,970 mt), compared to an estimate of 27,122 mt in the Arctic FMP based on 1990 survey data within a smaller survey of area of 98,803 km^2 in the northeast Chukchi Sea (NPFMC 2009).

3.3 Estimates of Natural Mortality

Natural mortality estimates varied substantially between methods and only the larger values resulted in realistic population growth rates in simulations. The natural mortality estimate based on longevity (Hoenig) was the lowest at 0.53, catch-curve analysis resulted in an estimated mortality of 1.40 (SE 0.22, p-value 0.008) and values for weight varying mortality (Lorenzen) ranged from 1.07 to 1.94 (Table 2). Using estimated mortalities, fecundity values from the Arctic Domain and abundance-at-age estimates (Table 2) as inputs into Leslie Matrix Models, we simulated population trajectories. The population growth rate for longevity based (Hoenig) M after 50 years was 102%, for catch curve M it was 25% and for weight varying (Lorenzen) M it was 2%. Using the fecundity values estimated from the Atlantic domain, the population growth rate were 5% to 17% higher with the largest difference being for weight varying M and the smallest difference for longevity based M. Assuming fecundity and maturity values similar to those estimated for Arctic cod in the Atlantic, simulations with the higher natural mortality rates result in a more stable population and therefore may be more representative of Arctic cod mortality rates in the Chukchi Sea.

3.4 Reconciling age-0 and age 1+ abundances

Using our best estimates for egg production, egg duration, egg mortality, larval duration and larval mortality, we estimated abundance of age-0 Arctic cod at roughly 44 million (Table 3), which is several orders of magnitude less than the 247 billion age-0 fish estimated from the 2013 acoustic survey. When we used our upper bound parameters (shortest egg and larval durations, lowest mortality rates and highest egg production), we estimated approximately 83 billion age-0 Arctic cod (Table 3). Using our lower bound parameter estimates, we estimated only 832 age-0 Arctic cod (Table 3). These results suggest that not enough eggs are produced to account for the large number of age-0s estimated by the acoustic surveys.

4. Discussion

The Arctic Eis surveys provide the first comprehensive assessment of the abundance and distribution of Arctic cod throughout the US portion of the Chukchi Sea. Our results show that that adult Arctic cod are demersal throughout the region and are broadly distributed on the shelf over a broad range of temperatures, but at relatively low abundances. In contrast, young-of-year fish were concentrated at very high densities in the Northeast Chukchi Sea, primarily in winter water or at the interface between Bering Chukchi summer water and winter water. The observed number of adults over the US portion of the shelf is unlikely to account for the large number of offspring observed on the shelf. This suggests 'missing biomass' of adults or advection from outside the study region. A second key conclusion could be that you provided the first estimates of natural mortality and that simulations suggest high mortality rates for Arctic cod or something along those lines. This could be a single introductory paragraph before you get into more detail below.

4.1 Environmental and biological influences on Arctic cod distribution

Temperature was strongly linked to the distribution of age-0 Arctic cod, who were more frequently encountered in the northern half of the survey area, where temperatures were cooler. In general, cool Arctic waters extended further south in and Arctic cod were more wide-spread and approximately 3 times as abundant as in 2012 (De Robertis et al. 2017b). The larger extent of warmer waters in 2012 may indicate restricted availability of suitable habitat for juvenile Arctic cod and may reflect lower levels of spawning, limited advection into the region or reduced egg and larval survival in 2012. Where age-0 Arctic cod were present, CPUE increased non-linearly with temperature to a peak near 7°C, the temperature of maximum growth rate of laboratory-reared juvenile Arctic cod (Laurel et al. 2015). In contrast, in the Barents Sea the majority of age-0 Arctic cod occur between 2.0–5.5 °C (Eriksen et al. 2015). However, we used near sea surface temperature for our analysis and while age-0 Arctic cod were typically observed in near-surface waters, they often extended from the surface to near the bottom in warmer waters and therefore experience lower temperatures on average.

Contrary to our expectation, age-0 Arctic cod CPUE decreased with the density of *Calanus*, which are major prey for small Arctic cod in the Chukchi Sea (Gray et al 2016). However, schools of Arctic cod feeding resulted in local depletion of *Calanus* spp. in Allen Bay in the Canadian High Arctic (Hop et al. 1997). Furthermore, zooplankton biomass was negatively correlated with biomass of planktivorous fish during August through early October in the Barents Sea, suggesting top down control (Stige et al. 2014). We observed a similar negative relationship, suggesting that the high densities of age-0 Arctic cod in the water column may be depleting zooplankton locally in the Chukchi Sea.

Model results suggest that the distribution of age-1+ Arctic cod was also related to temperature and possibly salinity with a decrease in CPUE at the highest temperatures and at lower salinities. Higher temperatures, lower salinities and lower nutrients are characteristic of the Alaska Coastal Current (ACC), which flows northward along the coast of Alaska (Danielson et al. 2017). Though Arctic cod occurred throughout the survey area, the lowest densities occurred in the warmest and freshest waters of the ACC with a steep decline in CPUE when temperatures exceeded 6 °C. In contrast, saffron cod (*Eleginus gracilis*), a potential competitor, were most abundant in these warmer coastal waters. They are generally considered a coastal species and the growth rate of juvenile saffron cod exceeds that of Arctic cod at temperatures above about 10 °C (Laurel et al. 2016) and adults have a faster growth rate and maximum length compared to Arctic cod (Helser et al. 2017). Integrated *Chla* and zooplankton collected during the surface trawl survey were not significantly related to Arctic cod CPUE from the bottom trawl survey, possibly reflecting the temporal mismatch between surface and bottom trawl surveys that were conducted from two different research vessels.

4.2 Biomass, natural mortality and reproductive potential estimates

Given the levels of uncertainty and corrections for survey area, our estimates of biomass are not substantially different from past biomass estimates of Arctic cod in the US Chukchi Sea. Using data from a 1990 survey of the northeast US Chukchi Sea (Barber et al. 1997), which covered a more limited survey area and resulted in a much lower biomass estimate (NPFMC 2009). If we assume that the 1990 biomass distribution was consistent throughout the area corresponding to the Arctic Eis survey area, the total 1990 biomass estimate expands to 57,090 mt, which is well within the 95% confidence intervals of our estimate (26,583 – 66,970 mt). In this study, we adjusted for gear selectivity, but excluded age-0 Arctic cod from the biomass estimate (≤ 7 cm) because they are largely pelagic and not effectively sampled by the large-mesh bottom trawl. Goddard et al. (2014) estimated an unadjusted area-weighted biomass of 31,536 mt (S.E. 210,914 mt) using the 2012 survey data. There was apparent interannual variability in catch between the eight stations that were repeatedly sampled in both 1990 and 1991. The average density of Arctic cod in 1991 was only 22% of the 1990 value for these stations (NPFMC 2009), although the difference was not statistically significant due to large variability among stations and/or small sample sizes. Similarly, temporal fluctuations in biomass estimates for Arctic cod have been observed in the Russian Chukchi Sea (Datsky 2015). Biomass estimates have ranged from 12,600 mt in 2008 up to 674,200 mt in 2003, with the most recent estimate being 45,700 in 2010 (Datsky 2015). While this at least in part reflects large sampling uncertainty, there is a potential for considerable temporal variability in both the Russian and US portions of the Chukchi Sea, which highlights the need for repeated systematic surveys to accurately estimate total biomass and changes in biomass of Arctic cod and other species of interest.

Only the highest estimated natural mortality rates were consistent with a stable population given our assumptions about fecundity, maturity and age composition. Weight varying natural mortality estimates predicted annual mortality of 66% to 86%, while natural mortality estimates based on catch-curve analysis predict 75% annual mortality. In contrast, natural mortality estimates used in the Arctic FMP predicted that only 37% of Arctic cod die annually (NPFMC 2009). The relatively high values of mortality and low survival estimated from catch-curve analysis and body weight are plausible given Arctic cod's ecological role as the major prey for many seabirds and marine mammals (Welch 1992) and potentially high rates of post-spawning mortality (Hop et al. 1995).

Given their low biomass, small size and remote location from fishing ports, the potential for a viable Arctic cod fishery in the Chukchi Sea is low. Although the higher natural mortality rate and the larger survey area would result in a higher maximum sustainable yield (MSY) for the population than the estimate from NPFMC (2009), harvesting Arctic cod in the Chukchi Sea would not be consistent with policies of the North Pacific Fishery Management Council that limit the directed harvest of ecologically important forage species in other areas such as the Bering Sea (NPFMC 2015).

Based on relatively low abundances of age-1+ and high abundances of age-0 Arctic cod, de Robertis et al. (2017b) hypothesized that the Northeast Chukchi Sea serves as a nursery area for Arctic cod. To test this hypothesis, we estimated the number of age-0 Arctic cod that could be produced by the observed population of adult Arctic cod in the survey area using estimated reproductive potential, early life survival and stage duration. We conclude that it is unlikely that mature females in the survey area can produce enough eggs to yield the estimated number of age-0s observed during acoustic surveys. This suggests that either mature fish are migrating into the Chukchi to spawn in the winter, that age-0 fish originate from a larger spawning population outside the study area with the Chukchi Sea serving as a nursery area, or that we are underestimating the abundance of mature Arctic cod in the study area. Arctic cod have been observed to form dense schools in shallow water (Welch et al. 1993) and our sampling may have missed such dense aggregations. Some caution is required in interpreting our results, as we borrowed life history parameters from other regions and even other species in the case of egg mortality. Although we chose conservative (i.e. low) estimates of walleye pollock egg mortality from the literature, it is possible that the egg mortality rate for Arctic cod is even lower because Arctic cod eggs are slightly larger than those of walleye pollock and are usually found beneath the ice, where predation is likely to be low.

While we gained insight into the ecology and population dynamics of Arctic cod through analyzing new survey data, many aspects of the biology of Arctic cod remain unknown. Generally, more information is needed on spawning locations, the timing of spawning, their winter distribution, and early life history parameters. There is also need for more consistent monitoring through periodic systematic surveys such as the Arctic Eis survey to assess changes in the status of the Arctic cod populations over time. In addition to estimates of biomass obtained from such surveys, a reliable fishery stock assessment requires estimates of age at maturity, fecundity and age structure that are specific to the stock of interest and are not currently available. Finally, Arctic cod in the US Chukchi Sea are almost certainly part of a larger stock with a much broader geographic distribution. This is supported by our analysis of egg production and survival to the late juvenile stage, which suggests that the Northeast Chukchi Sea may serve as an important nursery area for Arctic cod in the region.

Our results provide a snapshot of the abundance, distribution and dynamics of Arctic cod in the Chukchi Sea at a time of rapid change, but the future of Arctic cod in our study region is uncertain. The Arctic is warming roughly two times as fast as the rest of the globe, which will likely impact cold-adapted Arctic cod. This warming is evident in a reduction of sea-ice extent and thickness (Stroeve et al. 2014) and an increase in temperatures throughout the Arctic at a rate of roughly 0.5 °C per decade in the Chukchi Sea (Jeffries et al. 2014). Although the consequences of these climate changes for fishes in the Pacific Arctic are poorly understood, sub-arctic gadids such as Pacific cod (*Gadus macrocephalus*) or walleye pollock may expand into the Chukchi Sea (Hollowed et al. 2013) as they have temperature dependent growth rates that exceed those of Arctic cod above 2 °C (Laurel et al. 2015) and therefore may outcompete Arctic cod during the summer months. As the waters continue to warm, suitable habitat may be further restricted for age-0 Arctic cod, but may also result in faster growth (Bouchard and Fortier 2008; Laurel et al. 2015). Therefore, the future of Arctic cod in the northern Bering Sea and Chukchi Sea is highly uncertain and future surveys will be required to monitor their response to a changing climate.

5. Acknowledgements

We thank the captains and crews of the F/V Alaska Knight and the F/V Bristol Explorer. A special thanks to the numerous Arctic Eis scientists that aided in sample collection. This study was funded in part by the Bureau of Ocean and Energy Management (BOEM) Award # M12AC00009 and in part with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, U.S. Fish and Wildlife Service, U.S. Department of the Interior (contracts #s: 10-CIAP-010; F12AF00188). Additional funding for graduate student support was provided by the North Pacific Research Board Graduate Research Award, J. Frances Allen Scholarship, Dr. H. Richard Carlson Scholarship, and the Al Tyler Memorial Scholarship.

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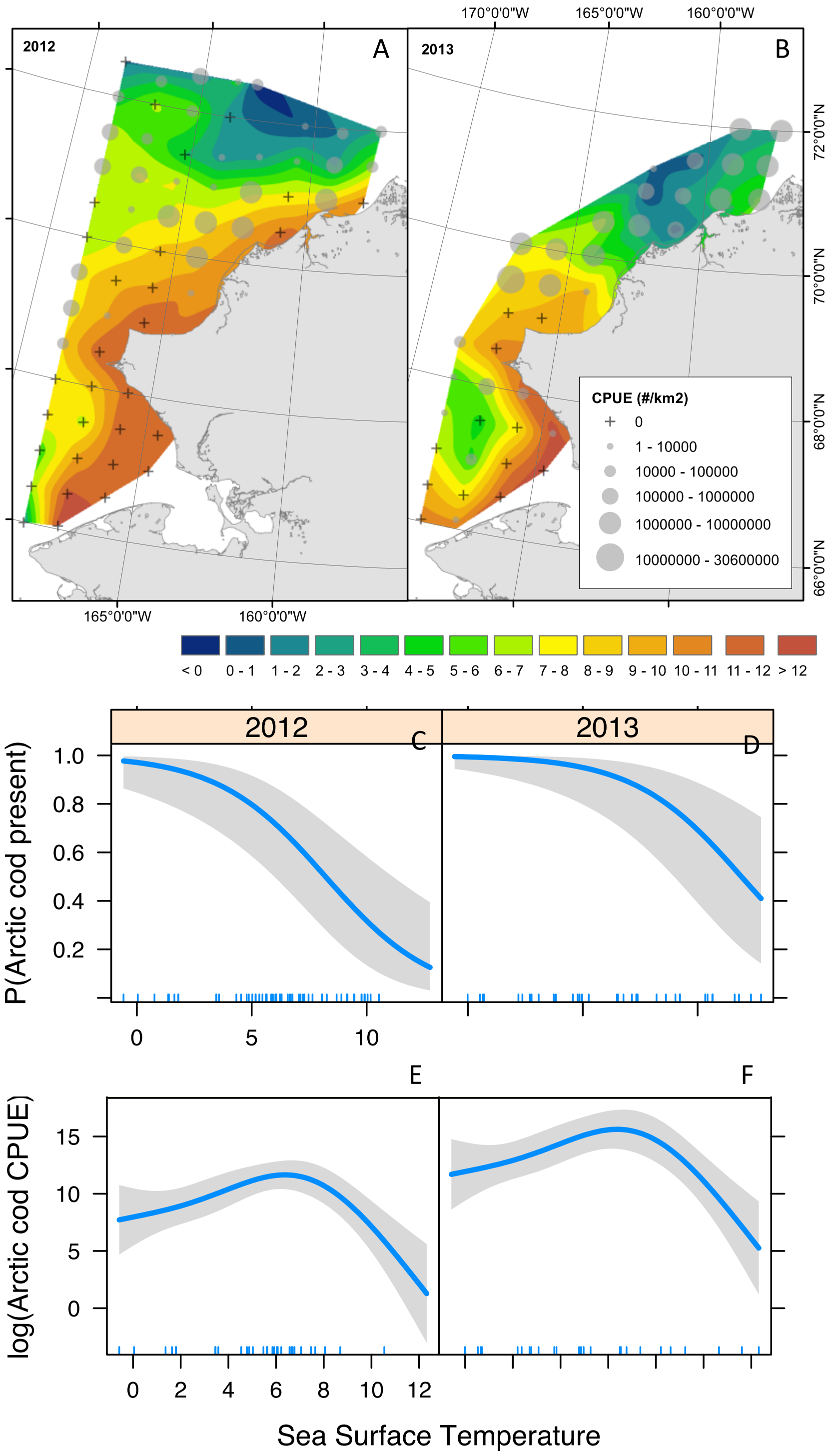
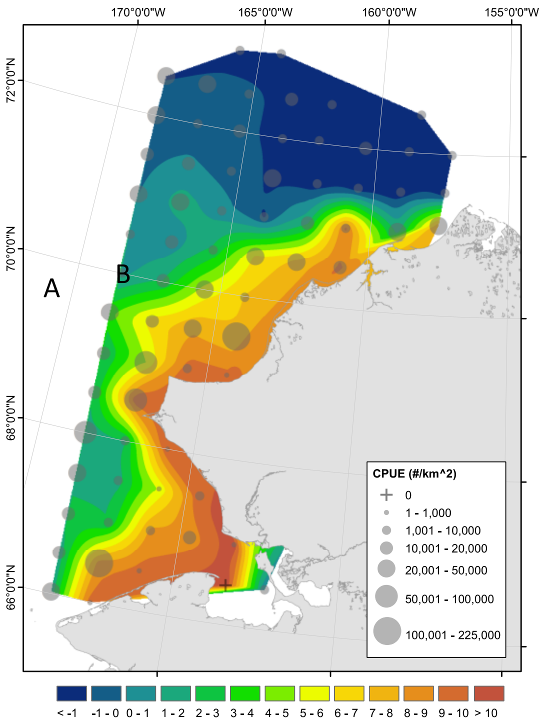
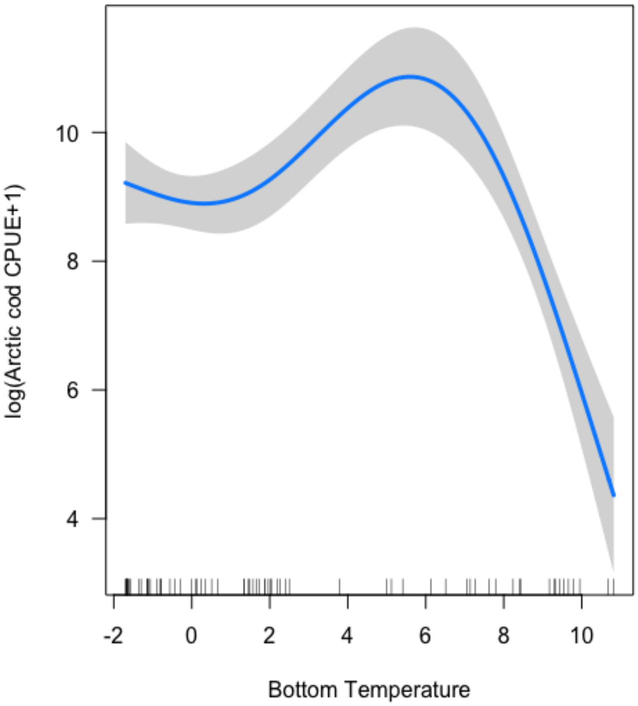
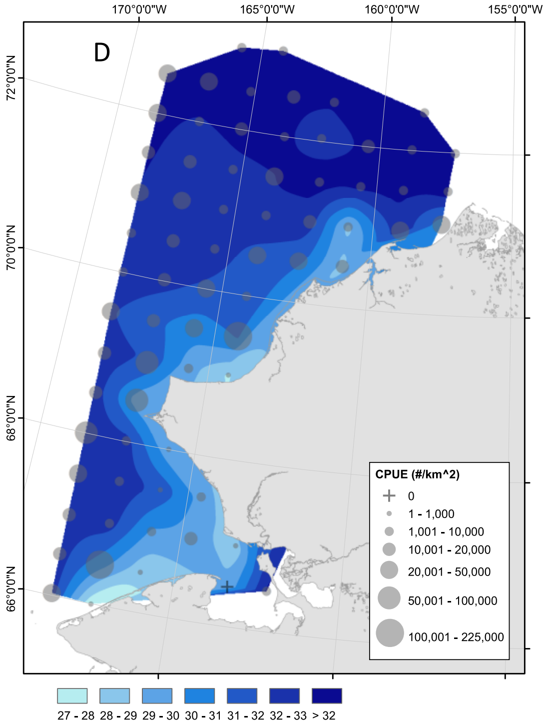


Figure 1. Catch-per-unit-effort (CPUE) of age-0 Arctic cod at surface trawl stations (grey circles) and nearest neighbor interpolated sea surface temperature (SST, color contours) in 2012 (A) and 2013 (B), probability of catching age-0 Arctic cod versus SST from best-fit presence/absence model

(Table 1a) for 2012 (C) and 2013 (D) and model predicted log(age-0 CPUE-where–present) versus SST from best-fit model (Table 1b) in 2012 (E) and 2013 (F).







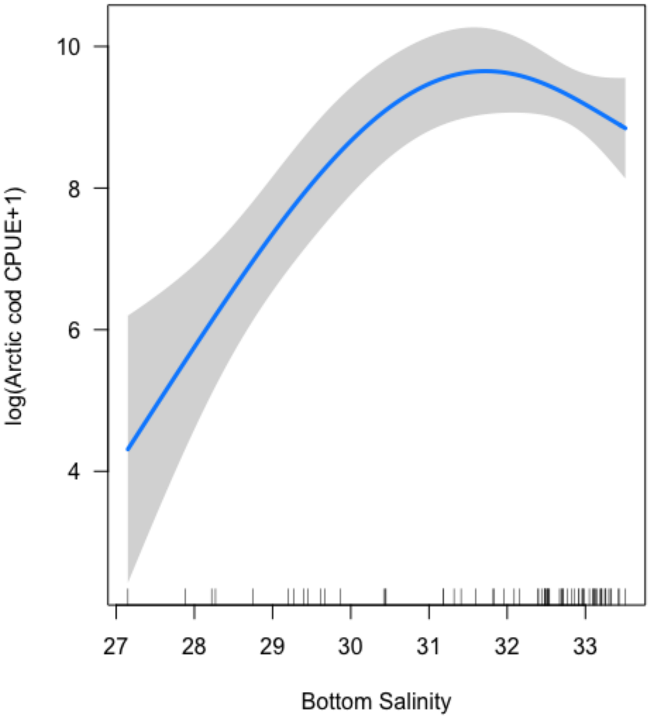


Figure 2. Age 1+ Arctic cod CPUE (grey circles) and nearest neighbor interpolated bottom temperature (A) and bottom salinity (C) maps (color contours). Model predicted ln(age-1+ CPUE +1) versus bottom temperature (B) and salinity (D). Relationships between CPUE and temperature and salinity were modeled separately.

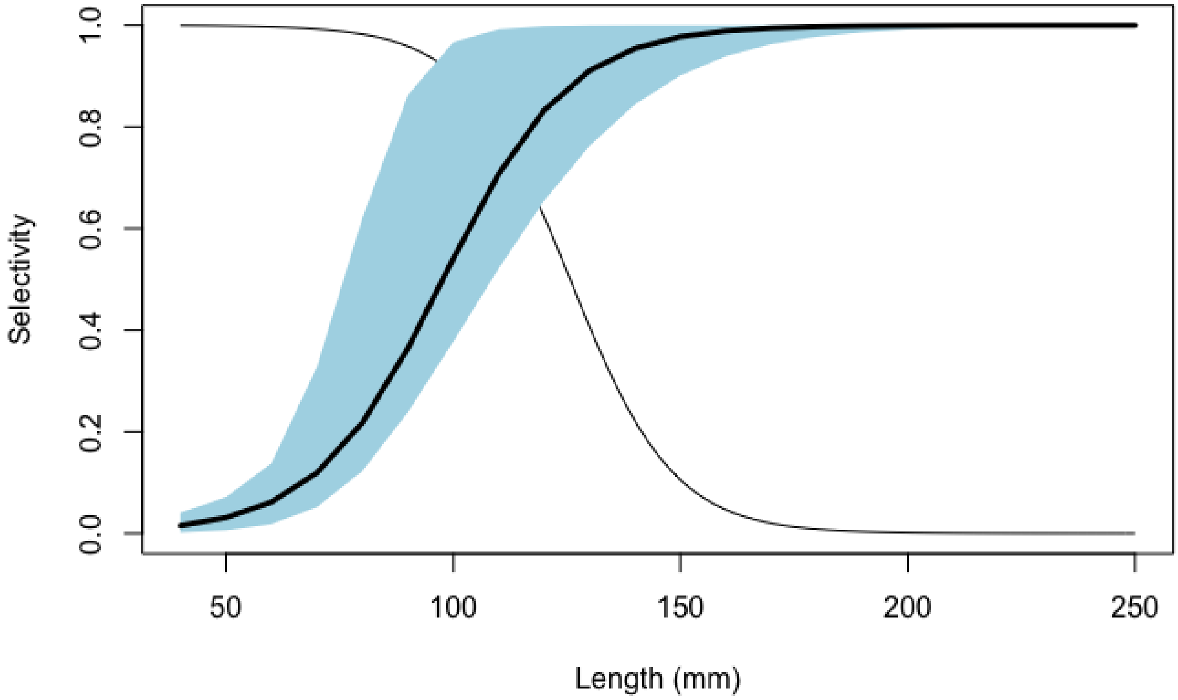


Figure 3. Modeled EBT selectivity curve (thick black line) with 95% confidence band based on bootstrapping (shaded polygon) and modeled PSBT selectivity curve (thin black line).

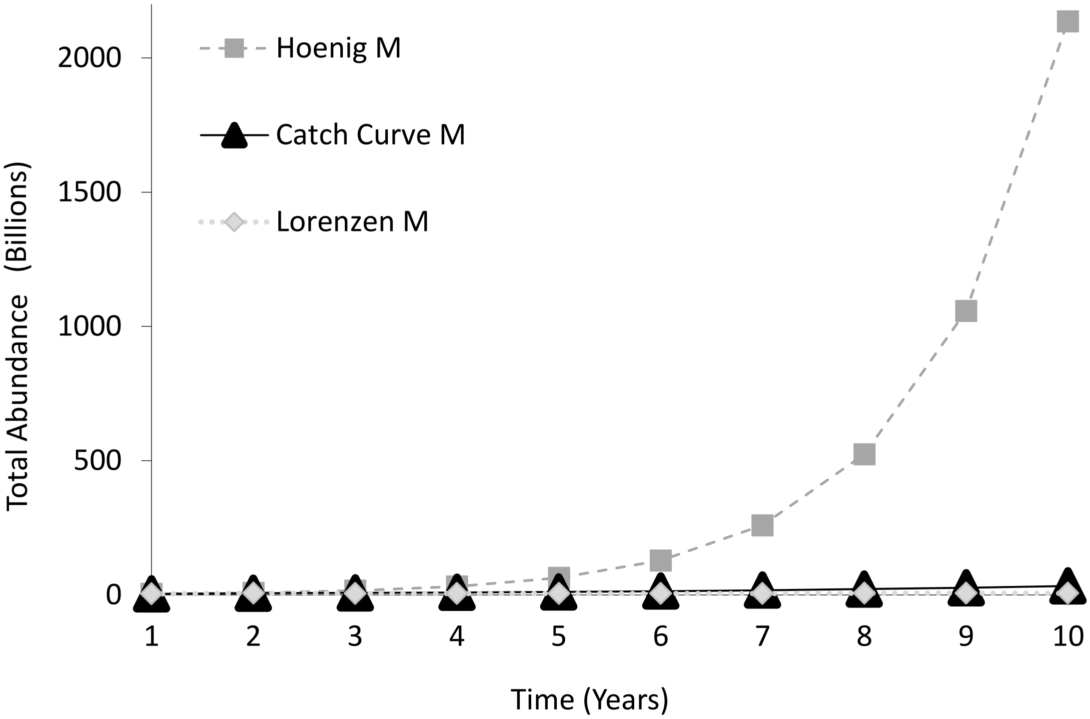


Figure 4. Simulated population trajectories from a Leslie Matrix model for three methods of estimating natural mortality over a ten year span: catch-curve (triangles), longevity-based (Hoenig, squares) and weight-varying (Lorenzen, diamonds). Fecundity was estimated using the maturity schedule from the Arctic domain.

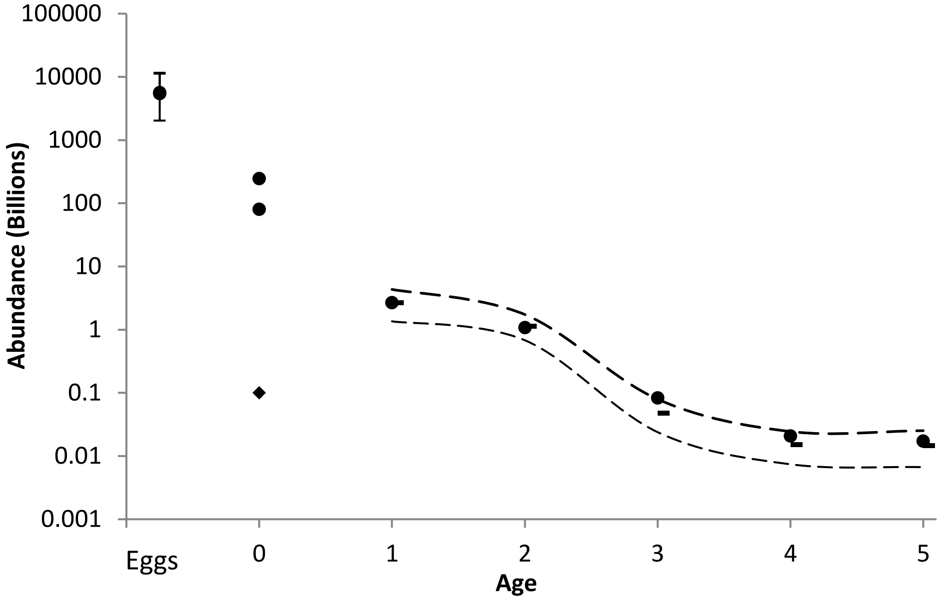


Figure 5. Abundance at age for eggs through age 5. Bootstrap means are depicted with dashes and survey estimates are shown with circles. Bootstrap estimated 95% confidence interval is shown with a dashed line. Age-0 estimates are from the 2012 and 2013 acoustic surveys (De Robertis et al. 2016b) are also shown with circles and estimated age-0s based on number of eggs and literature values of early life survival (diamond; parameters row 1 in Table 3). Estimated egg production (equation 7) with bootstrap estimated 95% confidence intervals.

Table 1. Generalized Additive Model fits for models of age-0 Arctic cod presence/absence (a), CPUE-where-present (b), age 1+ Arctic cod (c) and full data set of age 1+ Arctic cod (d). Model associated degrees of freedom (DF), ΔAIC values, R^2 and number of samples (n) are also listed. Rectangular borders highlight selected best-fit models. Significance of individual terms is indicated at four levels (p-values: *** < 0.001; ** < 0.01; * < 0.05).

	Model parameters	DF	ΔAIC	R^2	n
a)	Additive models, binomial response: age-0 presence/absence				
	Year + SST*** + Chla + Cal* + Cape + Lion	8.7	0.4	0.30	93
	Year* + SST*** + Cal* + Cape* + Lion	7.1	0.0	0.28	93
	Year* + SST*** + Cal* + Cape*	6.0	0.3	0.27	93
	Year* + SST*** + Cape	5.2	2.9	0.26	93
	Year + SST***	3.0	6.0	0.20	93
	SST***	2.0	7.8	0.18	93
b)	Additive models, response: log(age-0 CPUE-where-present)				
	Year*** + SST** + Chla* + Cal + Cape + Lion	10.6	4.5	0.38	56
	Year*** + SST** + Chla* + Cape + Lion	9.6	3.8	0.40	56
	Year*** + SST*** + Chla* + Lion	8.7	1.9	0.40	56
	Year*** + SST*** + Chla*	7.7	0.0	0.41	56
	Year*** + SST***	5.7	6.4	0.31	56
c)	Additive models, response: log(age-1+ CPUE + 1)				
	BT + Bsal*** + Chla + Cal	6.9	3.7	0.30	57
	BT + Bsal*** + Cal	5.9	2.1	0.31	57
	Bsal*** + Cal	5.4	0.3	0.32	57
	Bsal***	4.4	0.0	0.31	57
d)	Additive models, all stations, response: log(age 1+ CPUE + 1)				
	BT*** + Bsal*	7.7	0.0	0.52	71
	BT***	5	6.3	0.45	71
	Bsal***	4.3	20.6	0.32	71

Table 2. Gear selectivity adjusted abundance at age, age-length key for Arctic cod S and N of 68.3 N, mean length (cm) and weight at age, proportion mature at age, gross and net fecundity at age estimated from the Arctic and Atlantic domain maturity schedules (Nahrgang et al. 2014), and instantaneous mortality rates.

		Length range (cm)		Mean Length	Mean Weight	Maturity		Gross Fecundity		Net Fecundity		Instantaneous Mortality Rate		
Age	Abundance	South	North	(cm)	(g)	Arctic	Atlantic	Arctic	Atlantic	Arctic	Atlantic	Longevity	Catch Curve	Weight -based
1	2693669430	8 - 11	8 - 11	10.0	8.2	0.11	0.33	6199	4492	825	1735	0.53	1.40	1.94
2	1080503357	12 - 14	12 - 13	12.4	15.4	0.60	0.53	10560	8093	6539	4308	0.53	1.40	1.60
3	83506461	15 - 16	14 - 15	14.4	23.8	0.84	0.67	13431	12482	11466	9026	0.53	1.40	1.40
4	20841380	17	16	16.1	32.9	0.97	1.00	19335	24381	18755	24381	0.53	1.40	1.27
5	17365241	18	17	17.3	40.2	0.97	1.00	21906	24381	21374	24381	0.53	1.40	1.20
6+	25966429	≥19	≥18	19.7	58.2	1.00	1.00	33441	24381	33441	24381	0.53	1.40	1.07

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Table 3. Predicted age-0 Arctic cod abundance calculated from Equation 15 and associated parameters: egg production, instantaneous daily egg mortality rate, days spent as an egg (hatch time from spawning), daily larval mortality, and time spent as a larva prior to sampling.

Variable	Lower	Mean	Upper	Based on
Egg production	3.62E+12	5.94E+12	8.86E+12	Length distribution, Arctic maturity schedule (Nahrgang et al. 2014 and bootstrapped 95% CI)
Egg stage duration (days)	90	56	28	Minimum, max and mean literature values in Rass 1968, Aronovich et al. 1975, Graham and Hop 1995 and Ponomarenko 2000
Egg mortality (day^{-1})	0.14	0.09	0.05	Estimates from walleye pollock (*Gadus chalcogramma*) +/- 50% (Kim 1989)
Hatch to sampling (days)	215	162	92	95% CI (Lengths from acoustic trawl and length hatch date regression from Bouchard and Fortier 2011)
Larval mortality (day^{-1})	0.046	0.042	0.037	Larval *B. saida* Canadian Beaufort (Bouchard et al. 2014)
Age-0 estimate	832	43,653,999	83,292,139,995	

Appendix N.

Ontogenetic, spatial and temporal variation in trophic level and diet of Chukchi Sea fishes

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Date
September 11, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
C	Carbon
N	Nitrogen
ACW	Alaska Coastal Water
BCSW	Bering Chukchi Summer Water
MW	Melt Water
CWW	Chukchi Winter Water
SIA	Stable Isotope Analysis

List of Oral and Poster Presentations

Marsh JM, Mueter FJ, Quinn TQ II, Iken K, Danielson S (February 25, 2016) Population dynamics, distribution and diet of Arctic cod (*Boreogadus saida*) in the eastern Chukchi Sea Ocean Sciences Meeting, New Orleans LA

Marsh JM, Mueter FJ, Iken K, Danielson S (August 17, 2015) Ontogenetic and spatial variation in the trophic roles of Chukchi Sea Fishes. Annual AFS Meeting, Portland. OR.

Marsh JM (April 25, 2015) A cold-adapted fish in a warming sea. Cod chronicles and salmon stories. Community outreach event, Juneau, AK.

Marsh JM, Mueter FJ, Iken K, Danielson S (January 23, 2015) Ontogenetic, temporal and spatial variation in the trophic roles of Chukchi Sea fishes. AMSS, Anchorage, AK.

Marsh JM, Mueter FJ, Gray B, De Robertis A (April 9, 2014) Distribution and trophodynamics of Arctic cod (*Boreogadus saida*) in the eastern Chukchi and northeastern Bering Seas. Ecosystem Studies of the Sub-Arctic Seas (ESSAS) Annual Science Meeting, Copenhagen, Denmark.

Marsh JM, Mueter FJ (January 20, 2014) Ontogenetic and environmental influences on the trophic roles of Chukchi Sea fishes. AMSS, Anchorage, AK (poster).

Marsh JM, Mueter FJ (October 9, 2013) Ontogenetic and spatial variation in the trophic roles of Chukchi Sea fishes. 40th Annual Alaska Chapter Meeting of the AFS, Fairbanks, AK (poster).

Marsh JM, Mueter FJ (March 26, 2013) Trophic dynamics of Chukchi Sea saffron cod. 28th Lowell Wakefield Symposium, Anchorage, AK (poster).

Proposed Objectives and Study Chronology

The proposed objectives were to (1) determine trophic levels of common marine and anadromous fish species in the eastern Chukchi Sea, (2) examine spatial and temporal variability in the stable isotope composition, and (3) construct a food web model for the fish community of the eastern Chukchi Sea based on stable isotopes. In the following report, we address objectives 1 and 2. Because we collected few prey items, food web models were not constructed. Instead, we assessed the spatial variability in the stable isotopic composition of the fish community for each water mass to examine and compare community level measures, such as, isotopic niche space, trophic redundancy and trophic separation across water masses. Fish samples were collected via surface, midwater and bottom trawls during the 2012 and 2013 Arctic Eis cruises. In addition, *Calanus* spp. samples were collected during paired oblique bongo tows during the 2012 and 13 surface trawl surveys. Laboratory work was completed in the fall of 2014. The stable isotope data used in this study has been uploaded to AOOS Arctic Eis Ocean Workspace and will be made available to the public. This report has been submitted as a manuscript and has been accepted to the Arctic Eis special issue of Deep-Sea Research Part II.

Abstract

Climate warming and increasing development are expected to alter the ecosystem of the Chukchi Sea, including its fish communities. As a component of the Arctic Ecosystem Integrated Survey, we assessed the ontogenetic, spatial and temporal variability of the trophic level and diet of key fish species in the Chukchi Sea using N and C stable isotopes. During August and September of 2012 and 2013, 16 common fish species and two primary, invertebrate consumers were collected from surface, midwater and bottom trawls within the eastern Chukchi Sea. Linear mixed-effects models were used to detect possible variation in the relationship between body length and either $\delta^{13}C$ or $\delta^{15}N$ values among water masses and years for 13 fish species with an emphasis on Arctic cod (*Boreogadus saida*). We also examined the fish community isotopic niche space, trophic redundancy, and trophic separation within each water mass as measures of resiliency of the fish food web. Ontogenetic shifts in trophic level and diet were observed for most species and these changes tended to vary by water mass. As they increased in length, most fish species relied more on benthic prey with the exception of three forage fish species (walleye pollock, *Gadus chalcogrammus*, capelin, *Mallotus villosus*, and Pacific sandlance, *Ammodytes hexapterus*). Species that exhibited interannual differences in diet and trophic level were feeding at lower trophic levels and consumed a more pelagic diet in 2012 when zooplankton densities were higher. Fish communities occupied different isotopic niche spaces depending on water mass association. In more northerly Arctic waters, the fish community occupied the smallest isotopic niche space and relied heavily on a limited range of intermediate $\delta^{13}C$ prey, whereas in warmer, nutrient-rich Bering-Chukchi summer water, pelagic prey was important. In the warmest, Pacific-derived coastal water, fish consumed both benthic and pelagic prey. Examining how spatial gradients in trophic position are linked to environmental drivers can provide insight into potential fish community shifts with a changing climate.

1. Introduction

Marine ecosystems can be defined and compared by their trophic structure (Lindeman 1942), which may be altered through climate-driven changes in productivity (bottom-up processes), or through predator removals by fishing and alterations in predator range (top-down processes). For example, following a climate shift to a warm regime in the 1970s in the Gulf of Alaska, a community-wide trophic restructuring occurred. The system switched from an ecosystem dominated by benthic crustaceans and forage fish to one dominated by higher trophic level predatory groundfish (Anderson and Piatt, 1999), leading to an increase in trophic level (TL) of the fishery catches from the 1970s through the early 1990s (Urban and Vining, 2008). Conversely, in the North Atlantic, fishing pressure on predatory groundfish, combined with oceanographic changes, resulted in a switch from an ecosystem dominated by demersal fishes to one dominated by small pelagic fishes, benthic crustaceans and bivalves (Frank, 2005). Most likely, the effects of climate and fishing pressure worked synergistically to restructure that ecosystem (Kirby et al., 2009). Therefore, while it can be difficult to tease apart the effects of climate change and fisheries removals on ecosystem structure, the combined effects can be dramatic.

Commercial fishery removals are currently prohibited in the US Arctic, i.e., the eastern Chukchi and western Beaufort seas (NPFMC, 2009), a region impacted by extreme seasonality and pronounced climate change (ACIA, 2004). By 2100, air and sea temperatures in the Arctic are expected to rise an additional 5° C and 1.5° C, respectively, under moderate carbon emission scenarios (IPCC 2013). Moreover, the annual average Arctic sea ice extent has shrunk by 3.5 – 4.1% per decade, with larger decreases of 9.4% per decade (1979-2012) occurring in the summer (IPCC 2013). It has been suggested that the central Arctic Ocean will be seasonally ice-free as early as 2040 (Holland, et al., 2006; Wang and Overland, 2012). With warming and a longer open-water season there is an increased interest in shipping, oil exploration and development/expansion of commercial fisheries. Until the fisheries ban is lifted and/or the Arctic Ocean is seasonally ice-free, the Arctic Ocean offers an opportunity to study effects of climate change with limited confounding from anthropogenic activities.

Future effects of continued climate warming and potential anthropogenic disturbances might have large impacts on the Chukchi Sea ecosystem. Warming waters and reduced extent of the Bering Sea cold-pool, a persistent pool of cold (<2°C) bottom water formed during sea ice brine rejection that acts as a thermal barrier to the expansion of subarctic fishes northward (Mueter and Litzow, 2008), may facilitate earlier seasonal migrations (Moss et al., 2009) or the establishment of some subarctic fishes in the Arctic (Hollowed et al., 2013). These changes could alter Chukchi food web structure through changes in predation and competition for food resources. Also, earlier ice retreat and a prolonged open-water season could lead to earlier phytoplankton blooms and extended growing seasons (Kahru et al., 2011). Observed and future changes in phytoplankton bloom timing and composition (Li et al., 2009), along with changes in zooplankton composition, increases in abundance (Ershova et al., 2015) and grazing pressure (Lane et al., 2008), could possibly weaken the currently strong pelagic-benthic coupling. Currently, cold temperatures in the spring and summer limit zooplankton growth and reproduction; therefore, much of the primary production (ice algae and phytoplankton) is not heavily grazed and settles from the water column to support high benthic biomass (Coyle and Pinchuk, 2002; Questel et al., 2013). These effects will most likely vary spatially, as water mass structure has a strong influence on the community composition and food web structure of the biota (Eisner et al., 2012; Iken et al. 2010). Fishes provide important links between lower and upper trophic levels, as well as between benthic and pelagic communities. Therefore, changes in trophic structure experienced by the fish community may alter the efficiency of the food web with important consequences for upper trophic level species, including seabirds and mammals important to subsistence in coastal communities.

The pelagic and demersal fish biomass in the Chukchi Sea is generally low compared with invertebrate biomass (Stevenson and Lauth, 2012). In previous surveys, 59 demersal fish species in 17 families have been identified in the Chukchi Sea (Barber et al., 1997; Norcross et al., 2010, 2013). However, only 4 families and 10 species comprise the majority of the demersal fish community (~90%): Gadidae (Arctic cod *Boreogadus saida,* saffron cod *Eleginus gracilis*), Cottidae (Hamecon *Artediellus* *scaber*, Arctic staghorn sculpin *Gymnocanthus tricuspis*, shorthorn sculpin *Myoxocephalus scorpius*), Pleuronectidae (Bering flounder *Hippoglossoides robustus,* yellowfin sole *Limanda aspera,* Alaska plaice *Pleuronectes quadrituberculatus*), and Zoarcidae (polar eelpout *Lycodes polaris*) (Barber et al., 1997; Norcross et al., 2013). Even fewer species have been observed in the pelagic fish community with the dominant species being Pacific herring (*Clupea pallasii*), juvenile chum salmon (*Oncorhynchus keta*), juvenile Arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*) and Pacific sandlance (*Ammodytes hexapterus*) (Eisner et al., 2012). These species tend to be segregated into three groups: cold-adapted polar species, coastal species, and Pacific species (Barber et al., 1997; Norcross et al., 2010). Moreover, species richness declines from warmer sub-arctic waters to cooler Arctic waters in the northern Chukchi Sea (Mueter et al., 2013), as well as from nearshore to offshore (Barber et al., 1997; Piatt and Springer, 2003). In previous surveys of the Chukchi Sea, Arctic cod have consistently been one of the most dominant species, in terms of both biomass and abundance, in both pelagic and demersal trawls (Barber et al., 1997; Eisner et al., 2013; Norcross et al., 2010, 2013). This species plays a crucial role in the ecosystem as important prey for many migrating seabirds (Matley et al., 2012) and marine mammals (Bluhm et al., 2008; Crawford et al., 2015; Loseto et al., 2009). Arctic cod are considered a key species linking upper and lower trophic levels in a relatively simple food web (Whitehouse et al., 2014).

To evaluate potential future changes in the fish community it is necessary to understand the diets of different species. Stable isotope analyses provide an alternative and complementary approach to the more traditional stomach content diet analyses. Two stable isotopes, ^{15}N and ^{13}C, are commonly used to characterize trophic status and dynamics. The ratio of heavy to light nitrogen relative to a standard (δ^{15}N) is used to assess trophic level based on a distinct stepwise enrichment from prey to consumer (Minagawa and Wada, 1984; Post, 2002). In contrast, δ^{13}C is conserved throughout the food web with minimal enrichment between trophic levels (0-1‰) and can be used to track diet sources and general feeding habitats; e.g., phytoplankton tends to be more depleted in ^{13}C than benthic primary producers (France, 1995). Unlike stomach content analysis, stable isotope analysis integrates only food items assimilated by consumers, accurately representing a transfer of organic matter between trophic levels, and integrates diet over time-scales ranging from weeks to months, depending on the tissue analyzed (Miller, 2006).

Previous studies using C and N stable isotopes to examine the diets and trophic levels of fauna in the Chukchi Sea have primarily examined benthic organisms, including fishes, but have been limited by small samples sizes and/or spatial coverage (Feder et al., 2011; Iken et al., 2010; McTigue and Dunton, 2014). Studies of a few replicates (usually 1-9 specimens of each fish species collected per water mass) have found differences in fish trophic levels between water masses. Because trophic level (based on δ^{15}N) often increases with body length (e.g., Jennings et al., 2002; Marsh et al., 2012) it is important to consider the trophic position of fish species throughout their life history. For example, the stable isotope signatures of different size classes of five common fish species within a limited region of the northeastern Chukchi Sea typically had higher δ^{15}N values in larger size classes of Bering flounder (*H. robustus*), Arctic cod, polar eelpout (*L. polaris*), Arctic staghorn sculpin (*G. tricuspis*) and stout eelblenny (*Anisarchus medius*) (Edenfield et al., 2011). Here we build on the previous work by conducting a spatially comprehensive stable isotope study.

As a component of the Arctic Ecosystem Integrated Survey, this project presents a unique opportunity to assess the ontogenetic, spatial and temporal variability of the trophic level and diets of key fish species in the eastern Chukchi Sea using C and N stable isotope data, complementing ongoing stomach content studies in the region. In addition, we use community level measures to quantify isotopic niche space, trophic redundancy and trophic separation within each water mass. Our specific objectives are to: (1) create isoscapes of C and N stable isotope ratios based on the primary consumer *Calanus* spp. to quantify and visualize spatial isotopic gradient at the base of the pelagic food web; (2) describe the ontogenetic diets and trophic level of common marine and anadromous fish species in the eastern Chukchi Sea; (3) assess spatial variability in the stable isotopic composition of the fish community by size class; and (4) assess the trophic role of a key species, Arctic cod, within the Chukchi Sea fish food web relative to water mass characteristics. We hypothesize that individual species have unique trophic levels (based on δ^{15}N) that change with body length and that diet source (based on δ^{13}C) changes with body length. We further hypothesize that the stable isotope composition of fishes varies spatially across the Chukchi Sea, reflecting different source waters and communities.

2. Methods

2.1. Study Region

The Chukchi Sea is a broad, shallow (typical depth 50 m) continental shelf region marked by extreme seasonality: dark ice-covered winters versus long days and open water in the summer. Many biological processes are timed to coincide with the spring sea ice retreat, such as migration of fish, seabirds and marine mammals (e.g. Bluhm et al., 2007; Mecklenburg et al., 2011), advection of larval fish and plankton and the timing of the phytoplankton bloom (Kahru et al., 2011). Typically, the ice retreat begins in May to early June with increased solar radiation and advection of warmer waters from the Bering Sea. Three water masses flow northward through the Bering Strait: the nutrient-rich, relatively colder, and more saline Anadyr Water (west), the warmer, fresher and nutrient-depleted Alaska Coastal Water (ACW) in the east, and a shelf mixture of these two water masses with intermediate nutrients levels, temperatures and salinity known as Bering Shelf Water (central) (Coachman et al., 1975). Mixing between the Anadyr Water and the Bering Shelf Water produces the combined Bering Chukchi Summer Water (BCSW) (Danielson et al., this issue). There is typically a strong density front separating the Alaska Coastal Current and the Bering Shelf Water (Grebmeier et al., 1988). An additional water mass resulting from brine rejection during ice formation in winter is the colder and more saline Chukchi Winter Water (CWW; Danielson et al., this issue). In late summer, CWW is commonly found in the lower portion of the water column on the northern Chukchi shelf, often but not always topographically confined to the Hanna Shoal region. The relatively fresh and cold Melt Water (MW) derived from pack ice melt can occupy surface waters in the open water season following the receding ice edge. Finally, the dense and saline (>33.5) Atlantic Water (ATL) is observed in the near-bottom waters (> 200 m depth) at the mouth of Barrow Canyon on the continental slope (Danielson et al., this issue). The distribution and spatial extent of these water masses within the eastern Chukchi Sea is likely to vary in response to both local atmospheric forcing and variability in oceanic advection (Weingartner et al., 2005).

These water masses are key in structuring zooplankton, pelagic fish and demersal fish communities in the northern Bering and southern Chukchi Seas (Eisner et al., 2012; Hopcroft et al., 2010; Norcross et al., 2010; Sigler et al., this issue). Specifically, the fish communities are split into a coastal group in the ACW, a "Pacific-dominated" group in the BCSW, and true Arctic fishes in the CWW (Norcross et al., 2010). The BCSW is characterized by high primary and secondary productivity due to high nutrient availability, a large influx of zooplankton advected from the south, and high benthic biomass (Grebmeier et al., 1988; Walsh et al., 1989). The CWW also tends to have high nutrient concentrations, while the ACW has the lowest concentrations of nutrients and marine carbon during the summer (Walsh et al., 1989).

There is strong connectivity between the water masses and marine communities in the northern Bering and Chukchi seas because of the northward flow through the Bering Strait. Aside from nutrients, heat and freshwater, the Pacific water brings with it biota into the Chukchi Sea. The net northward flow (~0.8 Sv annually) of Pacific Ocean water through the narrow (~80 km) and shallow (<50 m) Bering Strait to the Arctic Ocean is driven by a sea surface height difference between the fresher Pacific Ocean and the more saline Atlantic Ocean (Aagaard et al., 2006). Transport through the Bering Strait varies on interannual, seasonal and shorter time scales related to the position of the Aleutian Low and local winds (Danielson et al., 2014). The flow is greatest in the summer months and least in the winter when the Bering Strait and Chukchi Sea are covered with ice and opposing winds are strong (Woodgate, 2005a). There are occasional wind-driven reversals in flow between November and March (Woodgate et al., 2006). About 20% of the northward flow is comprised of ACW, which is present from May through December (Woodgate, 2005b). Although flow through the Bering Strait is clearly important to the fish community, the role of advection versus local production in structuring and maintaining the fish communities in the Chukchi Sea is poorly understood.

2.2. Sample Collection

All samples for this study were collected during two comprehensive fisheries oceanographic surveys in August/September 2012 and 2013 within the eastern Chukchi Sea (Figure 1). Surveys included oceanography, acoustics, zooplankton, and surface and midwater trawls conducted aboard the F/V Bristol Explorer. During the standardized grid survey, stations were sampled every ~55 km (61 stations in 2012 and 40 in 2013) with additional stations for oceanographic and plankton collections every ~ 28 km along E-W transects (45 stations in 2012 and 62 in 2013). Pelagic fish samples were collected with a 400/601 Cantrawl from the upper 25-30 m of the water column at each main station and opportunistically at locations with a strong acoustic signal by midwater trawls using the same 400/601 Cantrawl as well as a modified Marinovich trawl (2013 only). The 400/601 Cantrawl net was 198 m long with a 122 m headrope and had mesh tapering from 162 to 1.2 cm at the cod-end liner, while the modified Marinovich trawl was ~31 m long with meshes tapering from 6.4 to 0.3 cm at the cod-end liner. Zooplankton samples were collected using 60-cm (505 µm mesh) and 20-cm (153 µm mesh) paired bongos obliquely towed from near bottom to the surface. At each station a conductivity, temperature and depth meter (CTD) collected data throughout the water column (SBE 9-11 plus or FastCat CTD, Sea-Bird Electronics, Inc, Bellevue, WA). In 2012 only, demersal fishes and benthic invertebrates were collected concurrently at 71 main stations aboard the F/V Alaskan Knight, using an 83-112 Eastern bottom trawl (EBT; 25.3 m head rope, a 34.1 m footrope and 32 mm mesh cod-end liner) and, at selected stations, a plumb staff beam trawl (4.1 m headrope, 5.1 m footrope and a 4 mm mesh cod-end liner) (Fig 1). An RDI Citadel CTD was attached to the headrope of the EBT.

Diets by size, as inferred from stable isotopes, were assessed for the most common fish species in the Chukchi Sea (Norcross et al., 2010; Eisner et al., 2012), as well as less common species including capelin and walleye pollock (Table 1). We also collected pelagic and benthic primary consumers as baseline organisms to define the natural spatial and temporal isotope variation at the base of the food web (Table 1). When available, 30 specimens per species were collected from each water mass (Alaska Coastal Water, Bering Chukchi Summer Water, Melt Water (surface) and Chukchi Winter Water (bottom)), based on post-hoc analyses of CTD data, for stable isotope analysis. A sample size of 30 was selected in order to detect a 0.25 change in trophic level over 80% of the maximum length of a given species with 80% power (Galván et al., 2010). Fishes were identified to species, total length measured to the nearest mm, labeled with haul information, and individually frozen for further processing. Where available, 30 *Calanus* spp. were collected from the 150 μm mesh bongo and frozen to a glass slide at each surface trawl station to represent pelagic baseline consumers. Up to 3 bivalves (*Serripes groenlandicus*) were retained as a benthic baseline consumer at each station on the bottom trawl survey, as this species presents a long-lived integrator of carbon and nitrogen available to benthic organisms. Due to limited spatial coverage of *S. groenlandicus*, only *Calanus* spp. were used to convert study organism δ^{15}N values to trophic level and to correct for both δ^{15}N and δ^{13}C baseline variation (see analysis section). In addition to being a prey item for all of the surface trawl caught and some of the bottom trawl caught fish species, *Calanus* spp. also was chosen as a baseline organism because samples were available from most of the sampling sites, allowing us to quantify spatial differences in the baseline values of δ^{15}N. Moreover, *Calanus* spp. were collected throughout the water column and has some degree of spatial overlap with all of the targeted fish species.

2.3. Sample processing

In the lab, samples were prepared for stable isotope analysis (SIA). From minimally thawed fishes, approximately 0.5 g of dorso-lateral muscle were excised with skin and bones carefully removed. For smaller (age-0) fishes, the head, guts and tail were removed and the remainder was retained for SIA.

Also, muscle tissue from *S. groenlandicus* samples, and whole-body *Calanus* spp. (8-12 per sample x 3 samples/station) were analyzed for $\delta^{15}N$ and $\delta^{13}C$. Samples were placed into 20 ml glass scintillation vials, freeze-dried and pulverized with a glass rod. For each sample, 0.2-0.5 mg of muscle tissue, or homogenized copepods were weighed out and enclosed in a tin capsule for SIA. Samples were analyzed at the Alaska Stable Isotope Facility (UAF) for nitrogen and carbon stable isotopes using a Costech ECS4010 elemental analyzer interfaced through a CONFLO III to a Finnigan Delta^{plus}XP isotope ratio mass spectrometer (IRMS). Results are presented in delta (δ) notation in per mil (‰) calculated using the following formula:

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1{,}000$$

where *X* is ^{15}N or ^{13}C and *R* is the ratio of heavy to light isotope ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) for a given element. The standards are Vienna Pee Dee Belemnite for $\delta^{13}C$ and atmospheric air for $\delta^{15}N$. The isotope ratio mass spectrometer precision values were 0.17‰ for $\delta^{13}C$ and 0.32‰ for $\delta^{15}N$ based on the standard deviation of replicates of peptone, which were run on every 10th sample ($n = 290$). About 15 samples with unlikely values, which may have resulted from sample contamination or mechanical error, were re-analyzed for C and N stable isotopes. The newer values replaced the original values and were used in analyses.

2.4 Data analysis

Lipids tend to be relatively more depleted in ^{13}C than proteins (DeNiro and Epstein, 1977). To account for varying lipid contents in our samples (fishes and bivalves), we used an arithmetic lipid normalization equation generalized for aquatic organisms (Post et al. 2007):

$$\delta^{13}C' = \delta^{13}C - 3.32 + 0.99 \cdot C{:}N$$

where $\delta^{13}C'$ is the lipid normalized value, $\delta^{13}C$ is the value from the bulk tissue, and C:N is the carbon to nitrogen ratio for each sample. *Calanus* copepods tend to have a much higher lipid content than fish muscle, thus a similar arithmetic lipid normalization equation specifically for copepods was applied to *Calanus* samples (El-Sabaawi et al., 2008)

$$\delta^{13}C' = \delta^{13}C - 1.85 + 0.38 \cdot C{:}N$$

2.4.1 Isoscapes

We constructed smooth spatial surfaces, or isoscapes, of $\delta^{15}N$ and $\delta^{13}C$ for baseline organisms to visualize variability at the base of the food chain and to correct the fish stable isotope values for this baseline variation. Both $\delta^{15}N$ and $\delta^{13}C$ values of primary producers can vary in space and time (Goericke and Fry, 1994; Holst Hansen et al., 2012; Schell et al., 1998; Vander Zanden and Rasmussen, 1999). In order to compare fish stable isotope values across the eastern Chukchi Sea, it is important to correct for these natural spatial variations because, for example, elevated $\delta^{15}N$ values could result either from fish feeding at a higher trophic level or from a higher baseline $\delta^{15}N$ value. Therefore, we corrected for baseline variation by subtracting estimated $\delta^{15}N$ and $\delta^{13}C'$ anomalies for the primary consumer *Calanus* spp. from the corresponding values for each fish species at a given location.

Stable isotope anomalies for the baseline organism throughout the study region were estimated by fitting a geospatial model to observed anomalies in $\delta^{15}N$ or $\delta^{13}C'$ for *Calanus* spp. The observed anomalies were computed by subtracting the mean values for $\delta^{15}N$ or $\delta^{13}C'$ across all stations from the station-specific means. Models were fit via universal or ordinary kriging, a geostatistical interpolation technique that exploits spatial autocorrelation (nearby values will tend to be more similar) in the observed anomalies, after removing any trends. Specifically, we first removed linear spatial trends from $\delta^{13}C'$, but not from $\delta^{15}N$ because no linear trends in $\delta^{15}N$ were apparent. We then used weighted least squares to fit exponential semi-variogram models to the residuals for $\delta^{15}N$ and $\delta^{13}C'$, respectively. Models were fit separately for 2012 and 2013 to account for interannual differences in baselines. For all semi-variogram models, the nugget was set to 0.2 to account for moderate within station variability. Predicted values were then estimated over a grid covering the entire study area to construct *Calanus* spp. δ^{15}N and δ^{13}C' isoscapes for visual assessment. Raw δ^{15}N and lipid normalized δ^{13}C' stable isotope values for each fish sample were adjusted ($\delta^{15}N_{adj}$ and $\delta^{13}C_{adj}$) by subtracting the kriged δ^{15}N and δ^{13}C baseline anomalies from the corresponding values for fish at each sampling location. Geospatial models were fit using the R package geoR (Diggle and Ribeiro, 2007; Ribeiro and Diggle, 2001). Two unrealistic 2013 *Calanus* spp. replicate samples were removed prior to analysis. The δ^{15}N values of these samples were >3‰ different than the other two replicates at the same station and were assumed to be due to an error.

In addition to the adjusted N isotope ratio ($\delta^{15}N_{adj}$), we computed the corresponding trophic levels of each sample to provide values in a more intuitive framework. Trophic levels relative to the baseline were estimated from $\delta^{15}N_{adj}$ values for each fish sample (Post, 2002) and the trophic levels of individual species and communities were compared across water masses. We assumed that δ^{15}N has a constant enrichment of 3.4‰ from diet to consumer (Minagawa and Wada 1984; Post 2002). In order to estimate the TL based on δ^{15}N data, we used the following equation:

$$TL_i = \left(\frac{\left(\delta^{15}N_{adj,i} - \delta^{15}N_{ref}\right)}{3.4}\right) + TL_{ref}$$

where TL_i is the trophic level of each individual *i*, $\delta^{15}N_{adj,i}$ is the adjusted nitrogen stable isotope ratio for each individual *i*, $\delta^{15}N_{ref}$ is the estimated mean δ^{15}N value for the baseline organism *Calanus* spp. in either 2012 or 2013, and TL_{ref} is the TL of 2.0 assigned to the generally herbivorous *Calanus* spp. (Hobson et al., 2002; Wang et al., 2015).

Finally, we ran linear regressions of the unadjusted δ^{15}N and δ^{13}C' values for each fish species on the modeled baseline values to determine how much variation in the fish stable isotope values were explained by the baseline variation.

2.4.2 Water mass classification

Water mass structure in the Chukchi Sea is known to influence community composition (Eisner et al., 2013) and food web structure (Iken et al., 2010); therefore, we defined water masses for use in further analyses of trophic structure. Water masses were defined based on temperature-salinity (T-S) characteristics that could reflect different times of formation, spatial distributions, or ecological importance. Near-bottom temperatures and salinities represent averages over the bottom 5 m of the CTD profile, and surface layer values are averages from the upper 10 m of the water column. T-S plots were visually assessed for modes such that the resulting water masses had similar characteristics to previously defined water masses in the Chukchi Sea (Alaska Coastal Water = ACW, Bering Chukchi Summer Water = BCSW, Melt Water = MW, Chukchi Winter Water = CWW) (Coachman et al., 1975; Danielson et al., this issue; Eisner et al., 2013; Gong and Pickart, 2015; Weingartner, 1997). Often the mixed layer depth (transition zone between the lower density surface water and higher density bottom layer) was less than 10 m, while the vertical spread of the surface trawl net averaged 17 m and the actual tow depth extended roughly 5 m below that depth. We paired the observed surface and bottom water mass types at each sampling location into distinct water mass structures, including ACW, ACW/BCSW, BCSW, MW/BCSW, BCSW/CWW and MW/CWW, where MW/CWW, for example, denotes surface Melt Water overlaying Chukchi Winter Water and ACW denotes the presence of Alaska Coastal Water throughout the water column.

2.4.3 Ontogenetic shifts

To address objective 2, we modeled $\delta^{13}C'_{adj}$ or $\delta^{15}N_{adj}$ for each species as a function of body length, water mass, and year. We pooled all fishes from the 2012 surface trawl survey and bottom trawl survey to assess ontogenetic shifts in trophic roles between water masses. To examine interannual variability in trophic roles, only fish collected during surface trawl surveys in 2012 and 2013 were used. Prior to model fitting, $\delta^{13}C'_{adj}$ and $\delta^{15}N_{adj}$ values for fish collected in 2013 were further adjusted by the differences in mean $\delta^{13}C'$ and $\delta^{15}N$ values for *Calanus* spp. between years to compare isotopic enrichment relative to the respective baselines. Linear mixed-effects models were used to quantify how $\delta^{13}C'_{adj}$ or

$\delta^{15}N_{adj}$ vary with body length and how this relationship varies among water masses and between years (the latter for surface trawl-caught species only). The isotope ratios ($\delta^{13}C'_{adj}$ or $\delta^{15}N_{adj}$) were modeled as a function of length for each species because ontogenetic shifts in feeding often result in changes of trophic level and foraging habitat. These relationships are often not linear and we observed curvature in some plots of isotope values against raw length that suggested a log-linear relationship, thus three alternative models were fit allowing for either a linear, log-linear or quadratic relationship between length and $\delta^{13}C'_{adj}$ or $\delta^{15}N_{adj}$. The effects of water mass and year were analyzed separately. The full quadratic model includes main effects for year (surface trawl samples only) and water mass, and separate slopes for length by year and/or water mass, as well as random effects by station:

$$Y_{tkji} = \alpha_{tk} + \beta_{1tk}(Length) + \beta_{2tk}(Length)^2 + a_j + b_j(Length) + \varepsilon_{tkji}$$

where α_{tk} is the intercept for year *t* and water mass *k*, β_{1tk} is the coefficient (slope) for length in year *t* and water mass *k*, β_{2tk} is a quadratic coefficient for length^2 in year *t* and water mass *k*, a_j and b_j are random effects that capture station-specific deviations (station *j*) from the mean intercept and slope for a given year and water mass and ε_{tkji} is a residual for the *i*th sample. The random effects a_j and b_j are assumed to follow a bivariate normal distribution:

$$\begin{bmatrix} a_j \\ b_j \end{bmatrix} \sim N(0, \mathbf{\Psi_1})$$

where $\mathbf{\Psi_1}$ is a 2x2 variance-covariance matrix with variances σ_a^2 and σ_b^2 and covariance $\sigma_{a,b}$.

The residuals, ε_{tkji} are assumed to follow a normal distribution with mean 0 and variance σ_ε^2 and are assumed to be independent of the random effects. To find the optimal structure of the random component of the model, we compared the fit of the full model with random slopes (b_j) and intercepts (a_j) to a model with random intercepts only and to a model with no random component besides the residuals. All candidate models were compared using Akaike's information criterion (AIC) to identify the random structure that is most consistent with the data (Akaike, 1974). After we selected the random effects structure, the fit of the full model was compared to all possible reduced models and alternative models with ln(length), for which the full model is shown below:

$$Y_{tkji} = \alpha_{tk} + \beta_{tk}(\ln(Length)) + a_j + b_j(\ln(Length)) + \varepsilon_{tkji}$$

We used AIC to identify the model that was most consistent with the data. When the difference in AIC values was < 2, the more parsimonious model (fewer parameters) was selected. Maximum likelihood estimation was used for model comparisons, while restricted maximum likelihood estimation (Harville, 1977) was used for final parameter estimates. All linear mixed-effects models were fit using the ‘nlme’ package version 3.1-119 (Pinheiro et al., 2015) in the statistical program R (R Core Team, 2014). Goodness of fit was assessed using marginal R^2 (proportion of variance explained by the fixed factor(s) alone) and conditional R^2 (proportion of variance explained by both the fixed and random factors in combination) for linear mixed effects models (Nakagawa and Schielzeth, 2012) and the R^2 for linear models. Results from the best-fit models whose conditional R^2 exceeded 0.2 were visualized as follows. The estimated fixed effects showing the relationship between length and $\delta^{13}C'_{adj}$ or $\delta^{15}N_{adj}$ were plotted for each species and for each of the most common water masses (ACW, BCSW and MW/CWW) sampled in 2012.

2.4.4 Arctic cod

To visualize differences in the isotopic niche space of Arctic cod between years, water masses and size class, standard ellipse areas (multivariate mean ± SD) were estimated and plotted using the R package ‘siar’. Standard ellipse areas contain 40% of the data points (area encompassing $\delta^{13}C'_{adj}$ and $\delta^{15}N_{adj}$ values on a $\delta^{13}C$-$\delta^{15}N$ bi-plot - the larger the area, the more varied the diet).

We examined elemental carbon to nitrogen ratios (C:N) as an index of lipid content and body condition. Higher lipid tissues have higher C:N (McConnaughey and McRoy, 1979) and may indicate a higher relative body condition. Specifically, we modeled C:N for Arctic cod as a function of body length, water mass, and year using the equations in section 2.4.3. To examine potential differences between water masses, we included all Arctic cod sampled in 2012 in our analysis. We also tested for potential interannual differences between the surface trawl caught Arctic cod in 2012 and 2013. Only fish that were sampled in water masses that occurred in both years were included in this analysis. Three outlying C:N values with standardized residuals that exceeded 5 were removed from the analysis because they potentially included non-muscle tissue.

2.4.5 Community isotopic space

To compare fish community trophic structure between water masses we estimated the community isotopic niche space and associated metrics in each water mass (Layman et al., 2007). The isotopic niche space is a measure of diet breadth of the fish community, here defined as the area contained within the smallest convex hull polygon surrounding the mean $\delta^{15}N_{adj}$ and $\delta^{13}C'_{adj}$ for each species-size class combination within each water mass. We calculated mean nearest neighbor distance as a measure of trophic redundancy (smaller distances implying higher redundancy), mean distance to centroid as a measure of trophic separation, $\delta^{15}N_{adj}$ range as a measure of food chain length and $\delta^{13}C'_{adj}$ range as a measure of diversity of basal food sources (Layman et al., 2007). These metrics were calculated using the R package ‘siar’ (Jackson et al., 2011; Parnell and Jackson, 2013). Only species - age class combinations with n≥4 in each water mass were included in this analysis.

3. Results

3.1. Water mass classification

Four water masses were observed in both years (ACW, BCSW, MW, CWW), while Atlantic Water (AW) was observed in 2013 only at a single deep station in Barrow Canyon (Figure 1). There was a nearshore-to-offshore gradient of decreasing water temperature with the warmer and fresher ACW nearshore and the relatively cool more saline BCSW offshore. North of approximately 71°N, the surface and bottom waters were cooler (<2°C) and the fresh and cold MW and cold saline CWW were the dominant water masses. In 2013, the ACW was absent north of 70°N with CWW dominating both nearshore and offshore.

3.2. Isoscapes

Calanus spp. baseline isoscapes for both $\delta^{13}C'$ and $\delta^{15}N$ showed strong spatial gradients with some differences between 2012 and 2013 (Figure 2). Modeled carbon stable isotope values ranged from -24.2‰ to -19.5‰ with similar ranges in both years, although 2013 values were on average enriched in ^{13}C by ~0.8‰. In both years, $\delta^{13}C'$ values were highest in BCSW just north of Bering Strait and decreased to the northeast. Nitrogen stable isotope values ranged from 8.0‰ to 10.8‰ over both years, averaging 9.5‰ in 2013 and 10.1‰ in 2012. In both years, the lowest values were observed within and just north of Bering Strait. In 2012, there was also a nearshore-offshore gradient with higher $\delta^{15}N$ values nearshore. In 2013, a similar gradient was observed, but only in the southern part of the study area, with baseline $\delta^{15}N$ values peaking at 162°W and declining further east towards Barrow.

The differences in baseline values explained between 0 and 41% of the variation in unadjusted $\delta^{15}N$ and $\delta^{13}C'$ values for each fish species. The baseline variability in $\delta^{15}N$ explained > 20% of the variation in the $\delta^{15}N$ values for hamecon and shorthorn sculpin, while the baseline variability in $\delta^{13}C'$ explained > 20% of the variation in the $\delta^{13}C'$ values for Arctic cod, capelin, Pacific sandlance, shorthorn sculpin, Bering flounder, slender and stout eelblennies, and Arctic staghorn sculpin. These fishes were collected both demersally and pelagically.

3.3. Ontogenetic shifts

For fish samples collected in 2012, mean $\delta^{15}N_{adj}$ values spanned nearly two trophic levels based on a 3.4‰ $\delta^{15}N$ enrichment, with values typically increasing between the age-0 and age1+ groups (Figure 3; Tables 1, 2 and 3). Fish collected in the bottom trawl had $\delta^{13}C'_{adj}$ signatures more similar to the Greenland cockle, an epibenthic suspension feeder, whereas the surface trawl caught fish signatures were more similar to *Calanus* spp. Polar eelpout (Lpo) and Arctic staghorn sculpin (Gtr) had the highest mean trophic level, while age-0 Pacific sandlance (Ahe_0) had the lowest value.

For 10 out of the 13 species trophic level ($\delta^{15}N_{adj}$) increased with body length, and the relationship often varied by water mass (Figure 4; Table 4a). A notable exception was Pacific herring (Cpa) for which trophic level decreased with body length over the observed size range (Figure 4). Modeled trophic levels for walleye pollock (Gch) and capelin (Mvi) dipped at intermediate lengths, though the model for the latter had a very low marginal R^2 of 0.08. For saffron cod (Egr), Bering flounder (Hro), Arctic staghorn sculpin, shorthorn sculpin (Msc), and slender eelblenny (Lfa) trophic level increased most rapidly at shorter lengths (Figure 4; Table 4a). The relationship with length varied by water mass for 8 out of 13 species (Table 4a) with a wider range of $\delta^{15}N_{adj}$ values in the MW/CWW and BCSW than in the ACW (Figure 4). In the ACW, model fits overlapped for intermediate sized walleye pollock, Arctic cod, saffron cod and Bering flounder (Figure 4).

Similar to $\delta^{15}N_{adj}$, the $\delta^{13}C'_{adj}$ values for 8 out of 13 species increased with ontogeny, indicating a switch from pelagic to benthic prey with size (Figure 4; Table 4b). The relationship varied by water mass for four species: saffron cod (Egr), Bering flounder (Hro), Arctic staghorn sculpin and stout eelblenny. Several pelagic species (walleye pollock, Pacific sandlance and capelin) showed no trend in $\delta^{13}C'_{adj}$ with ontogeny or differences among water mass structure (Table 4b). Though selected models for Arctic cod and Hamecon (Asc) indicated relationship with length and $\delta^{13}C'_{adj}$, the length term explained little of the variability in $\delta^{13}C'_{adj}$ values (Table 4b).

Interannual differences were observed in the relationship of $\delta^{15}N_{adj}$ with length for Arctic cod (Figure 5), capelin, and Pacific herring and in the mean $\delta^{15}N_{adj}$ for saffron cod (Table 5a). All of these species showed consistent enrichment in ^{15}N in 2013 compared with 2012. The difference increased with length for Arctic cod (Figure 5) and capelin. Interannual differences were also observed in the relationship of $\delta^{13}C'_{adj}$ with length for Arctic cod (Figure 6) and in the mean $\delta^{13}C'_{adj}$ for saffron cod, capelin, and Pacific herring (Table 5b). In 2012, saffron cod, capelin and Pacific herring had lower $\delta^{13}C'_{adj}$ values indicative of a more pelagic diet. For several of these species, samples from the 2012 and 2013 surface trawl surveys consisted almost entirely of similar-sized juveniles (Arctic cod, saffron cod, shorthorn sculpin and chum salmon); therefore, detecting ontogenetic shifts over their entire life history was not possible based on these surveys alone. Nevertheless, trends in both $\delta^{15}N_{adj}$ and $\delta^{13}C'_{adj}$ over the available size range were evident for many of these species.

3.4 Arctic cod

There was a high degree of overlap in the standard ellipse areas of age-0 Arctic cod between water masses (MW/CWW and BCSW) and between years, moderate overlap between age 1+ Arctic cod from the MW/CWW and from the BCSW within the same year, and almost no overlap of age 1+ Arctic cod between 2012 and 2013 (Figure 7). In 2012, it appears that age 1+ Arctic cod fed more pelagically in the BCSW than in the MW/CWW. Furthermore, age 1+ Arctic cod had a more pelagic diet in 2012 than in 2013. Age-0 Arctic cod had similar and overlapping isotopic niche spaces in both years and water masses, indicating a similar diet regardless of year or water mass. Older Arctic cod exhibited a broader isotopic space than age-0 fish. It should be noted that only three age 1+ Arctic cod were sampled for stable isotopes in the BCSW in 2013.

In 2012, regardless of length, Arctic cod sampled in the MW/BCSW, BCSW and BCSW/CWW had the highest C:N values, while cod in MW/CWW had intermediate values and cod in ACW/BCSW and ACW had significantly lower C:N values (Figure 8). The best-fit model included a quadratic length term and different intercepts for each water mass structure (marginal $R^2=0.33$; conditional $R^2=0.58$). When 2012 and 2013 surface trawl samples were analyzed together, no difference was detected between years or water masses. It should be noted that most of the Arctic cod sampled in the surface trawls were age-0 or age-1 (<12 cm).

3.5 Community isotopic space

Fish community isotopic space metrics varied by water mass (Figure 9; Table 6). The fish community in the ACW had the largest range in $\delta^{13}C'_{adj}$ values (-22.3 to -18.0‰), indicating the highest diversity in basal resources and resulting in the largest total area (isotopic niche space), the largest mean nearest neighbor distances (MNND, lowest redundancy) and the largest distance to the centroid (highest trophic diversity). In contrast, the MW/CWW had a much smaller $\delta^{13}C'_{adj}$ range (-21.3 to -19.2‰), total area (isotopic niche space) and MNND (Figure 9; Table 6), implying higher trophic redundancy. The fish community in the BCSW fell largely between the other two water masses in terms of the above characteristics, but had the shortest mean distance to the centroid and a $\delta^{13}C'_{adj}$ range from -22.3 to -19.0‰. Based on the lower $\delta^{13}C'_{adj}$ range of fish community in the BCSW, the fishes seem to be relying on more pelagic prey than the fish community in the MW/CWW, which has intermediate values. All three communities had similar ranges for $\delta^{15}N_{adj}$ (BCSW: 11.6 to 16.1‰; MW/CWW: 11.7 to 16.3‰; ACW: 12.4 to 17.1‰), suggesting that the food chain lengths were similar among communities. However, values in the ACW were slightly higher on average (corresponding to a difference of <0.3 trophic levels).

4. Discussion

4.1 Isoscapes

Isoscapes revealed temporal and spatial variation in the $\delta^{15}N$ and $\delta^{13}C'$ signatures of primary consumers, *Calanus* spp. Isotopic values of primary production have been shown to vary spatially, seasonally and based on species composition (McMahon et al., 2006; Soreide et al., 2006). These differences in baseline isotopic values are linked to nutrient availability (e.g., new [nitrate] vs. regenerated production [ammonium] (Ostrom et al., 1997)), primary productivity (species composition and bloom progression (Soreide et al., 2006; Tamelander et al., 2009)), and microbial degradation (Lovvorn et al., 2005; McTigue et al., 2015; McTigue and Dunton, 2014; North et al., 2014), all of which can be influenced by water mass characteristic and currents.

In both 2012 and 2013 we observed a decline in $\delta^{13}C$' values from the southwest corner of the survey region to the northeastern Chukchi shelf. Similar trends were found in sediment $\delta^{13}C$ values in the northeastern Chukchi Sea (McTigue et al., 2015). The highest $\delta^{13}C$ values were observed in the highly productive Bering Strait region with values decreasing to the northeast. Often, higher $\delta^{13}C$ values are associated with rapid growth rates of phytoplankton (Goericke and Fry, 1994). Generally, $\delta^{13}C$ at the base of the food web decreases with increasing latitude because phytoplankton preferentially uptake $^{12}CO_2$ during photosynthesis and at lower temperatures CO_2 dissolves more readily, increasing the pool of CO_2, which results in a proportionally higher uptake of the lighter $^{12}CO_2$ (reviewed in Fry and Sherr, 1984). In addition, terrestrial carbon tends to be relatively depleted in ^{13}C (Naidu et al., 2000) and $\delta^{13}C$ values were lower along the coast, possibly due to the riverine influence in the Alaska Coastal Current (ACC) (Iken et al., 2010). Similarly, some zooplankton sampled along the coast in the southeast Chukchi Sea (Kotzebue Sound) in the ACW were relatively depleted in $\delta^{13}C$ compared with zooplankton sampled more offshore in the BCSW (Feder et al., 2011). In the present study, relatively high $\delta^{13}C$' values were observed near Hanna Shoal in 2012, but not in 2013 when the ACC did not extend as far north. The elevated values in 2012 could be due to regeneration of carbon in the relatively stagnant water surrounding Hanna Shoal (Day et al., 2013) or the availability of sea-ice algae, as they tend to be enriched in ^{13}C (Soreide et al., 2006). Regenerated C and N, which has been reworked by microbes, tends to have enriched ^{13}C and variable ^{15}N values (McTigue and Dunton, 2014).

In both 2012 and 2013, baseline $\delta^{15}N$ increased to the northeast although lower values were observed in the far northeastern region in 2013. A previous isotope study in the Bering, Chukchi and Beaufort seas found a similar increase in $\delta^{15}N$ values of planktonic organisms with latitude over a much broader spatial scale, which was attributed to isotopic discrimination and higher nutrient availability in the south (Schell et al., 1998). In the southern Chukchi Sea, Feder et al. (2011) observed larger $\delta^{15}N$ values in copepods in the ACW than farther offshore. The decline in $\delta^{15}N$ values in the northern Chukchi Sea in 2013 may be related to the absence of ACW above 70°N in that year as a result of changes in circulation patterns (Danielson et al., this issue), as the ACW tends to have relatively higher $\delta^{15}N$ values, potentially from nitrogen limitation (Lee et al. 2007).

Natural spatial variations in the isotope values at the base of the food web propagate up to higher trophic levels and need to be accounted for when comparing trophic level of animals over large areas. For example, large-scale spatial differences in $\delta^{15}N$ (ranging from 9.7 to 20.9‰) for yellowfin tuna across the equatorial Pacific and western Indian Oceans were explained by differences in baseline $\delta^{15}N$ values, not diet (Lorrain et al., 2015). In the present study the differences in baseline values explained between 0 and 41% (majority > 20%) of the variation in unadjusted $\delta^{13}C'$ values and between 0 and 31% (only 2 species > 20%) of the variation in unadjusted $\delta^{15}N$ values. Likely, the baseline variability explained less of the variation in the $\delta^{15}N$ values than the $\delta^{13}C'$ values because there is a large effect of size on $\delta^{15}N$ for most species. In order to account for the natural baseline variability, we had to make several assumptions. Specifically, we assumed that the sampled fishes and the baseline organism *Calanus* spp. have similar turnover rates and movement patterns. Turnover rate, which is the rate of change in tissue isotopic composition based on tissue replacement due to growth and metabolic processes (MacAvoy et al., 2001), tends to vary with organism size and tissue type. For example, smaller fish tend to have faster turnover rates because they typically have higher metabolic and growth rates (Jennings et al., 2008). The complete isotopic turnover in fish muscle can take anywhere from months (Miller, 2006) to a few years (Hesslein et al., 1993), while shifts in isotopic signatures resulting from diet changes are often observable much sooner. For an Arctic amphipod (*Onisimus litoralis*) the half-life turnover rate was roughly 20 days (Kaufman et al., 2008) and isotopic changes in Arctic bivalves were evident after 4 weeks (McMahon et al., 2006). Presumably, the turnover rate of calanoid copepods would be similar to or faster than the rates for the larger Arctic amphipods. Therefore, turnover times in the fish consumers, which are typically several months (Miller, 2006), likely do not match the turnover times in their prey. This difference may lead to some error when calculating trophic level or estimating diet source. Moreover, movement patterns may vary, as larger fish may be more mobile or sedentary, while *Calanus* spp. are more subject to currents. This is potentially problematic, especially in regions with steep gradients in baseline isotope values (i.e., the southwest corner in the BCSW for carbon in 2012 and northeast region in the MW/CWW for nitrogen in 2013). Furthermore, baseline ^{15}N values are more depleted in the Bering Sea (Dunton et al., 1989; Schell et al., 1998) and larger fish migrating through Bering Strait into the highly productive Chukchi Sea may have isotopic signatures reflecting their diet in the Bering Sea. Most likely, some of the larger fish have different turnover rates and movement patterns, thus their current isotope signatures may reflect diets at different spatial and time scales. For example, in this study some age 1+ Arctic cod collected in the BCSW had unexpectedly low $\delta^{13}C'_{adj}$ values (lower than the mean *Calanus* spp. values). This is likely due to a temporal or spatial mismatch with the baseline organism.

4.2 Trophic roles and ontogenetic shifts

As we hypothesized, the trophic positions of several fish species shifted with ontogeny and often varied with water mass and year. We observed a general increase in trophic level ($\delta^{15}N$) with body size, which has been observed in many ecosystems (Jennings et al., 2002; Marsh et al., 2012; Sherwood and Rose, 2005; Werner and Gilliam, 1984). Typically, as fish grow, their gape size, swimming speed, and energetic demands increase (Scharf et al., 2000). This often leads to consumption of larger, more energy-rich and higher trophic level prey to meet these demands. In addition, fish may change or expand their foraging range as they grow (Werner and Gilliam, 1984). We observed shifts in foraging habitats with increasing length. Typically, younger fish fed in the pelagic zone and increased the proportion of benthic prey as they grew. However, the pelagic forage fish Pacific sandlance and capelin exhibited only pelagic $\delta^{13}C'$ signatures throughout ontogeny.

Several studies have examined fish diets within the eastern Chukchi Sea (Coyle et al., 1997; Edenfield et al., 2011; Frost and Lowry, 1983; Gray et al. 2015, this issue; Iken et al., 2010; Whitehouse et al. this issue) and some have examined ontogenetic diet shifts and regional variability (Coyle et al. 1997; Edenfield et al., 2011; Gray et al. 2015, this issue). Within the Chukchi Sea, Arctic cod, Arctic staghorn sculpin, Bering flounder, shorthorn sculpin and saffron cod are considered generalists that consume a broad range of prey types depending on the local prey available (Coyle et al., 1997; Gray et al., this issue; Whitehouse et al., this issue). In the present study, with the exception of shorthorn sculpin, diet source and trophic level varied by water mass. Similar to the present study, during 1990 and 1991 spatial differences in Arctic cod, Bering flounder and Arctic staghorn sculpin diets were observed between ACW, BCSW and in the MW/CWW (Coyle et al., 1997). Resource partitioning occurs between these species in shared habitats (Coyle et al., 1997; Gray et al. this issue; Whitehouse et al. this issue). However, dietary overlap was observed between similarly sized Arctic and saffron cods (average length roughly 15 cm) collected in the ACW near Point Hope (Coyle et al. 1997). We found that intermediate length Arctic and saffron cods (~10 – 15 cm) sampled in the ACW had nearly identical trophic levels and similar δ^{13}C values, suggesting a very similar trophic niche and a high potential for competition. In addition to regional dietary differences, shifts with ontogeny have been observed for stout eelblenny, Arctic cod, Arctic staghorn sculpin, Bering flounder and shorthorn sculpin in the northeastern Chukchi Sea (Edenfield et al. 2011; Gray et al. 2015, this issue), which corresponds to increasing trophic levels and increasing importance of benthic prey items with length in the current study.

4.3 Arctic cod

Trophic level, diet and body condition of Arctic cod (C:N) varied with body length, water mass and year for Arctic cod. Age-0 Arctic cod occupied a similar isotopic niche space in different water masses, while larger Arctic cod consumed a broader diet of higher trophic level prey that varied by water mass. Our results are consistent with stomach content studies that examined diet over a shorter time scale. Arctic cod are considered generalist zooplanktivores, with diet reflecting local prey availability (Bradstreet et al., 1986). In addition to varying with time and location, Arctic cod diets have been observed to vary with body size (Coyle et al., 1997; Cui et al., 2012; Edenfield et al., 2011; Gray et al., 2015; Rand et al., 2013). In the northeastern Chukchi Sea, age-0 Arctic cod exclusively consumed small, pelagic prey, mainly calanoid copepods (Gray et al., 2015). Similarly, small Arctic cod (7 – 11 cm) in the northern Bering Sea occupied a narrow niche feeding mainly on copepods, while larger Arctic cod (14 – 22 cm) had a broader dietary niche (Cui et al., 2012). In the northeastern Chukchi Sea, diets of larger Arctic cod (> 7 cm) had a higher proportion of benthic prey compared with smaller Arctic cod (≤ 7 cm), though pelagic zooplankton remained the primary food (Gray et al., 2015). In the present study we found Arctic cod to expand their foraging range as they grow and consume higher trophic level prey, but this varied by water mass. In 2012, age 1+ Arctic cod in the BCSW fed mainly on pelagic prey, while cod in the MW/CWW incorporated more benthic prey. Moreover, we found significantly higher C:N values in cod from nutrient-rich BCSW than in cod from the nutrient-poor ACW, with relatively low zooplankton densities. This pattern in C:N ratios likely indicates a diet of lipid-rich *Calanus* spp. in the BCSW. The difference between water masses corresponds to a diet study in the early 1990s in the Chukchi Sea, in which Arctic cod collected in the ACW had no *Calanus* spp. in their stomachs, while the energy dense *Calanus* spp. were the dominant prey for Arctic cod collected in the BCSW (Coyle et al., 1997). Similarly, Arctic cod has higher energy densities offshore and near Barrow Canyon, as opposed to nearshore in the ACW (J. Vollenweider, pers. comm.). We hypothesize that fish in offshore waters (BCSW and MW) may have an advantage over those in coastal waters in terms of prey quality or quantity if higher energetic values reflect the ability to allocate energy to lipid storage.

Differences in the spatial extent of Pacific water masses in the Chukchi Sea between 2013 and 2012 may explain higher $\delta^{13}C'_{adj}$ and $\delta^{15}N_{adj}$ values of age-1+ Arctic cod in 2013 than 2012, indicating a more benthic diet in 2013. Specifically, ACW and BCSW in 2013 did not extend as far north on the NE Chukchi shelf and these waters were colder, fresher and had fewer nutrients on average to support pelagic production, possibly reflecting less inflow through Bering Strait (Danielson et al., this issue). Reduced advection into the Chukchi Sea, lower temperatures and/or less nutrients, in turn, may have resulted in lower densities of *Calanus* spp. observed in 2013, especially in the northern half of the survey area (Pinchuk and Eisner, this issue). Because of this lack of suitable pelagic prey, Arctic cod may have relied more on benthic prey resulting in higher observed $\delta^{13}C'_{adj}$ and $\delta^{15}N_{adj}$ values.

4.4 Isotopic niche space

In addition to spatial variation in intraspecific trophic positions, regional variation in the isotopic niche space of the fish communities suggests differences in food web structure among water masses. Observed differences in isotopic niche space between water masses appear to be a combination of fish species composition and prey availability. Fewer fish species were sampled in the colder MW/CWW. A narrower prey base was observed in the Arctic MW/CWW with intermediate $\delta^{13}C'_{adj}$ values, which suggests a higher reliance on benthic prey and corresponds to a high benthic biomass surrounding Barrow Canyon (Fox et al., 2014; Grebmeier, 2012; Grebmeier et al., 2006). The isotopic turnover rates for fish muscle tissues integrate diet over the past few months (Miller, 2006), so the stable isotope signatures from fishes collected in the MW/CWW may reflect diets of fishes during a time preceding ice-retreat. During ice-cover, fishes within this region may have been largely limited to benthic or ice-associated prey. A more pelagic resource base (lower $\delta^{13}C'_{adj}$) was observed in the BCSW, which is known for high primary and secondary productivity in the water column. These results support previous studies delineating two separate ecosystems with different food web structures in the northeastern Chukchi Sea: a pelagic dominated system in the BCSW and a more benthic driven ecosystem in the MW/CWW (Day et al., 2013).

Fish communities and species with higher resilience are more likely to withstand disturbances resulting from climate change. Community resilience depends on functional redundancy (multiple species with a similar niche space), complexity (many species, many trophic linkages) and resource availability (nutrients and primary production) (Blanchard et al., 2011; Rice et al., 2013; Rosenfeld, 2002). As previously mentioned, in the Chukchi Sea resource and nutrient availability is linked to oceanographic processes, including waters advected through Bering Strait. It is unknown how flow through Bering Strait might change under climate warming, but the Chukchi Sea on the whole may become more like the present-day Bering Sea shelf (earlier ice-retreat, more pelagic system). Warmer and fresher waters may favor smaller phytoplankton that are more likely to be retained in the surface waters (Li et al., 2009).

Also, the warmer water may enhance zooplankton growth and reproduction. Smaller phytoplankton and enhanced grazing pressures would presumably weaken benthic-pelagic coupling. The Arctic fish community in the MW/CWW had the smallest isotopic niche space (lowest complexity and trophic diversity), a limited resource base, but a slightly higher trophic redundancy. On the other hand, the BCSW community draws on a broader resource base and had over twice the isotopic niche space and higher trophic diversity. This seems to imply a competitive advantage and when the Bering Sea influence is larger (i.e., BCSW extends farther north), the community associated with this water mass may displace the species-poor Arctic fish community. Central to the Arctic community is the Arctic cod, which was present in all water masses and showed some diet adaptability, indicating some resilience to ecosystem changes. However, age-0 Arctic cod occupied a narrow isotopic niche space and did not occur in the ACW, indicating that they are more vulnerable than adults to a changing prey field that might result from a changing climate.

Limited accessibility due to remoteness, seasonal ice cover and the high costs of sampling have until recently limited the number of surveys in the Chukchi Sea, an extremely dynamic region experiencing pronounced climate warming (Wang et al., 2013). Although numerous studies have sampled demersal fishes in the Chukchi Sea over recent decades (Norcross et al 2010), this was the first spatially comprehensive, synoptic fisheries oceanographic survey across water masses in the US portion of the Chukchi Sea. As such, this project provides a benchmark for isotopic values of key demersal and pelagic fish species throughout the eastern Chukchi shelf. Against this benchmark, future changes in response to climate warming and anthropogenic activities (e.g., oil exploration, shipping, fisheries, tourism) can be monitored. For many of the fish species in the Chukchi Sea, we demonstrated that diet varies with body-length, region (water mass) and year. Our estimates of trophic levels and energy pathways for common fish species in the Chukchi Sea can also inform food web models, such as the Ecopath model developed at the Alaska Fisheries Science Center (Whitehouse et al., 2014).

Acknowledgements

We thank the captains and crews of the F/V Alaska Knight and the F/V Bristol Explorer. A special thanks to the numerous Arctic Eis scientists that aided in sample collection. We also thank Alexei Pinchuk and Michael Stekoll for use of laboratory equipment; Edward Cokelet for bottom trawl temperature and salinity values; and Lauren Divine and Kenneth Dunton for constructive discussions. We appreciate the feedback from three anonymous reviewers that helped improve this manuscript. This study was funded in part by the Bureau of Ocean and Energy Management (BOEM) Award # M12AC00009 and in part with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, U.S. Fish and Wildlife Service, U.S. Department of the Interior (contracts #s: 10-CIAP-010; F12AF00188). Additional funding for graduate student support was provided by the North Pacific Research Board Graduate Research Award, J. Frances Allen Scholarship, Dr. H. Richard Carlson Scholarship, and the Al Tyler Memorial Scholarship.

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Figures

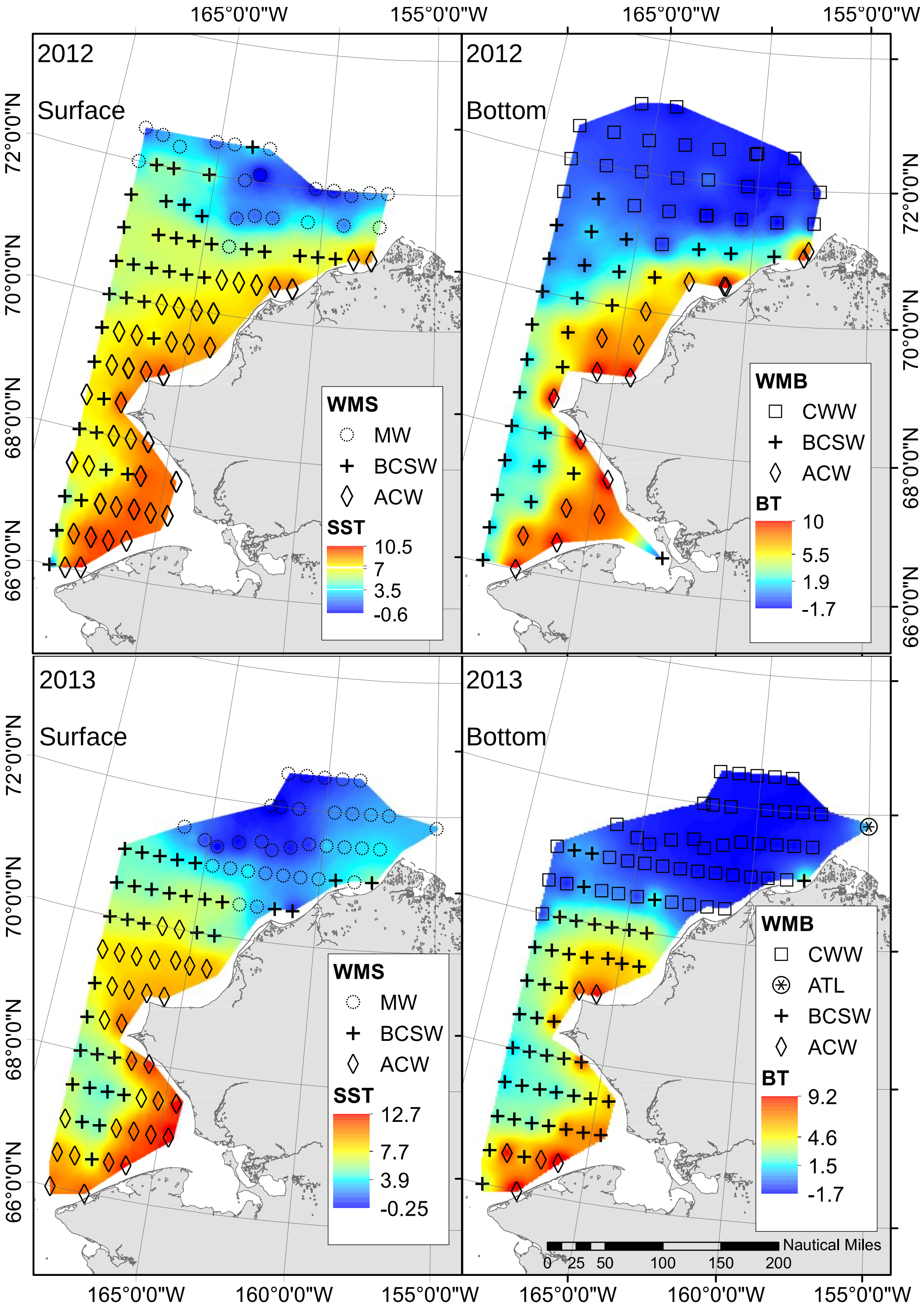

Figure 1. Station locations in 2012 (top) and 2013 (bottom) with near surface (left) and near bottom (right) water temperatures and surface water mass classifications (MW = Melt Water, BCSW = Bering Chukchi Summer Water and ACW = Alaska Coastal Water) and near bottom (right) water temperatures and bottom water mass classifications (CWW = Chukchi Winter Water, ATL =

Atlantic Water, BCSW and ACW). Temperatures were interpolated using inverse distance weighting tool in ArcGIS 10.1.

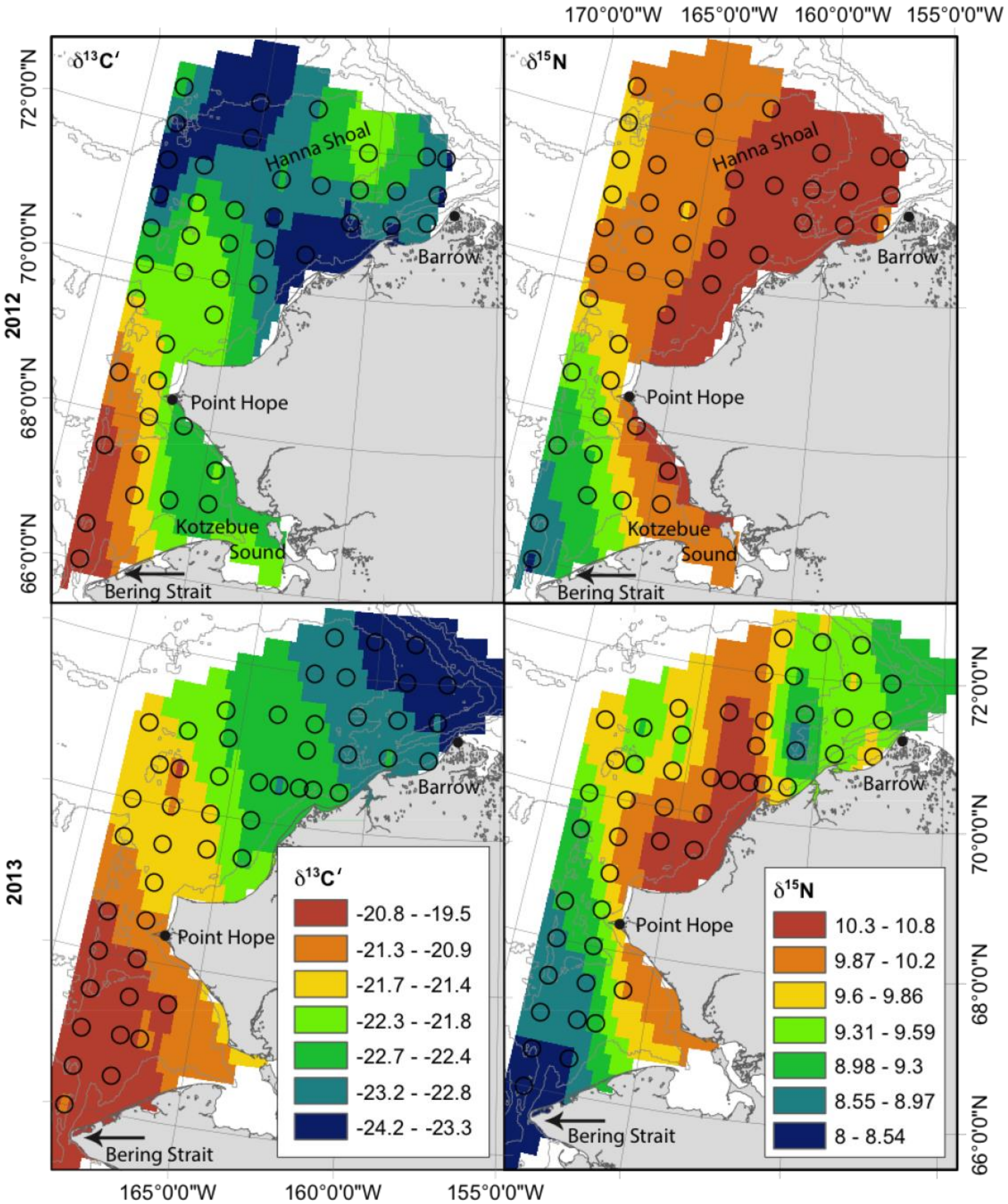

Figure 2. 2012 (top) and 2013 (bottom) *Calanus* spp. $\delta^{13}C'$ (left) and $\delta^{15}N$ (right) isoscapes. *Calanus* spp. sampling locations are shown with open circles.

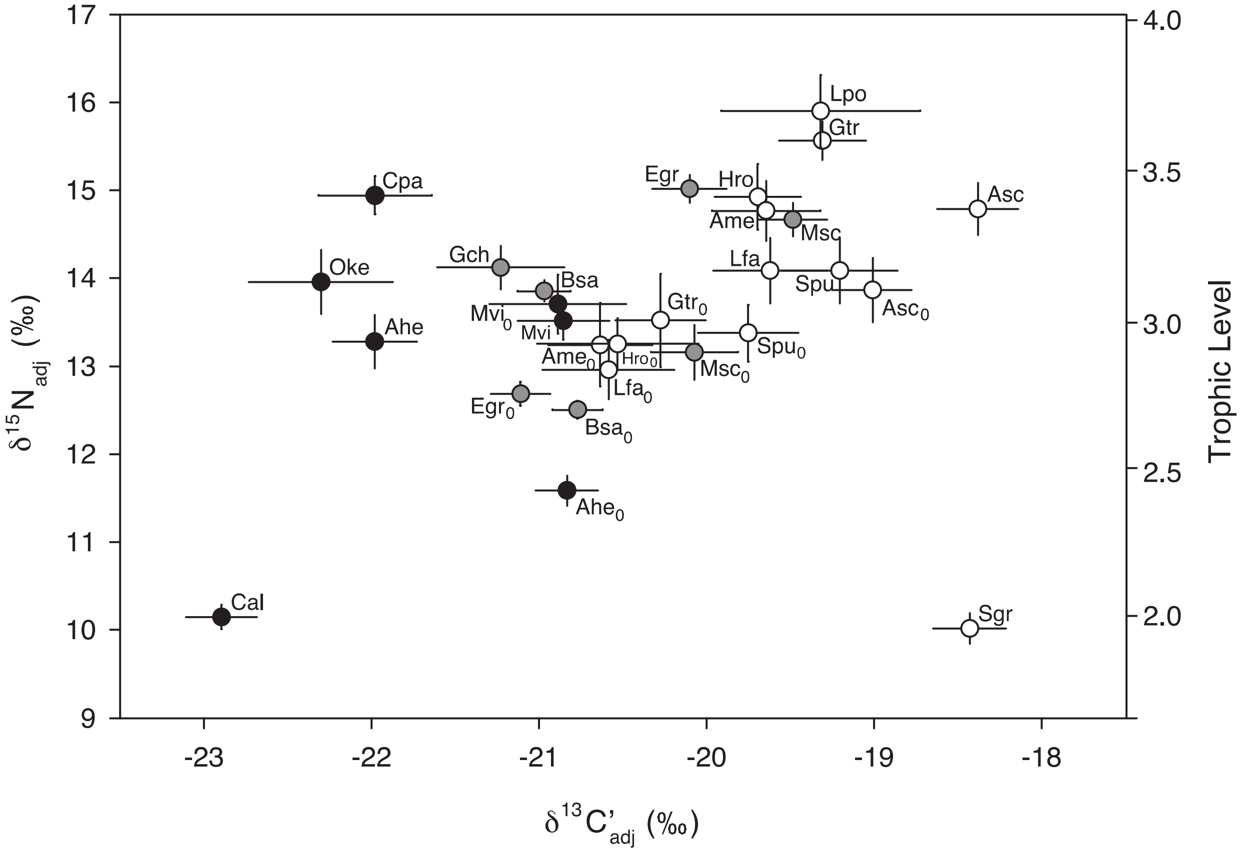

Figure 3. Overall 2012 mean carbon isotope values (± 2 SE) and mean nitrogen isotope values (± 2 SE) for each species by age group (age-0 with subscript '0' and/or age-1+ without subscript) in the eastern Chukchi Sea. Species collected during the bottom trawl survey only are shown with open circles, species collected during the surface trawl survey only are shown with black circles and species collected during both surveys are shown in gray. For species codes, see Tables 1 and 3.

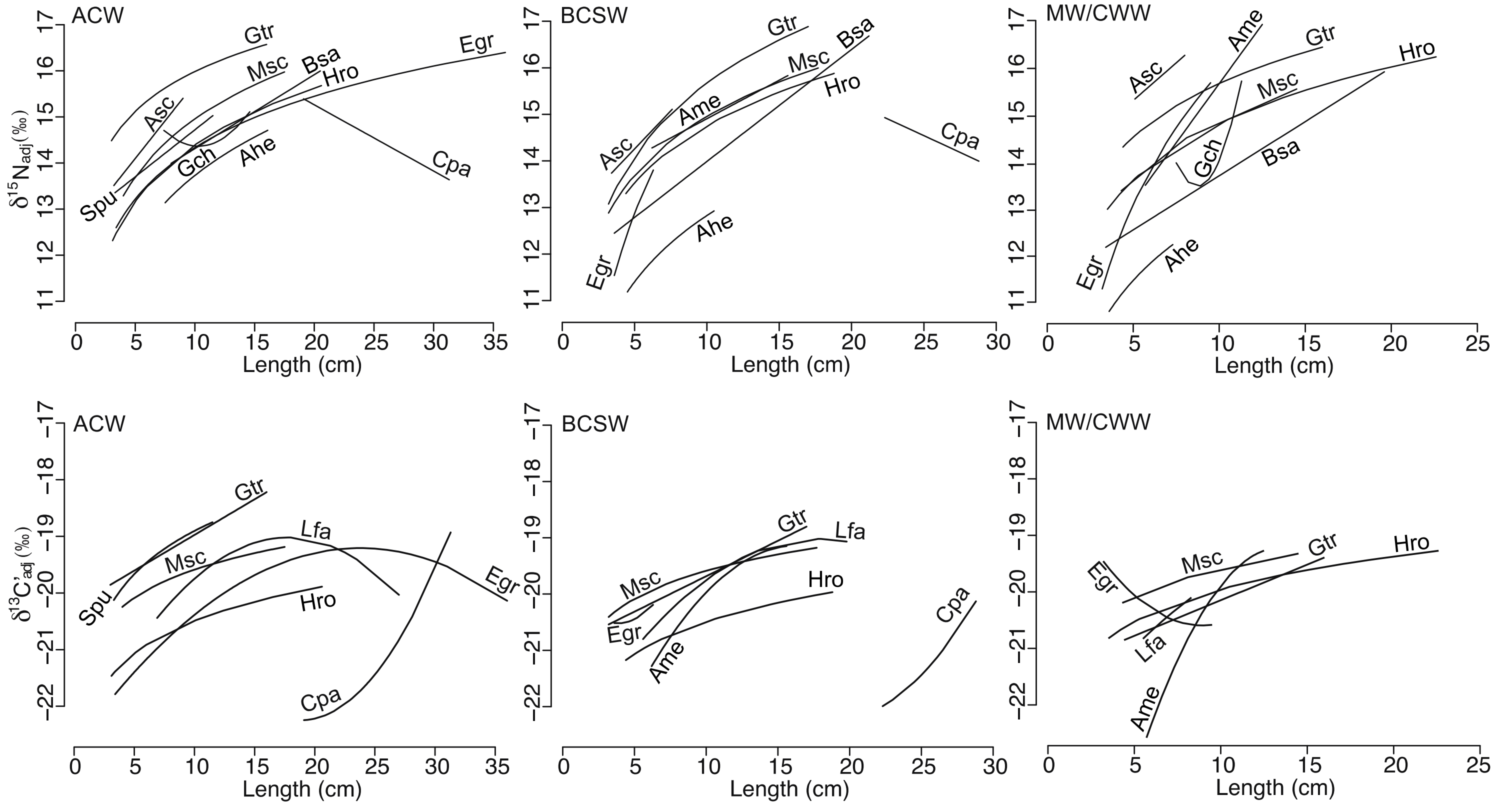

Figure 4. Modeled relationships between $\delta^{15}N_{adj}$ (top row) or $\delta^{13}C'_{adj}$ (bottom) and fork length for each species by water mass showing ontogenetic shifts in trophic level and feeding habitat/ diet source, respectively, based on 2012 samples. Water masses shown are Alaska Coastal Water (ACW), Bering Chukchi Summer Water (BCSW) and Melt Water over Chukchi Winter Water (MW/CWW). See tables 1 and 3 for species codes and Table 4 for corresponding best-fit models. Walleye pollock, Pacific sandlance, Arctic cod, and capelin showed no trends in $\delta^{13}C'_{adj}$ with ontogeny or differences among water masses, and are not shown.

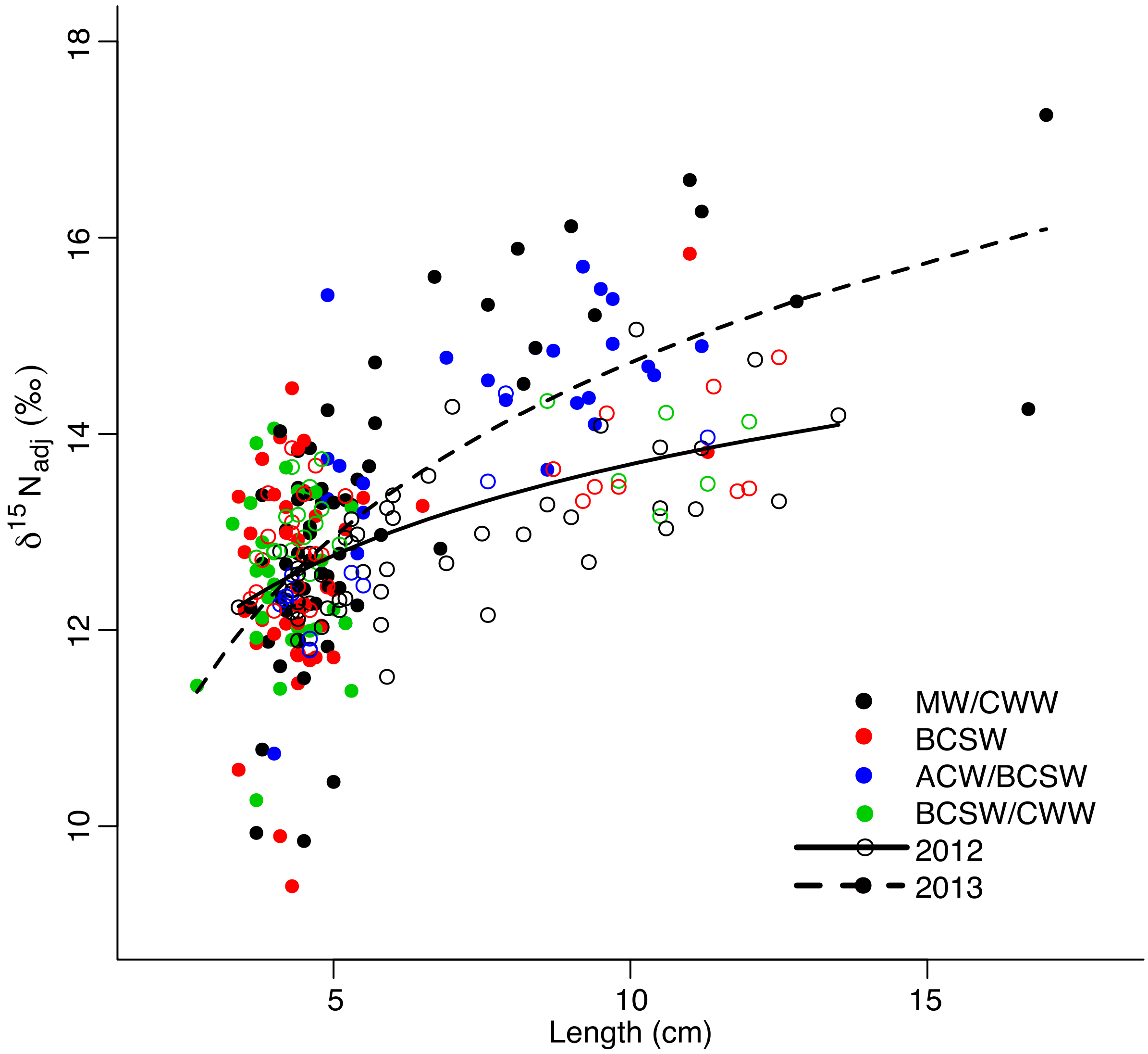

Figure 5. Modeled relationships between $\delta^{15}N_{adj}$ and fork length for Arctic cod by year (surface trawl only). See Figure 4 for water mass abbreviations.

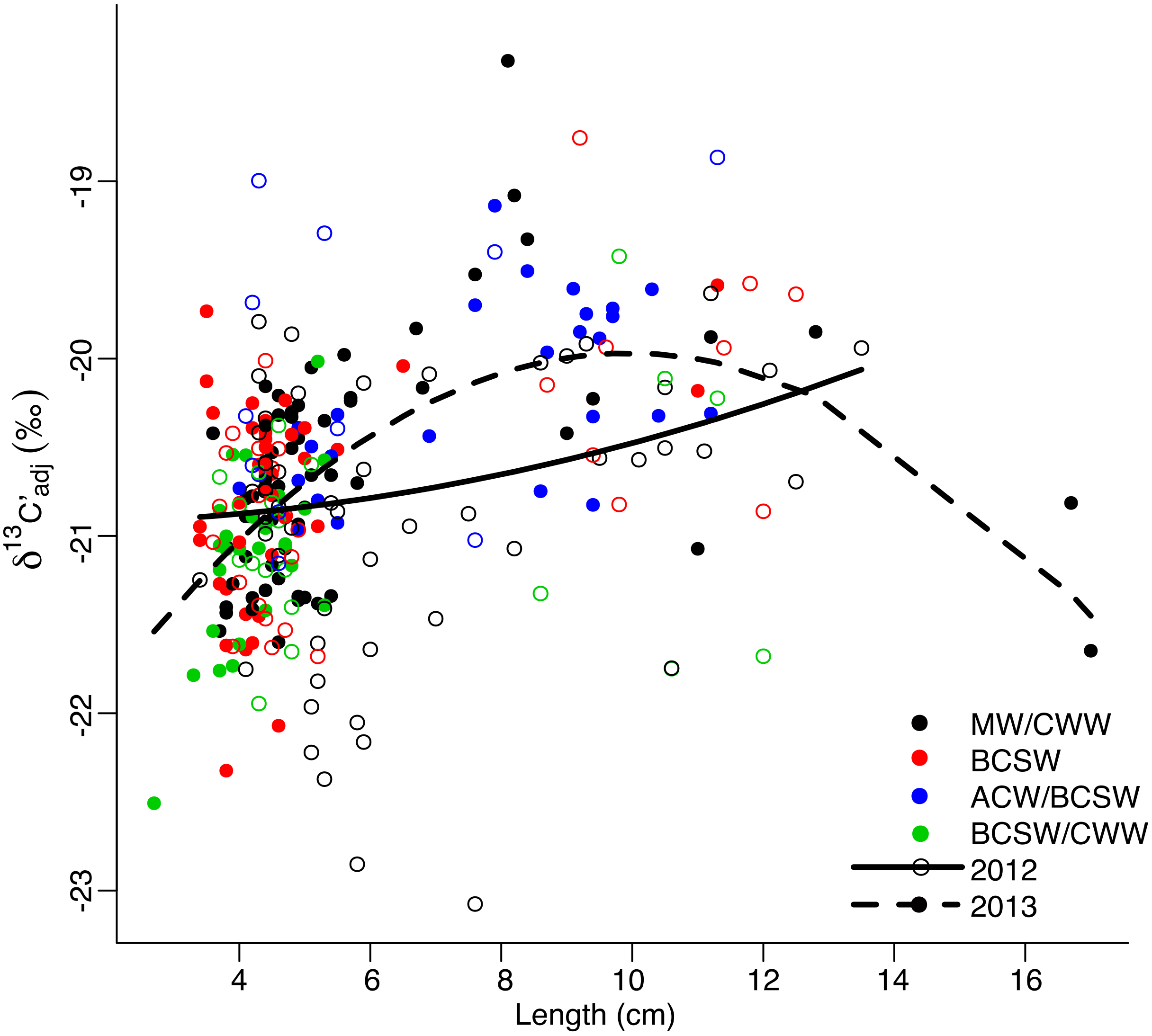

Figure 6. Modeled relationships between $\delta^{13}C'_{adj}$ and fork length for Arctic cod by year (surface trawl only). See Figure 4 for mater mass abbreviations.

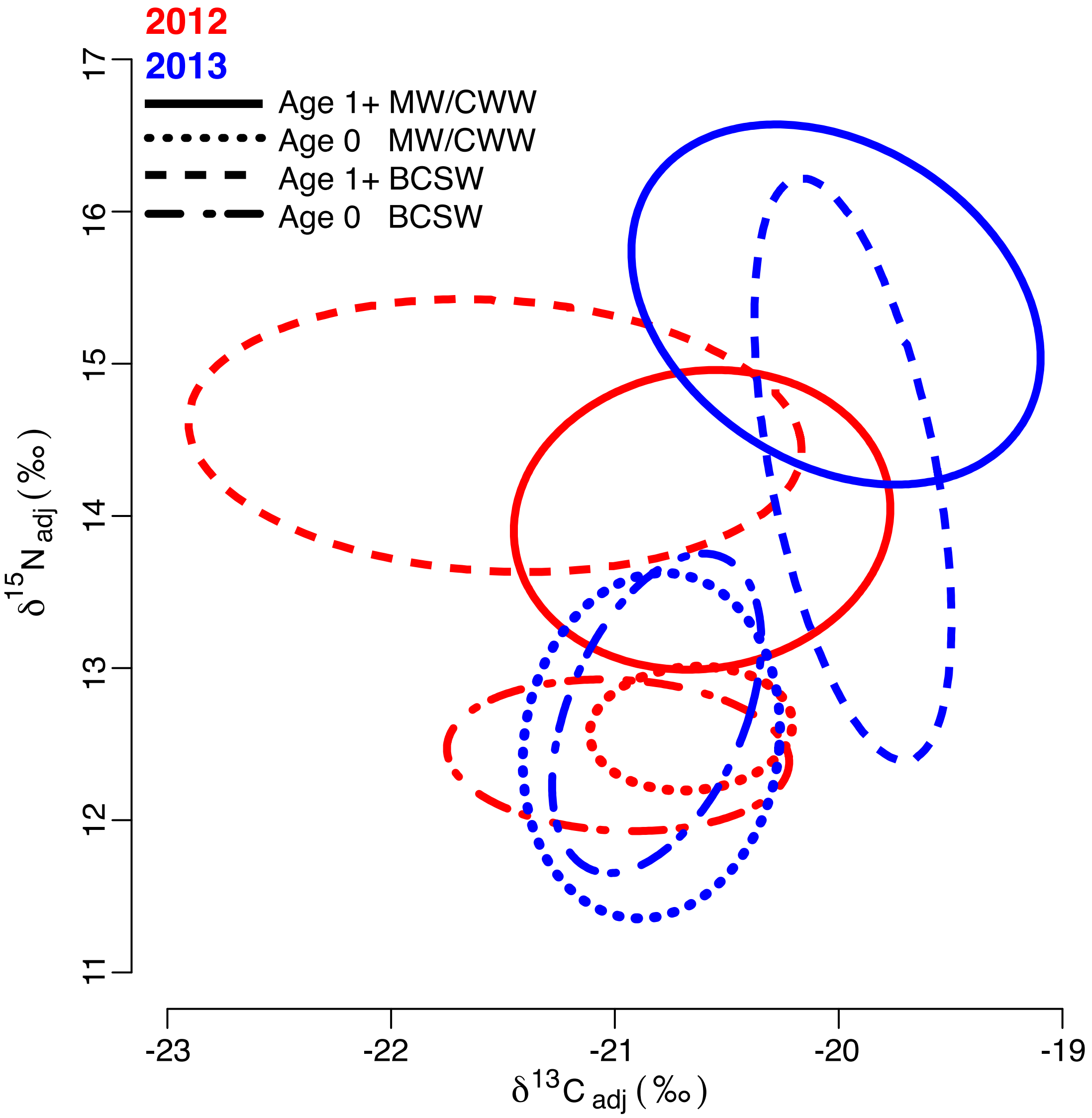

Figure 7. Scatter plot of $\delta^{15}N_{adj}$ and $\delta^{13}C_{adj}$ values for age-0 and age-1+ Arctic cod collected during 2012 (red) and 2013 (blue) surface trawl in the Melt Water/Chukchi Winter Water (MW/CWW) and Bering Chukchi Summer Water (BCSW) water masses with standard ellipse areas representing isotopic niche space for each year/age/water mass combination.

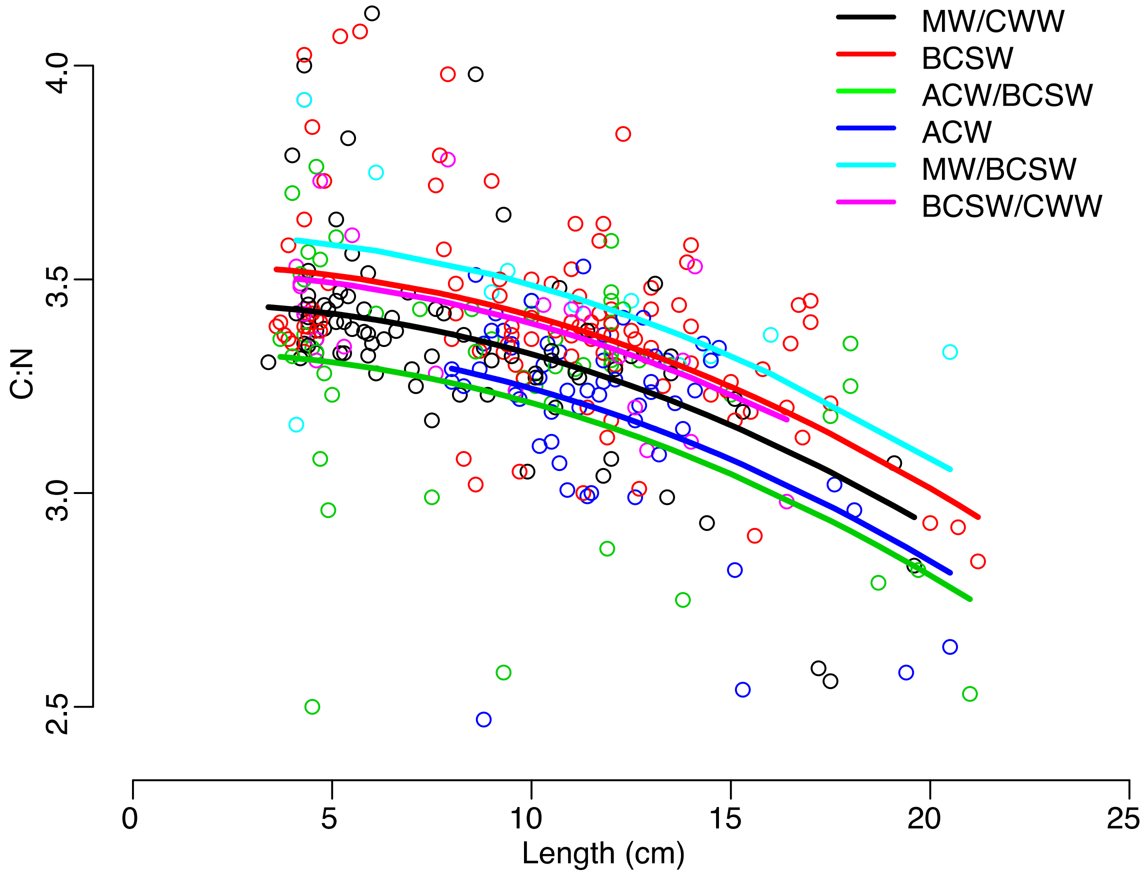

Figure 8. Modeled relationships between the C:N and fork length by water mass for 2012 Arctic cod (conditional r^2 = 0.33 and marginal r^2 = 0.58).

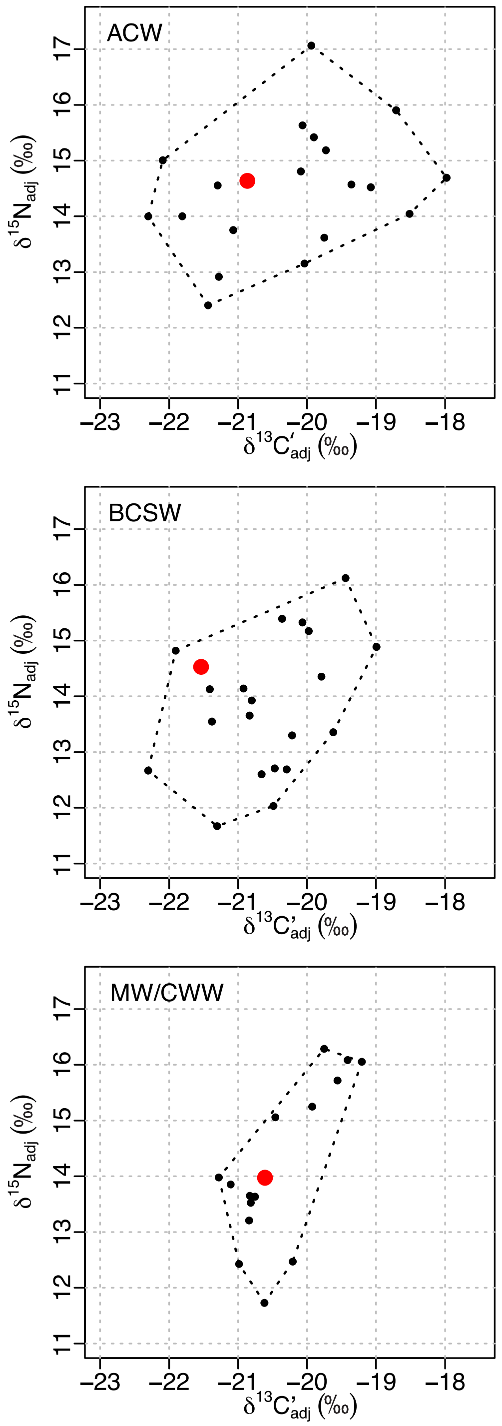

Figure 9. Convex hulls encapsulating isotopic niche space ($\delta^{15}N_{adj}$ vs $\delta^{13}C_{adj}$) of fish community by water mass structure in 2012. Each point is a mean value by species and size class (age 1+ and age 0s). The red circles are the mean value for Arctic cod age 1+.

Table 1**.** Fish and invertebrate samples collected for stable isotope analysis during the 2012 surface trawl survey in the eastern Chukchi Sea by age class (age-0, age-1+, mature fish (Mat) or juvenile salmon (Juv)), including sample size (N), species/age abbreviation code, fork length range (cm), average raw δ^{15}N ± SD (‰), average $\delta^{15}N_{adj}$ ± SD (‰), trophic level (TL), average raw δ^{13}C ± SD (‰), average lipid-normalized δ^{13}C' ± SD (‰), and average $\delta^{13}C'_{adj}$ ± SD (‰).

	Surface 2012									
Species (Common name)	Age	Code	N	Size range	δ^{15}N (SD)	$\delta^{15}N_{adj}$ (SD)	TL	δ^{13}C (SD)	δ^{13}C' (SD)	$\delta^{13}C'_{adj}$ (SD)
Boreogadus saida (Arctic cod)	0	Bsa$_0$	79	3.4 – 6.0	12.8 (0.6)	12.6 (0.4)	2.7	-21.4 (0.8)	-21.3 (0.7)	-20.8 (0.7)
	1+	Bsa	47	6.6 – 13.5	13.9 (0.6)	13.9 (0.8)	3.1	-20.6 (1.0)	-20.6 (1.0)	-20.7 (1.3)
Eliginus gracilis (Saffron cod)	0	Egr$_0$	40	3.2 – 5.9	12.8 (0.6)	12.7 (0.6)	2.7	-21.2 (0.6)	-21.2 (0.6)	-21.0 (0.7)
	1+	Egr	18	6.9 – 13.9	14.9 (0.4)	15.3 (0.6)	3.6	-20.0 (0.8)	-20.1 (0.8)	-20.7 (0.9)
Gadus chalcogrammus (Walleye pollock)	1+	Gch	15	9.4 – 12.3	14.1 (0.3)	15.0 (0.5)	3.4	-20.7 (0.3)	-20.8 (0.3)	-22.4 (0.9)
Myoxocephalus scorpius (Shorthorn sculpin)	0	Msc$_0$	18	3.2 – 4.7	13.3 (0.9)	12.7 (0.7)	2.9	-19.8 (0.6)	-19.8 (0.6)	-20.0 (0.7)
	1+	Msc	10	6.5 – 15.3	15.4 (0.9)	15.4 (1.0)	3.6	-19.6 (0.8)	-19.9 (0.7)	-20.0 (1.0)
Mallotus villosus (Capelin)	0	Mvi$_0$	26	4.4 – 7.5	13.8 (0.7)	13.7 (0.9)	3.1	-21.4 (0.5)	-21.3 (0.6)	-20.9 (1.0)
	1+	Mvi	77	7.6 – 13.1	13.4 (0.8)	13.6 (0.9)	3.0	-20.8 (0.8)	-20.7 (0.9)	-20.9 (1.3)
Clupea pallisii (Pacific herring)	Mat	Cpa	46	19.1 – 31.3	14.4 (0.6)	14.9 (0.7)	3.4	-21.4 (0.9)	-20.9 (0.7)	-22.0 (1.1)
Ammodytes hexapterus (Pacific sandlance)	0	Ahe$_0$	50	3.6 – 7.0	11.6 (0.7)	11.6 (0.6)	2.4	-21.8 (0.6)	-21.3 (0.6)	-20.8 (0.7)
	1+	Ahe	37	7.2 – 16.1	13.1 (0.7)	13.3 (0.9)	3.0	-21.9 (0.9)	-21.6 (0.8)	-22.0 (0.8)
Oncorhynchus keta (Chum salmon)	Juv	Oke	30	9.1 – 15.1	13.7 (0.6)	14.0 (1.0)	3.1	-21.4 (0.5)	-21.5 (0.6)	-22.3 (1.2)
Calanus spp. (Copepod)	--	Cal	135	--	10.1 (0.7)	--	2.0	--	-23.2 (1.3)	-22.9 (1.2)

Table 2. Fish and invertebrate samples collected for stable isotope analysis during the 2013 surface trawl survey in the eastern Chukchi Sea by age class (age-0, age-1+, mature fish (Mat) or juvenile salmon (Juv)), including sample size (N), species/age abbreviation code, fork length range (cm), average raw $\delta^{15}N \pm$ SD (‰), average $\delta^{15}N_{adj} \pm$ SD (‰), trophic level (TL), average raw $\delta^{13}C \pm$ SD (‰), average lipid-normalized $\delta^{13}C' \pm$ SD (‰), and average $\delta^{13}C'_{adj} \pm$ SD (‰).

Surface 2013

Species (Common name)	Age	N	Size range	$\delta^{15}N$ (SD)	$\delta^{15}N_{adj}$ (SD)	TL	$\delta^{13}C$ (SD)	$\delta^{13}C'$ (SD)	$\delta^{13}C'_{adj}$ (SD)
Boreogadus saida (Arctic cod)	0	123	2.7 – 5.8	12.1 (1.0)	12.0 (1.0)	2.7	-20.4 (0.9)	-20.2 (0.9)	-20.0 (0.6)
	1+	57	6.2 – 17.4	14.5 (1.0)	14.6 (1.0)	3.5	-20.1 (0.6)	-20.1 (0.6)	-18.8 (0.7)
Eliginus gracilis (Saffron cod)	0	32	3.3 – 5.8	13.3 (0.5)	13.4 (0.9)	3.1	-20.9 (0.8)	-21.0 (0.9)	-21.8 (1.3)
Gadus chalcogrammus (Walleye pollock)	1+	2	9.0 – 10.8	15.1 (1.1)	15.8 (1.7)	3.8	-19.4 (0.6)	-19.5 (0.5)	-20.8 (0.7)
Myoxocephalus scorpius (Shorthorn sculpin)	0	50	2.6 – 5.2	12.9 (1.1)	12.8 (0.8)	3	-19.3 (0.9)	-19.2 (1.1)	-19.8 (0.8)
Mallotus villosus (Capelin)	0	39	4.2 – 7.3	13.9 (1.0)	13.8 (1.2)	3.3	-21.6 (0.7)	-21.9 (1.0)	-21.2 (0.9)
	1+	58	7.4 – 12.5	13.9 (0.7)	13.8 (1.0)	3.3	-20.3 (0.6)	-20.4 (0.6)	-20.7 (0.9)
Clupea pallisii (Pacific herring)	Mat	36	21.1 – 27.4	15.0 (0.8)	15.4 (1.2)	3.7	-22.1 (0.9)	-21.7 (1.1)	-22.6 (1.2)
Ammodytes hexapterus (Pacific sandlance)	0	54	3.4 – 6.8	11.3 (0.8)	10.9 (0.9)	2.4	-21.6 (0.9)	-21.1 (1.0)	-20.6 (0.8)
	1+	30	6.9 – 15.5	13.1 (0.8)	12.9 (1.0)	3	-20.5 (0.5)	-20.4 (0.6)	-20.7 (0.9)
Oncorhynchus keta (Chum salmon)	Juv	30	11 – 15.4	13.5 (0.9)	13.3 (1.1)	3.1	-20.9 (0.5)	-20.8 (0.3)	-21.7 (0.5)
O. gorbuscha (Pink salmon)	Juv	30	8.1 – 14.0	12.7 (1.2)	13.1 (1.7)	3.1	-20.9 (0.6)	-20.6 (0.7)	-21.8 (1.1)
Calanus spp. (Copepod)	--	146	--	9.3 (1.1)	9.5 (1.2)	2	-22.8 (1.4)	-22.1 (1.3)	-22.2 (1.4)

Table 3. Fish and invertebrate samples collected for stable isotope analysis during the 2012 bottom trawl survey of the eastern Chukchi Sea by age class (age-0 and age-1+), including species/age abbreviation code, sample size (N), fork length range (cm), average raw δ^{15}N ± SD (‰), average δ^{15}N$_{adj}$ ± SD (‰), and average δ^{13}C'$_{adj}$ ± SD (‰).

Species (Common name)	Age	Code	N	Size range	δ^{15}N (SD)	δ^{15}N$_{adj}$ (SD)	TL	δ^{13}C (SD)	δ^{13}C' (SD)	δ^{13}C'$_{adj}$ (SD)
Boreogadus saida (Arctic cod)	0	Bsa$_0$	13	4 – 6.1	12.6 (0.6)	12.5 (0.6)	2.7	-20.8 (1.1)	-20.6 (0.9)	-20.5 (0.8)
	1+	Bsa	195	6.3 – 21.2	14.4 (1.0)	14.6 (0.9)	3.3	-20.4 (0.6)	-20.5 (0.7)	-21.0 (1.2)
Eliginus gracilis (Saffron cod)	0	Egr$_0$	24	3.9 – 6.0	13.2 (0.5)	12.9 (0.5)	2.8	-21.2 (0.7)	-21.2 (0.7)	-21.2 (0.7)
	1+	Egr	87	6.1 – 36.0	15.5 (0.8)	15.6 (1.0)	3.6	-19.4 (0.9)	-19.6 (0.9)	-20.0 (1.1)
Gadus chalcogrammus (Walleye pollock)	1+	Gch	29	7.4 – 14.6	14.2 (0.6)	14.0 (0.6)	3.2	-21.1 (0.5)	-21.2 (0.5)	-20.6 (0.8)
Myoxocephalus scorpius (Shorthorn sculpin)	0	Msc$_0$	6	3.9 – 4.8	13.2 (0.7)	13.0 (0.7)	2.8	-19.5 (0.3)	-20.0 (0.3)	-20.2 (0.3)
	1+	Msc	4	7.1 – 17.8	15.1 (0.6)	14.9 (0.8)	3.4	-19.2 (0.7)	-19.6 (0.7)	-19.4 (0.7)
Hippoglossoides robustus (Bering flounder)	0	Hro$_0$	35	3.1 – 6.9	13.8 (1.4)	13.8 (1.5)	3.1	-20.6 (0.9)	-20.8 (0.8)	-20.6 (0.9)
	1+	Hro	42	8.2 – 24.8	15.5 (1.3)	15.6 (1.2)	3.6	-19.0 (1.1)	-19.3 (1.2)	-19.7 (0.8)
Anisarchus medius	0	Ame$_0$	26	5.7 – 7.0	13.7 (0.7)	13.9 (0.7)	3.1	-20.6 (1.1)	-20.7 (1.2)	-20.6 (1.3)
(Stout eelblenny)	1+	Ame	48	7.2 – 15.6	15.2 (1.1)	15.4 (0.9)	3.6	-18.9 (1.0)	-19.2 (1.0)	-19.8 (1.0)
Lumpenus fabricii	0	Lfa$_0$	25	5.5 – 6.9	13.5 (0.9)	13.3 (0.9)	2.9	-21.1 (0.9)	-21.0 (0.9)	-20.6 (0.8)
(Slender eelblenny)	1+	Lfa	54	7.2 – 27.0	14.6 (1.4)	14.9 (1.1)	3.4	-19.0 (1.1)	-19.1 (1.1)	-19.6 (1.3)
Stichaeus punctatus	0	Spu$_0$	16	3.3 – 6.2	13.9 (0.6)	13.6 (0.6)	3.0	-19.9 (0.6)	-19.8 (0.6)	-19.8 (0.7)
(Arctic shanny)	1+	Spu	19	6.8 – 14.0	14.7 (0.8)	14.6 (0.8)	3.3	-19.1 (0.5)	-19.1 (0.5)	-19.2 (0.7)

Lycodes polaris (Polar eelpout)	All	Lpo	13	6.6 – 26.1	16.5 (0.7)	16.8 (0.8)	4.0	-18.8 (1.0)	-18.8 (0.9)	-19.3 (1.1)
Artediellus scaber (Hamecon)	0	Asc$_0$	34	3.2 – 5.7	14.4 (1.1)	14.2 (0.9)	3.2	-19.1 (0.7)	-19.1 (0.7)	-19.0 (0.7)
	1+	Asc	51	5.8 – 9.0	15.3 (1.1)	15.1 (1.0)	3.5	-18.7 (0.9)	-18.8 (0.9)	-18.4 (0.8)
Gymnocanthus tricuspis (Arctic staghorn sculpin)	0	Gtr$_0$	28	3.0 – 6.1	14.1 (1.4)	14.0 (1.6)	3.2	-20.3 (1.1)	-20.2 (1.0)	-20.3 (0.7)
	1+	Gtr	59	6.5 – 17.0	16.1 (0.9)	16.1 (0.8)	3.8	-19.0 (1.1)	-19.0 (1.1)	-19.3 (1.0)
Serripes groenlandicus (Greenland cockle)		Sgr	28	--	10.0 (0.5)	--	2.0	-19.1 (0.8)	-18.4 (0.6)	--

Table 4. Best-fit models with random effects structure (none, random intercept, or random intercept and slope) and resulting R^2 values for species-specific ontogenetic shifts in $\delta^{15}N_{adj}$ (A) and $\delta^{13}C'_{adj}$ (B) with water mass (combined 2012 surface and bottom trawl samples only). Also, p-values from likelihood ratio tests comparing each best-fit model with the corresponding intercept-only model (null model) with the same random effects structure are shown. Models tested include quadratic (Q(L)), log-linear (ln(L)) and linear (L) length terms with additive (+) or multiplicative (*, i.e. including an interaction term) effects of water mass (w). See methods for details. Only fish species that occurred in multiple water masses with adequate numbers were included in analysis. Bolded species model fits are shown in Figure 4.

A) Common name	Code	Best-fit model	Random effects	Marginal R^2	Conditional R^2	p-value
Arctic cod	Bsa	L * w	intercept	0.78	0.81	<0.0001
Saffron cod	Egr	ln(L) * w	intercept	0.68	0.91	<0.0001
Capelin	Mvi	Q(L)	intercept	0.08	0.72	0.0001
Pacific sandlance	Ahe	ln(L) + w	none	0.80*	--	<0.0001
Pacific herring	Cpa	L	intercept	0.23	0.71	<0.0001
Bering flounder	Hro	ln(L) + w	intercept	0.57	0.75	<0.0001
Arctic staghorn sculpin	Gtr	ln(L) * w	intercept	0.57	0.88	<0.0001
Shorthorn sculpin	Msc	ln(L)	intercept	0.59	0.91	<0.0001
Slender eelblenny	Lfa	ln(L)	intercept	0.18	0.76	<0.0001
Stout eelblenny	Ame	L * w	none	0.67*	--	<0.0001
Walleye pollock	Gch	Q(L) * w	intercept	0.28	0.8	<0.0001
Arctic shanny	Spu	L	none	0.44*	--	<0.0001
Hamecon	Asc	L + w	intercept	0.39	0.77	<0.0001

B) Common name	Code	Best-fit model	Random effects	Marginal R^2	Conditional R^2	p-value
Arctic cod	Bsa	Q(L)	intercept	0.01	0.75	0.02
Saffron cod	Egr	Q(L) * w	intercept	0.50	0.85	<0.0001
Capelin	Mvi	null	intercept	0.00	0.79	NA
Pacific sandlance	Ahe	null	intercept	0.00	0.68	NA
Pacific herring	Cpa	Q(L)	intercept	0.23	0.92	<0.0001
Bering Flounder	Hro	ln(L) + w	intercept	0.46	0.67	<0.0001
Arctic staghorn sculpin	Gtr	L + w	none	0.39*	--	<0.0001
Shorthorn sculpin	Msc	ln(L)	intercept	0.22	0.57	<0.0001

Slender eelblenny	Lfa	Q(L)	intercept	0.27	0.62	<0.0001
Stout eelblenny	Ame	Q(L) * w	intercept	0.45	0.82	<0.0001
Walleye pollock	Gch	null	intercept	0.00	0.84	NA
Arctic shanny	Spu	ln(L)	none	0.46*	--	<0.0001
Hamecon	Asc	Q(L)	intercept	0.03	0.93	0.02

*****adjusted R^2 from simple linear regression model

Table 5. Best-fit models with random effects structure (none, random intercept or random intercept and slope) and resulting R^2 values for species-specific ontogenetic shifts in $\delta^{15}N_{adj}$ (A) and $\delta^{13}C'_{adj}$ (B) with water mass and year (combined 2012 and 2013 surface trawl samples only). Also shown are p-values from a likelihood ratio test comparing each best-fit model with the corresponding intercept-only model (null model) with the same random effects. Models tested include quadratic (Q(L)), log-linear (ln(L)) or linear (L) length terms with additive (+) or multiplicative (*, i.e. including an interaction term) effects of water mass (w) and/or year (y). See methods for details. Model fits are shown in Figure 4.

A) Common name	Best-fit model	Random effects	Marginal R^2	Conditional R^2	p-value
Arctic cod	ln(L) * y	intercept	0.44	0.71	<0.0001
Pacific sandlance	L + w	intercept	0.63	0.84	<0.0001
Saffron cod	ln(L) + y	intercept	0.48	0.91	<0.0001
Capelin	Q(L) * y	intercept	0.28	0.80	<0.0001
Chum	ln(L)	intercept	0.09	0.75	0.0007
Shorthorn sculpin	ln(L)	intercept	0.47	0.51	<0.0001
Pacific herring	Q(L) * y	intercept	0.35	0.79	<0.0001

B) Common name	Best-fit model	Random effects	Marginal R^2	Conditional R^2	p-value
Arctic cod	Q(L) * y	intercept	0.21	0.52	<0.0001
Pacific sandlance	w	intercept	0.17	0.58	0.02
Saffron cod	L + y + w	intercept	0.66	0.91	<0.0001
Capelin	ln(L) + y	intercept	0.25	0.75	<0.0001
Chum	Q(L)	intercept	0.02	0.89	0.04
Shorthorn sculpin	ln(L) + w	none	0.23*	--	0.0006
Pacific herring	Q(L) + y	intercept	0.48	0.82	<0.0001

*****adjusted R^2 from simple linear regression model

Table 6. Isotope niche fish community metrics (Layman et al. 2007) by water mass. Metrics shown are total area, δ^{15}N range, δ^{15}C range, mean distance to centroid (CD), mean nearest neighbor distance (MNND) and standard deviation of nearest neighbor distance (SDNND). Water mass structures listed are Alaska Coastal Water (ACW), Bering Chukchi Summer Water (BCSW) and Melt Water over Chukchi Winter Water (MW/CWW).

Water Mass	Total Area	δ^{15}N Range (‰)	δ^{13}C Range (‰)	CD	MNND	SDNND
ACW	11.3	4.7	4.3	1.46	0.60	0.32
BCSW	8.8	4.4	3.3	1.28	0.50	0.32
MW/CWW	4.3	4.6	2.1	1.34	0.38	0.25

Appendix O.

Juvenile Chinook salmon abundance in the northern Bering Sea: Implications for future returns and fisheries in the Yukon River

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Date
December 4, 2015

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
MLD	Mixed Layer Depth
BASIS	Bering Aleutian Salmon International Survey
CPUE	Catch per Unit of Effort
CTD	Conductivity, Temperature, Depth
DNA	Deoxyribonucleic Acid
SNP	Single nucleotide polymorphism
NBS	Northern Bering Sea

List of Oral and Poster Presentations

Kathrine Howard and James Murphy. 2014. Research in Response to Declines of Far North Chinook Salmon. United States Arctic Research Commission. Anchorage, AK. September 15, 2014. (Oral presentation)

James Murphy. 2014. Marine Fisheries and Research Review. Joint Technical Committee of the Yukon River Panel, Vancouver, B.C. October 28-29, 2014. (Oral presentation)

Kathrine Howard. 2014. Yukon River Marine/Estuarine Juvenile Chinook Salmon Research. US/Canada Yukon River Panel. December 10, 2014. (Oral presentation)

James Murphy. 2015. Marine Fisheries and Research Review. Joint Technical Committee of the Yukon River Panel, Seattle WA. November 17-19, 2015. (Oral presentation)

James M. Murphy, Kathrine G. Howard, Jeanette C. Gann, Kristin Cieciel, William D. Templin, Charles M. Guthrie III. 2016. Juvenile Chinook salmon abundance in the northern Bering Sea: implications for future returns and fisheries in the Yukon River. Ocean Sciences Meeting. New Orleans, LA. February 21-26, 2016. (Poster presentation)

James M. Murphy, Kathrine G. Howard, Jeanette C. Gann, Kristin Cieciel, William D. Templin, Charles M. Guthrie III. 2016. Juvenile Chinook salmon abundance in the northern Bering Sea: implications for future returns and fisheries in the Yukon River. Salmon Ocean Ecology Meeting. Juneau, AK. March, 2016. (Presentation format TBD)

Proposed Objectives and Study Chronology

Study Objectives:

1.) Estimate stock-specific abundance of juvenile Chinook salmon in the northern Bering Sea.
2.) Provide forecasts of future returns of the Canadian-origin stock group of Chinook salmon to the Yukon River.
3.) Estimate early life-history survival of the Canadian-origin stock group of Chinook salmon from the Yukon River.

May 2012 – Dec 2014. Field collections. Develop and prepare cruise plans, cruise instructions, collection protocols, and cruise reports. Conduct field surveys. Complete quality control steps on field data and integrate all field data into a field database.

Nov 2012-Sep 2014. Conduct laboratory analysis on genetic stock identification using a single nucleotid polymorphism baseline of Chinook salmon and analyze CTD data for mixed layer depth.

Oct 2014 – Jun 2015. Develop and complete analytical methods for estimating stock-specific juvenile abundance estimates.

Jun 2015 – Aug 2015. Write manuscript on stock-specific juvenile abundance.

1. Abstract

Juvenile Chinook salmon (*Oncorhynchus tshawytscha*) abundance is estimated in the northern Bering Sea and used to provide guidance for future returns and fisheries on Canadian-origin Chinook salmon in the Yukon River. Abundance estimates are based on surface trawl catch data, mixed layer depth adjustments, and genetic stock composition of juveniles in the northern Bering Sea near the end of their first summer at sea (September). Estimated annual abundance range from 0.6 million to 2.55 million juveniles with an overall average of 1.44 million juvenile Chinook salmon from 2003 to 2014. Comparisons of juvenile and adult abundance provide an unique insight into the survival of Chinook salmon. Although the estimates of juvenile survival rates are relatively low (average of 5.2%), juvenile abundance is significantly correlated ($r = 0.88$, $p < 0.001$) with adult returns, indicating that much of the variability in survival occurs during earlier life stages (freshwater and initial marine). Survival of Chinook salmon during these early life-history stages has increased along with juvenile abundance and has important implications for future returns and fisheries in the Yukon River. The number of juveniles per spawner increased from an average of 26 (2003 to 2012) to an average of 54 in 2013 and 2014. Recent production declines in Chinook salmon have triggered closures of commercial, sport, and personal use fisheries and severe restrictions on subsistence fisheries in the Yukon River. The number of adults projected to return from juvenile abundance estimates indicate that fishing opportunities on the Canadian-origin stock group of Chinook salmon in the Yukon River could be restored as early as 2016.

2. Introduction

Recent production declines in Chinook salmon (*Oncorhynchus tshawytscha*) have had a critical impact on subsistence, commercial, and sport fisheries in the Yukon River and throughout Alaska. The loss of subsistence fishing opportunities in the Yukon and Kuskokwim rivers is particularly significant as over 80% of the subsistence harvest of Chinook salmon in Alaska occurs in these two river drainages (ADFG 2013). Other Pacific salmon species (*Oncorhynchus* spp.) in Alaska have not experienced similar production declines (NPAFC 2014); why Chinook salmon, in particular, are experiencing poor survival is unclear. While the need for information on the causes of poor survival in Chinook salmon is obvious, their complex stock and life-history dynamics also requires information on when and where production declines are occurring. Stock-specific and life-history based research on key Chinook salmon stocks as well as process studies on survival are needed to gain insight into the underlying production dynamics of Chinook salmon in the Yukon River and Alaska (ADFG 2013).

Canadian-origin Chinook salmon are harvested along the entire reach of the Yukon River (approximately 3,190 km in length) and are jointly managed by the United States and Canada as part of the Pacific Salmon Treaty (JTC 2015). Reduced harvest opportunities on Canadian-origin Chinook salmon have resulted in closures or severe restrictions to salmon fisheries throughout the Yukon River drainage. Management priority is given to meeting escapement (spawning abundance) objectives and subsistence harvests are given priority over other uses, including commercial and recreational harvests. The inability to meet Alaskan Chinook salmon subsistence needs has also resulted in restrictions (harvest and fishing gear) to summer chum salmon (*O. keta*) commercial fisheries in the Yukon River due to the incidental harvest of Chinook salmon in these fisheries (JTC 2015). Conservation concerns over Chinook salmon has also prompted significant effort by the North Pacific Fishery Management Council to limit and reduce Chinook salmon bycatch in eastern Bering Sea groundfish fisheries (Ianelli and Stram 2014, Stram and Ianelli 2015).

Yukon River Chinook salmon enter marine habitats at the highest latitude of nearly all stocks of Chinook salmon in North America and therefore have unique limitations and adaptations associated with winter ice in freshwater and marine habitats. Yukon River Chinook salmon have a stream-type life-history and typically spend one year in freshwater before migrating to the ocean (Gilbert 1922, Healey 1991). Canadian-origin Chinook salmon from the Yukon River typically begin their downstream dispersal out of natal rearing areas during their smolt stage (after their first winter in freshwater), however, some Canadian-origin stocks are known to disperse early, during their fry stage, and rear in tributaries within Alaska during their first summer growing season (Bradford et al. 2008, Daum and Flannery 2011). Early dispersal is believed to be controlled, at least in part, by active behavior of fry, linking it to competition or adaptive behavior within specific stocks of Chinook salmon (Daum and Flannery 2011). Competition and other density dependent processes in freshwater provide 1an important stabilizing force in freshwater production of salmon, which is why marine survival is frequently regarded as the primary driver of salmon production over time (Hare and Francis 1995, Mantua et al. 1997). However, freshwater survival may play a larger role in the production of Canadian-origin Chinook salmon than typically found in other stocks of salmon due to the extensive downstream migration (over 2,100 km) required to reach marine habitats as well as ice and temperature limitations in high latitude freshwater habitats (Bradford et al. 2001). Yukon River Chinook salmon typically enter marine habitats shortly after river ice breakup during the month of June, but marine entry can extend into the month of August (Martin et al. 1987, Hillgruber and Zimmerman 2009). Canadian-origin Chinook salmon typically spend 3 to 4 years at sea before returning to freshwater to spawn and contribute approximately half of the total production of Chinook salmon in the Yukon River (JTC 2015).

Yukon River juvenile Chinook salmon enter the shallow, vertically mixed coastal ecosystem of the northern Bering Sea and are captured during late summer (September) surface trawl surveys in this region. Surface trawl surveys were initiated in the northern Bering Sea in 2002 as part of the Bering Aleutian Salmon International Survey (BASIS) research program (NPAFC 2014) and have contributed to our understanding of the marine ecology of salmon (Andrews et al. 2009b, Farley et al. 2009b, Murphy et al. 2009) and other epipelagic fish species in the eastern Bering Sea shelf (Moss et al. 2009a, Coyle 2011, Heintz et al. 2013, Siddon et al. 2013, Andrews et al. In Press, Farley et al. In Press). Significant freshwater input from the Yukon River (average annual discharge 6,457 m^3/s) and other major rivers in western Alaska produce warm (7-10°C), turbid, and low salinity (20-32 PSU) marine habitats in the coastal region of the northern Bering Sea throughout much of the summer growing season for juvenile salmon, and drive northward flowing currents along the coast (Gann et al. 2013). High sediment loads within the Yukon River and shallow marine habitats adjacent to the Yukon River Delta and within Norton Sound produce high turbidity levels in nearshore marine habitats and within the Yukon River plume (Fig. 1). The middle domain (50-100 m) of the northern Bering Sea generally exhibits a two-layer water column with a well-mixed layer at the surface and a cold (< 2 °C) dense bottom layer. The cold bottom layer is a byproduct of the formation of winter sea ice and is known as the eastern Bering Sea cold pool (Danielson et al. 2011, Lauth 2011b).

Here we used surface trawl survey data to summarize the distribution and abundance of juvenile Chinook salmon in the northern Bering Sea. We compare juvenile and adult abundance estimates for the Canadian-origin stock group in the Yukon River, and review implications for their underlying production dynamics and the application of juvenile assessments to run size forecasts. We also provide guidance for fisheries management in the Yukon River based on juvenile assessments in the northern Bering Sea.

3. Methods

Surface trawl survey data in the northern Bering Sea are summarized from 2003 to 2014, excluding 2008 when no survey was conducted. Northern Bering Sea surveys are centered on the month of September with an average capture date for Chinook salmon of September 14. A Cantrawl model 400/601 (made by Cantrawl Pacific Ltd., Richmond, B.C.) rope trawl (typical vertical opening of 18 m and horizontal opening of 50 m) was used to capture juvenile Chinook salmon in the Northern Bering Sea aboard chartered commercial fishing vessels. A description of the trawl is provided in Murphy et al. (2003). The sampling grid used in the northern Bering Sea was based on latitude and longitude coordinates with a latitude grid distance of 55.56 km for all years except 2003 (111.12 km in 2003) and the longitude grid distance calculated from average latitude and a longitude grid of one degree for all years except 2003 (half a degree in 2003). Average annual trawl speeds were 4.25 knots and trawl duration at each station was set to 30 min. Fork lengths (FL) and weights of juvenile Chinook salmon are measured onboard and average lengths and weights were adjusted for sampling date by assuming a growth rate of 1 mm FL/day and 1.3% body weight per day based on scale growth models for juvenile Chinook salmon (Walker et al. 2013).

Area-swept catch per unit of effort (CPUE; catch per km^2) data were used to construct a multi-year distribution map of juvenile Chinook salmon in the northern Bering Sea. CPUE data were standardized by average effort as:

$$C\_std_{i,y} = \frac{C_{i,y}}{E_{i,y}} \bar{E},$$

where $C_{i,y}$ is the number of juvenile Chinook salmon captured at station i in year y, $E_{i,y}$ is the area swept in km^2 and $\bar{E}$, is the average effort (km^2). Zero catch boundary conditions were added to land masses, and the prediction surface was estimated with a neighborhood kriging model (ESRI 2001). The neighborhood kriging model was fit to surface trawl catch data by removing the spatial trend with a first order local polynomial function and a minimum of 5 and a maximum of 10 datapoints were used within each of four quadrants of the kriging model search radius and cross-validation statistics were used to optimize the prediction surface to observed data.

Area-swept abundance estimates for juvenile Chinook salmon were estimated by expanding average CPUE to the survey area within four spatial strata: 60° to 62°N, 62° to 64°N, Norton Sound, and Bering Strait. The southern spatial strata was extended to 59°N in 2005 as the juvenile distribution straddled the 60°N parallel in 2005. Effort was based on area swept by each trawl haul and calculated from net sonar measurements of trawl width (km) and measurements of distance trawled (km) from GPS coordinates of the start and end positions of the trawl haul using spherical earth coordinates as:

$$x = \cos^{-1}(\sin(lat_s)^2 + \cos(lat_e)^2 \cos(\Delta\mathrm{lon})) \times 6371,$$

where lat_s is the trawl start latitude position in radians, lat_e is the trawl end latitude position in radians, Δlon is the longitude distance between the start and end trawl positions in radians, and 6371 is the earth radius in km. Abundance, variance, and coefficients of variation were estimated for the juvenile abundance index from a bootstrap (Efron and Tibshirani 1986) resample distribution of average catch-per-unit-effort (CPUE) (1,000 bootstrap samples) with expansions to survey area by:

$$\widehat{N}_{y,s} = \overline{CPUE}_{y,s} G_{y,s} n_{y,s} \,,$$

$$\widehat{N}_y = \theta_y \sum_s \widehat{N}_{y,s} \,,$$

where $N_{y,s}$ is the juvenile abundance in year *y* and stratum *s*, $CPUE_{y,s}$ is the average catch rate (catch-per-unit-effort, catch per km^2), $G_{y,s}$ is the average sample grid area (km^2), $n_{y,s}$ is the number of stations, and θ_y is the mixed layer depth adjustment.

Mixed-layer depth expansions were applied to area-swept estimates of juvenile abundance to adjust for the vertical extent of juvenile salmon habitat. Mixed layer depth was defined as the depth where seawater density (Sigma theta) increased by 0.10 kg/m^3 relative to the surface (Danielson et al. 2011) and set to CTD (conductivity, temperature, depth) sensor depth (within 5 m of bottom) when the water column was vertically mixed and mixed layer depth was absent. Seawater density data were derived from temperature, salinity and pressure data collected with a Seabird Electronics SBE25 CTD (during 2003 and 2004) and a Seabird

Electronics SBE9-11 CTD for all other years. Mixed layer depth is used to approximate the vertical habitat for juvenile Chinook salmon as seawater temperatures below the surface mixed layer are generally the cold (< 2°C) temperatures of the eastern Bering Sea cold pool (Fig. 2) and are not suitable habitat for juvenile salmon (Brett 1952). Mixed layer depth adjustments to annual abundance estimates, θ_y, were estimated by:

$$\theta_y = \frac{\sum_i M_{i,y} C_{i,y}}{\sum_i C_{i,y}}$$

where $C_{i,y}$ is catch of juvenile Chinook at stations, *i*, and in year, *y*, and $M_{i,y}$, is equal to the ratio of mixed-layer depth to trawl depth when trawl depth is shallower than mixed layer depth, and 1.0 when trawl depth is below the mixed-layer depth.

Corrections for incomplete sampling in the Bering Strait region and the depth dependency in the spatial distribution of juvenile Chinook salmon in Norton Sound were applied to trawl catch data. Corrections for incomplete sampling in the Bering Strait during 2004, 2005, and 2006 were based on the juvenile distribution patterns during adjacent years (2003 and 2007). Approximately 15% of juvenile distribution was present in the Bering Strait region (excluding Norton Sound) in 2003 and 2007, and was used to estimate juvenile abundance in the Bering Strait during 2004, 2005, and 2006 when the Bering Strait region was not sampled. All of these years are considered to be warm years in the northern Bering Sea and therefore should have a higher degree of similarity in the expected distribution of juvenile Chinook salmon (Murphy et al. 2013). Shallow habitats in Norton Sound limit trawl sampling in Norton Sound. Footrope setbacks adjustments have been made to trawl bridals since 2010 to increase flexibility in vertical opening of the trawl and our ability to sample water depths shallower than 20 m. Trawl catches from 2010 to 2014 indicate that 76% of the juveniles are caught in depths deeper than 20 m, and less than 7% are caught in depths less than 18 m. With depth contours only available at 10m intervals, we approximated the effective survey area in Norton Sound by doubling the area of the 20 m depth contour (2,800 km^2) to arrive at the juvenile Chinook salmon area within Norton Sound of 5,600 km^2. This is intended to approximate the area of the 18 m depth contour.

Genetic stock composition estimates were produced from single nucleotide polymorphisms (SNP) data. Juvenile chinook salmon DNA was genotyped by both matrix-assisted laser desorption/ionization - time of flight (MALDI-TOF) genotyping as described previously (Guyon et al. 2010) using a Sequenom MassARRAY iPLEX platform or by using TaqMan (Applied Biosystems, Foster City, California) assays (Templin et al. 2011) for a 43 SNP baseline for Chinook salmon (Templin et al. 2011). Juvenile Chinook salmon were assigned to four genetically distinguishable Bering Sea stock groups: Russia, Coastal Western Alaska, Middle Yukon River, Upper Yukon River, and North Alaska Peninsula. The proportion of Upper Yukon River Chinook salmon was used to estimate the proportion of Canadian-origin Chinook salmon in the juvenile population using Bayesian mixed stock analysis (Pella and Masuda 2001). Variance estimates for the Canadian-origin juvenile abundance index is based on the joint variance of juvenile abundance and stock proportions within each year, V(XY), assuming independence of abundance and stock proportions as:

$$V(XY) = \mu_Y^2\sigma_X^2 + \mu_X^2\sigma_Y^2 + \sigma_X^2\sigma_Y^2,$$

where μ_X and σ_X^2 are the mean and variance of juvenile abundance within each year, respectively, and μ_Y and σ_Y^2 are the mean and variance of the Canadian-origin stock proportion within each year.

The number of Canadian-origin Chinook salmon returning to the Yukon River and the number of spawners (escapement) were reported by the S/Canada Joint Technical Committee of the Yukon River Panel (JTC 2015) and combined with juvenile abundance to describe stage-specific survival patterns. Adult assessment data (escapement and return) were scaled to juvenile year based on the assumption that all juveniles spend one year incubating in the gravel and one year rearing as fry in freshwater. Juvenile survival (ratio of adult returns to juvenile abundance) is used to describe survival during later life-history stages, and juveniles per spawner (ratio of juvenile abundance to spawner abundance) is used to describe survival during their early life-history period. Variance estimates of marine survival were based on the joint variance of juvenile abundance and adult returns (adult returns assumed to be measured with a coefficient of variation of 10%) with the Delta method for Taylor series approximation to the variance of random variables (Fournier et al. 2011) as:

$$Var\left(\frac{X}{Y}\right) = \left(\frac{\mu_Y^2 \sigma_X^2}{\mu_X^4}\right) + \left(\frac{\sigma_Y^2}{\mu_X^2}\right) - 2\left(\frac{\mu_Y}{\mu_X^3}\right)\rho\sigma_x\sigma_Y,$$

where μ_X and σ_X^2 are the mean and variance of Canadian-origin adult return by juvenile year, respectively, and μ_Y and σ_Y^2 are the mean and variance of the Canadian-origin juvenile abundance, and ρ is the correlation coefficient between juvenile and adult abundance.

Age-structured return projections for Canadian-origin Chinook salmon were constructed from juvenile abundance, average and standard deviation of marine survival, and average maturation rates. Canadian-origin Chinook salmon exhibit an odd and even year pattern in their maturation rate (JTC 2015); therefore, maturation rates for the juvenile projection models were based on the average brood year age composition for the previous three odd or even year brood years.

4. Results

Juvenile Chinook salmon are distributed within coastal habitats of the northern Bering Sea through most of their first summer at sea and are primarily distributed in shallow water depths (< 50 m) during surface trawl surveys (Fig. 3). While the mean location varies from year to year, the spatial center of their distribution is typically just west or southwest of the mouth of the Yukon River, indicating limited overall dispersal rates of juvenile Chinook salmon from the Yukon River in the northern Bering Sea. The average distance between the spatial mean and the mouth of the Yukon River from 2003 to 2014 is 140 km. The leading edge of the juvenile distribution is approximately 425 km from the mouth of the Yukon River.

Juvenile sample sizes used to estimate average length and weight ranged from 91 to 514, with an overall average of 213. Average fork lengths (FL) of juvenile Chinook salmon varied from 202 to 237 mm, with an overall average of 212 mm from 2003 to 2014 (Table 1). Average weight ranged from 75 to 172 g, with an overall average of 121 g. Average date corrections ranged from 8 to 10 days based on the timing of the survey. Date-corrected lengths ranged from 202 to 232 mm, with an overall average of 211 mm. Date-corrected weights ranged from 83 to 167 g, with an overall average of 120 g. The overall standard deviation of date corrected lengths and weights (28 mm FL and 52 g) are only slightly lower than observed lengths and weights (30 mm and 55 g).

Mixed-layer depth adjustments are based on the station level difference between trawl depth and mixed-layer depth, and ranged from 1.01 in 2009 to 1.43 in 2005 with an overall average adjustment of 1.16 (Table 2). Water column depths (bottom depths) that juvenile Chinook salmon were captured in ranged from 25.4 m in 2003 to 35.7 m in 2007 with an overall average of 30.1 m. Trawl (footrope) depth ranged from 14.6 m in 2003 to 22.2 m in 2010, with an overall average of 18.4 m. Mixed-layer depths ranged from 11.9 m in 2003 to 22.9 m in 2005, with an overall average of 17.6 m.

The proportion of Canadian-origin Chinook salmon in the northern Bering Sea ranged between 42% and 52%, with an overall average of 46% from 2003 to 2012 (Table 3). Genetic tissue sample sizes were similar to sample sizes used for length and weight (Table 1) for all years except 2005 and 2013 due to the loss of approximately 70% of the genetic tissue samples during these two years. Tissue samples recovered from the 2005 and 2013 surveys were not considered representative of juvenile population; therefore the annual average mixture estimates were applied to 2013, and mixture estimates from 2003 to 2007 were applied to 2005. Genetic analysis is not yet complete for 2014; therefore, average mixture estimates were applied to 2014. Mixture estimates include the estimated proportion and standard deviation of Canadian-origin Chinook salmon in the northern Bering Sea.

Estimates of juvenile abundance for the Canadian-origin stock group of Chinook salmon are based on area-swept juvenile abundance adjusted for mixed layer depth and the proportion of Canadian-origin Chinook salmon in the northern Bering Sea (Table 3; Fig. 4). The 2014 estimate is provisional as genetic and oceanographic data analyses are not complete. Abundance estimates range from 0.6 to 2.55 million juveniles with an overall average of 1.44 million juvenile Chinook salmon. Coefficient of variation of the abundance estimates range from 15% to 39% with an overall average of 26%. A coefficient of variation of 20% for average CPUE is typical for primary species captured in trawl based surveys on the eastern Bering Sea shelf (Lauth 2011b, Ianelli et al. 2014). Genetic assignment error adds additional variance to the abundance estimates, therefore the average variance (26%) is believed to be within a reasonable range. However, individual years have variance estimates that are quite large (e.g. 39% in 2009), which reduces the information level present in abundance estimates during these years. Variance estimates have generally increased since 2007. Estimates of juvenile survival range from a low of 0.035 in 2004 to a high of 0.068 in 2006 with an overall average of 0.052 from 2003 to 2010 (Table 3). Standard deviations of marine survival range from a low of 0.004 in 2004 to 0.016 in 2009, with an overall average of 0.008.

The number of juveniles per spawner are used to estimate the early life-history (freshwater and early marine) survival of Canadian-origin Chinook salmon (Table 3; Fig. 5). The 2014 estimate is provisional as the genetic and oceanographic data analyses are not complete. The number of juveniles per spawner declined from 44 in 2003 to a low average of 23 from 2005 to 2012, and an overall average of 26 between 2003 and 2012. The numbers of juveniles per spawner increased significantly in 2013 and 2014 with an average of 54 between these two years. The recent increase in the number of juveniles per spawner reflects an increase in survival during the early life-history stages of Canadian-origin Chinook salmon (freshwater and early marine) and provides a better measure of early life-history productivity than juvenile abundance.

The Pearson product moment correlation coefficient identifies that juvenile and adult abundance are significantly correlated for the Canadian-origin stock group of Chinook salmon in the Yukon River ($r = 0.88$, $p < 0.001$; Table 3). Linear regression model fit to juvenile and adult abundance with an intercept of zero accounts for 74% of the variation in recent adult returns (Fig. 6). These results emphasize the importance of early life-history stages (freshwater and early marine) to inter-annual variability in recent returns of Chinook salmon and stability in marine survival of juveniles.

The increase in juvenile abundance, particularly in 2013, and relative stable marine survival have important implications to future returns and fisheries in the Yukon River over the next several years. Guidance to fisheries management can be provided by age-structured pre-season run projections for the Canadian-origin stock group of Chinook salmon (Table 3). Runs are projected to increase over the next three years from a point estimate of 65,000 Chinook salmon in 2015 to 109,000 in 2017.

5. Discussion

Juvenile abundance can provide key information on the underlying production dynamics of salmon when combined with adult assessment data over periods of high and low productivity. Two critical periods are known to be present in salmon survival during their marine life-history stage (Beamish and Mahnken 2001). Predation-based mortality is believed to be critically important during their initial marine entry but begins to shift to nutritional-based sources of mortality as salmon outgrow the predation size window of most marine predators. The second critical period is believed to be dependent on the ability of salmon to reach a critical size or nutritional state required to survive their first winter at sea (Beamish and Mahnken 2001, Moss 2005, Farley et al. 2007). Estimates of juvenile survival between these two critical periods can provide important insight into the impact or role of the second critical period and mortality of salmon in the open ocean to their underlying production dynamics (Beamish et al. 2000).

Average survival of juvenile Chinook salmon in the northern Bering Sea is relatively low (average survival of 5.2%), indicating that mortality after their initial marine period (fist critical period) is still an important component of their overall production. Estimates of survival are higher than total marine survival in other wild Chinook salmon stocks in Alaska. Taku River

Chinook salmon smolt survival ranges from 1% to 6% with an overall average of 3% (1991 to 1998 brood years; Ed Jones, Alaska Department of Fish and Game, personal communication). However, juvenile survival in the northern Bering Sea is expected to be higher than total marine survival as it does not include mortality during their initial marine life-history stage (first critical period). The higher rate of survival obtained by sampling juveniles after their first critical period (near the end of their first growing season) in marine habitats should provide a higher level of stability than is present in total marine survival.

The significant correlation between juvenile and adult abundance for Canadian-origin Yukon River Chinook salmon indicates that subsequent marine survival has been relatively stable and that the second critical period has not contributed as much to the annual variation in survival as early life-history stages (freshwater and early marine). Other studies have found that correlations between abundance of early life stages of fish and recruitment into fisheries cycle in and out of significance and have been met with various degrees of success (Stige et al. 2013). Significant and stable correlations are present between juvenile and adult pink salmon abundance in southeast Alaska (Orsi et al. 2012), but not for Bristol Bay sockeye (Farley et al. 2011b). However, success is expected to vary with species, life-stage, adequacy of abundance estimates, and ecosystem stability.

The nutritional status of juvenile salmon is important to their overwinter survival, stability in marine survival, and process error in the relationship between juvenile and adult abundance. Lipid stores contribute to much of the variation in energy density of a fish, therefore nutritional status of a fish is typically evaluated with the combination of energy density and weight to arrive at an estimate of total energy (Heintz et al. 2013). Energy density of juvenile Chinook salmon in the northern Bering Sea increases with size and they typically reach an overall average energy density of 21.6 kj/g (dry weight) by September (Murphy et al. 2013, Moss et al. In Review). Although the energy density of juvenile Chinook salmon is similar to age-1 walleye pollock (*Gadus chalcogrammus*) in the Bering Sea at this time period (23.5 kj/g) (Siddon et al. 2013), they are approximately four to five times larger than age-1 pollock. Average weight of juvenile Chinook salmon in the northern Bering Sea is 121 g, average weight of age-1 pollock is in the range of 25-30 g. Significant and stable correlations are present between age-1 pollock abundance and recruitment (Stige et al. 2013), and provide support for stability in marine survival of juvenile Chinook salmon based on their nutritional status. Persistence of winter sea ice in the northern Bering Sea introduces a higher level of ecosystem stability than the southern shelf (Stabeno et al. 2012b), where most of the age-1 pollock occur (Hollowed et al. 2012). Yukon River Chinook salmon have a higher degree of adaptive resiliency to overwinter conditions through energy allocation patterns than is present in lower latitude stocks (Moss et al. In Review). Although size-selective mortality occurs in juvenile Yukon River Chinook salmon, mortality correction for size is within the measurement error of juvenile abundance and therefore it may not be possible to detect the effect of size on survival (Howard et al. In Review).

Variable maturation rates of Chinook salmon adds an additional source of process error in adult projections that is not necessarily reflected in marine survival. Maturation uncertainty increases when significant differences are present in adjacent juvenile year classes, such as 2012 and 2013. Size reductions in maturing Chinook salmon have occurred throughout Alaska and has generated concern over its impact (reduction) on fecundity and spawning effectiveness in wild Chinook salmon stocks as well as the intrinsic value of Chinook salmon to fishermen, particularly sport fishermen (Lewis et al. 2015). An improved understanding of factors contributing to maturity schedules of Chinook salmon will reduce uncertainty in juvenile projections and provide insight into declining size trends in Chinook salmon.

Measurement error in estimates of abundance and survival impacts attempts to make inferences on the stability of survival over time. Although both the accuracy and precision of juvenile abundance estimates are influenced by measurement error, accuracy is of particular concern due to the potential to incompletely sample juvenile distributions. Juvenile abundance may have been underestimated in 2005 and 2006 as these years resulted in the highest estimates of marine survival (6.1% and 6.8%, respectively) and lowest estimates of juveniles per spawner (20 and 17, respectively). The low average size of juveniles in 2006 (85 g) is inconsistent with high survival due to the presence of size-selective mortality in Yukon River Chinook salmon (Howard et al. In Review). The lowest estimate of juvenile survival (3.5%) occurred in 2004, and may reflect the cumulative impact of bycatch by groundfish fisheries in the eastern Bering Sea on the 2004 juvenile cohort. Bycatch levels of Chinook salmon increased substantially in 2006 and 2007 and both years impact the 2004 juvenile cohort as Chinook salmon are typically captured as bycatch after spending 2 and 3 years at sea (Ianelli and Stram 2014, Stram and Ianelli 2015). Fishery interceptions and bycatch are sources of measurement error that impact estimates of stock productivity based on terminal run size data (Eggers 2009).

Catch (herding) efficiency of surface trawl gear and depth dependence of Chinook salmon in Norton Sound add uncertainty in the level of measurement error present in juvenile abundance. Although no juvenile salmon were recovered in small mesh nets (pocket nets) placed in the large forward meshes of the trawl in 2012 and 2013, not all mesh sizes have been tested and catch efficiency could vary with sea state. Depth dependency of Chinook salmon in Norton Sound is not well understood and introduces uncertainty in abundance estimates when significant numbers are present in Norton Sound (this occurred in 2003 and 2013). The apparent depth dependency in juvenile Chinook salmon may be the result of an avoidance of high turbidity habitats associated within shallow nearshore habitats of Norton Sound by Chinook salmon.

Shallow bottom depths, presence of the cold pool, and coastal currents are important features of the northern Bering Sea ecosystem that impact our ability to sample juvenile distributions. Yukon River Chinook salmon typically enter the broad shallow shelf of the northern Bering Sea in June and remain in shallow water depths (<50 m) throughout most of their first summer at sea (September). The eastern Bering Sea cold pool (temperatures < 2°C) forms as a byproduct of winter sea ice, remains on the seafloor throughout the summer months, and varies in size with the winter sea ice extent (Danielson et al. 2011, Stabeno et al. 2012b). This also produces a highly stratified water column in the northern Bering Sea with the cold pool directly below the mixed layer. Shallow bottom depths and temperatures within the cold pool limit the vertical distribution of and permit surface trawls to effectively sample much of the vertical habitat of juvenile salmon. However, shallow bottom depths also introduce sampling challenges in nearshore habitats, particularly in Norton Sound.

Juvenile dispersal rates define, in part, the survey area required to sample through juvenile distributions. If we assume juveniles enter marine habitats during mid-June and are captured in mid-September, average dispersal rates are approximately 1.4 km/day, and juveniles at the leading edge have an approximate dispersal rate of 4.6 km/day. These dispersal rates are much lower than dispersal rates observed for stream-type Chinook salmon in the Gulf of Alaska, which migrate with coastal currents (19.1 km/day; Orsi et al. (2000)). Juveniles swim against the prevailing coastal current to exit the coastal northern Bering Sea prior to the formation of winter sea ice and this behavior may be the primary feature limiting their dispersal rates. Foraging behavior of Chinook salmon on larval capelin (*Mallotus villosus*) and Pacific sandlance (*Ammodytes hexapterus*) (Moss et al. In Review) in the coastal habitats of the northern Bering Sea may also be an important ecological feature contributing to reduced dispersal rates.

Stock-specific juvenile data are more informative than mixed-stock data as they can be directly linked to information available at other life-history stages. The Canadian-origin stock group is genetically distinct from other Chinook salmon stocks (Templin et al. 2011), they are a significant component (average of 45%) of the juvenile population in the northern Bering Sea, and information on adult returns are reasonably well defined (JTC 2015). This makes the Canadian-origin stock group of Chinook salmon a logical candidate for stock-specific abundance estimates in the northern Bering Sea. The average proportion of Canadian-origin Chinook salmon in the juvenile population (46%) is consistent with the adult population in the northern Bering Sea. Although Canadian-origin Chinook salmon typically account for 50% of the Yukon River returns (JTC 2015), we would expect a slightly lower proportion in the juvenile population due to the presence of Norton Sound Chinook salmon in the northern Bering Sea (Murphy et al. 2009). The proportion of Canadian-origin Chinook salmon is also relatively stable (Table 3), indicating that other stock groups of Chinook salmon (as an aggregate) are following a similar pattern observed in the productivity of Canadian-origin Chinook salmon. However, analysis of other stock groups will be required to adequately evaluate patterns in their productivity and survival.

The increase in juvenile abundance in 2013 and 2014 reflects an improvement in survival during early life-history stages (freshwater and early marine) of Canadian-origin Chinook salmon and provides an important contrast in the juvenile data. The average number of juveniles per spawner in 2013 and 2014 (54) was significantly higher than the overall average of 26 juveniles per spawner during previous survey years (2003 to 2012). This reflects an improvement in survival during the egg incubation and/or fry stages of Chinook salmon (Bradford et al. 2001, Neuswanger et al. 2015) or an improvement in smolt survival during downstream migration and the early marine stages of Chinook salmon (Bradford et al. 2008, Hillgruber and Zimmerman 2009).

Indirect evidence in both marine and freshwater habitats provide support for an increase in abundance of the 2013 juvenile cohort. Immature Chinook salmon increased in abundance on the eastern Bering Sea shelf in 2014. Catches of immature Chinook salmon during surface trawl surveys on the eastern Bering Sea shelf increased from an overall annual average of 15 (2003 to 2013) to 107 during 2014. Over 80% of these Chinook salmon were in the size range of immature age 3 Chinook salmon (between 320 and 600 mm FL), which are the 2013 juvenile cohort. However, distribution and migration of Chinook salmon alters their abundance on the eastern Bering Sea shelf in addition to stock abundance (Ianelli et al. 2010, Ianelli and Stram 2014). The proportion of age-4 (2013 juvenile cohort) Chinook salmon maturing and returning to the Yukon River and caught in the 2015 Pilot Station test fisheries was 21.3%, and is much higher than the historic average of 10.6% (Larry Dubois, Alaska Department of Fish and Game, personal communication).

A dedicated commitment to advance and improve methods used to estimate juvenile abundance, describe changes in marine survival, and improve forecast models will be needed to ensure juvenile data remain relevant to Canadian-origin Chinook salmon in the Yukon River over time. The potential for measurement error in the assessment of juvenile abundance (particularly undersampling the juvenile population) is high and additional work is needed to develop survey design criteria that are appropriately matched to juvenile migration and dispersal patterns. Adaptive designs are an efficient approach to balancing research objectives between large-scale ecosystem monitoring and juvenile Chinook salmon assessments by adding Chinook salmon sampling locations to a core survey area to accommodate for changes in juvenile distribution over time. Adaptive cluster sampling (Thompson and Seber 1996) is a design approach that can be used to estimate abundance with a specified target variance (e.g. coefficient of variation < 15%) to help maintain consistency in the information level provided by juvenile abundance over time.

Recent declines in the productivity of Chinook salmon and the associated challenge of allocating limited harvest throughout the drainage adds complexity to in-river fisheries management and subsistence harvest decisions by rural communities. Juvenile assessments provide a unique insight into status of Canadian-origin Chinook salmon and have the potential to help define fishery expectation up to 3 years in advance of actual implementation of fisheries. This helps management by providing additional time to develop and gather support for strategies consistent with stock status. The current escapement goal range for Canadian-origin Yukon River Chinook salmon is 42,500 to 55,000, international treaty allocates 20% to 26% of the harvest to Canadian fisheries, and an unrestricted subsistence harvests in Alaska typically requires approximately 30,000 Canadian-origin Chinook salmon. Therefore, we expect Alaskan subsistence and Canadian aboriginal harvests to be curtailed, to some extent, when run size is below the range of 80,000 to 90,000 Canadian-origin Chinook salmon (JTC 2015).

Age-structured projected return models based on juvenile abundance and survival provide the following pre-season guidance for fisheries management. The projected return in 2015 (65,000, range 52,000 to 78,000) is likely to provide escapement and Canadian harvest sharing requirements but not an unrestricted Alaskan subsistence harvest. The projected return in 2016 (75,000, range 60,000 to 90,000) is likely to provide for escapement, Canadian harvest sharing agreements, but Alaskan subsistence harvest restrictions may be required unless the return is within the upper end of the projected range. The projected return for 2017 (109,000 range 87,000 to 131,000) will likely provide for all management priorities (escapement, Alaskan subsistence, and Canadian harvest sharing agreements) with the potential for commercial, sport, and recreational harvests. This may also reduce or eliminate gear restrictions placed on summer Chum salmon commercial fisheries. Restoration of the subsistence fisheries for Chinook salmon in the Yukon River will be a significant turning point in the management of Yukon River salmon fisheries; juvenile data indicate that this could occur in 2016 and will likely occur by 2017.

6. Acknowledgments

Multiple funding sources have provided support for surface trawl surveys in the northern Bering Sea. The National Marine Fisheries Service provided the primary funding support for the surveys from 2003 to 2010. The Alaska Sustainable Salmon Fund and the Arctic Yukon Kuskokwim Sustainable Salmon Initiative provided funding support for the survey in 2011. The State of Alaska's Coastal Impact Assessment Program and the Arctic Yukon Kuskokwim Sustainable Salmon Initiative provided funding support through the University of Alaska, Fairbanks Arctic EIS research program in 2012 and 2013. The Alaska Department of Fish and Game's Chinook Salmon Research Initiative provided funding support for the 2014 survey. Vessels supporting the northern Bering Sea surveys include the F/V *Sea Storm* (2003-2007), F/V *Epic Explorer* (2009-2010), F/V *Bristol Explorer* (2011-2013), and the F/V *Alaskan Endeavor*

(2014). We wish to thank the many scientists, as well as the captains and crews of the chartered fishing vessels, which have made the northern Bering Sea surveys possible.

7. Disclaimers

The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Table 1. Sample sizes, average observed length and weight, average date adjustment, and average date corrected length and weight of juvenile Chinook salmon during surface trawl surveys in the northern Bering Sea (2003 to 2014).

Year	Sample Size (n)	Average Length (mm)	Average Weight (g)	Average Date Adjustment (days)	Date Adjusted Average Length (mm)	Date Adjusted Average Weight (g)
2003	233	202	104	0	202	104
2004	181	221	136	-2	219	132
2005	144	226	143	-8	218	134
2006	107	189	81	5	195	85
2007	271	237	172	-5	232	167
2008						
2009	135	216	123	8	222	131
2010	135	211	118	-5	206	113
2011	314	185	75	10	195	85
2012	91	207	115	-7	200	108
2013	514	222	143	-4	218	139
2014	328	218	138	4	222	143
Average	213	212	121	0	211	120

Table 2. Catch weighted average bottom depth, trawl (footrope) depth, and mixed layer depth (MLD), and MLD adjustments to area swept abundance estimates for juvenile Chinook salmon during surface trawl surveys in the northern Bering Sea (2003-2013).

Juvenile Year	Catch weighted bottom depth (m)	Catch weighted trawl depth (m)	Catch weighted MLD (m)	MLD adjustment
2003	25.4	14.6	11.9	1.22
2004	32.7	16.5	17.3	1.16
2005	35.2	16.4	22.9	1.43
2006	31.2	16.5	21.2	1.29
2007	35.7	17.1	17.4	1.18
2008				
2009	30.4	21.7	16.3	1.01
2010	27.6	22.2	16.6	1.05
2011	26.6	19.6	19.3	1.14
2012	28.9	19.7	19.6	1.15
2013	27.5	19.9	13.1	1.01
Average	30.1	18.4	17.6	1.16

Table 3. Abundance and survival estimates of Canadian-origin juvenile Chinook salmon based on surface trawl surveys in the northern Bering Sea (NBS) from 2003 to 2014. Abundance estimates are included for all Chinook stock groups in the northern Bering Sea and for the Canadian-origin stock group. The proportion of Canadian-origin Chinook salmon in the northern Bering Sea and coefficients of variation (CV) for the Canadian-origin juvenile abundance estimates are included. Spawner abundance, adult returns, and estimates of juveniles per spawner, juvenile survival, and the standard deviation (DS) of juvenile survival for Canadian-origin Chinook Salmon are also included.

Juvenile Year	NBS Juvenile Abund. (000s)	Canadian Stock Prop.	Canadian Juvenile Abund. (000s)	Canadian Juvenile Abund. (CV)	Canadian Spawner Abund. (000s)	Canadian Return (000s)	Juveniles per Spawner	Juvenile Survival	Juvenile Survival (SD)
2003	5,332	0.43	2,293	17%	53	107	44	0.047	0.005
2004	2,826	0.52	1,470	18%	42	52	35	0.035	0.004
2005	3,377	0.47[1]	1,596	15%	81	98	20	0.061	0.005
2006	1,801	0.46	828	20%	48	56	17	0.068	0.009
2007	3,390	0.48	1,627	32%	68	78	24	0.048	0.012
2008					63	59			
2009	1,804	0.47	848	39%	35	45	24	0.053	0.016
2010	1,939	0.42	814	26%	34	42	24	0.051	0.009
2011	3,456	0.44	1,521	37%	65		23		
2012	1,401	0.42	592	35%	32		18		
2013	5,597	0.46[2]	2,559	24%	46		55		
2014	3,722	0.46[2]	1,702[3]	23%[3]	33		52		
Avg.	3,150	0.46	1,441	26%	50	67	31	0.052	0.008

1 Stock proportion in 2005 based on average proportion from 2003 to 2007

2 Stock proportion in 2013 and 2014 based on overall average 2003 to 2012

3 Juvenile abundance estimates in 2014 are based on average stock proportions and mixed layer depth adjustments

Table 4. Age-structured projection and projection ranges of Canadian-origin Chinook salmon returns to the Yukon River based on juvenile abundance in the northern Bering Sea, average juvenile survival, and average maturation (2015 to 2017).

Return Year	Projected Age-4 Return (000s)	Projected Age-5 Return (000s)	Projected Age-6 Return (000s)	Projected Age-7 Return (000s)	Projected Total Return (000s)	Projection Range Total Return (000s)
2011						
2012	3					
2013	6	17				
2014	2	30	20			
2015	10	12	40	2	65	52-78
2016	6	51	15	2	75	60-90
2017	6[1]	35	67	2	109	87-131
2018			42	4		
2019				4		

1 Projected age-4 returns in 2017 based on average projected return from 2012 to 2016

Figure 1. A natural color satellite image of the coastal northern Bering Sea shelf, Norton Sound, and Yukon River Delta from the NASA Earth Observatory System (EOS) on August 8, 2012. This Image was made available by the Land Atmosphere Near-real time Capability for EOS (LANCE) AQUA satellite operated by the NASA/GSFC Earth Science Data and Information System (ESDIS) with funding provided by NASA/HQ.

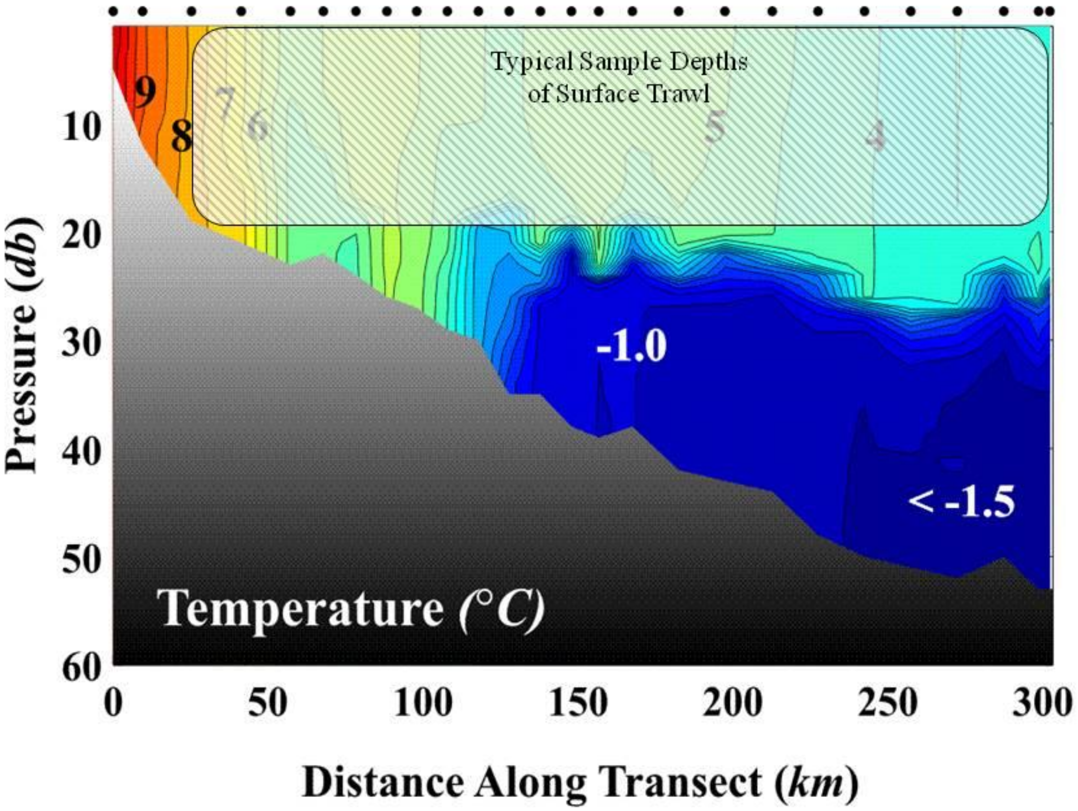

Figure 2. Typical sampling depths of the surface trawl in relation to water column temperatures in the northern Bering Sea. Temperature data is from 15-16 July, 2009 along latitude 62°N, from Danielson et al. (2011). Sample locations are indicated by black dots above the figure and the grey/black polygon indicates bottom depth.

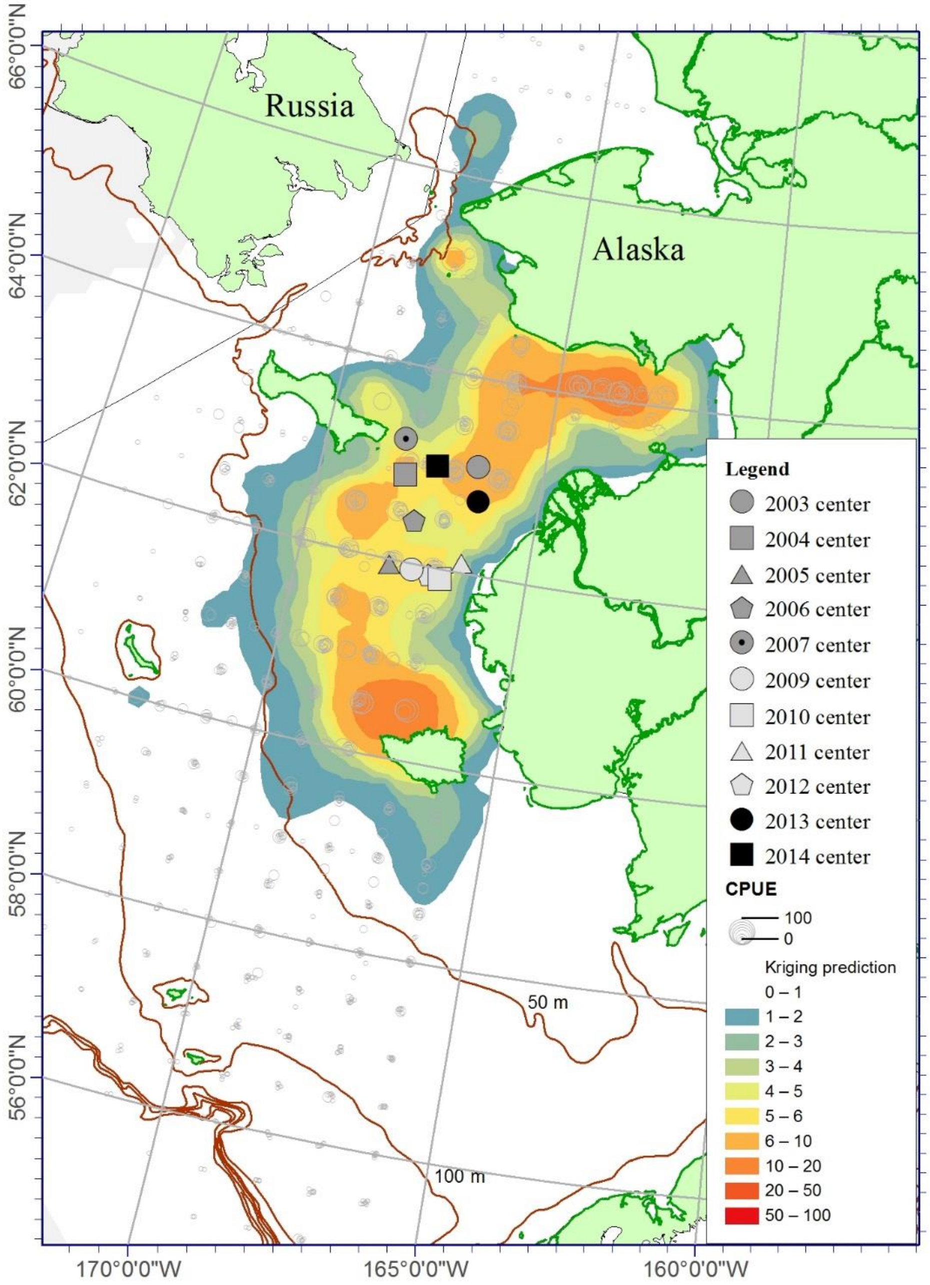

Figure 3. Spatial distribution of juvenile Chinook salmon based on catch data (CPUE, catch-per-km^2 scaled to average effort) from surface trawl surveys in the northern Bering Sea, 2003 to 2014. Color contours are from the neighborhood kriging prediction surface of CPUE (circles) and shaded symbols identify the spatial center of juvenile Chinook salmon distributions by year.

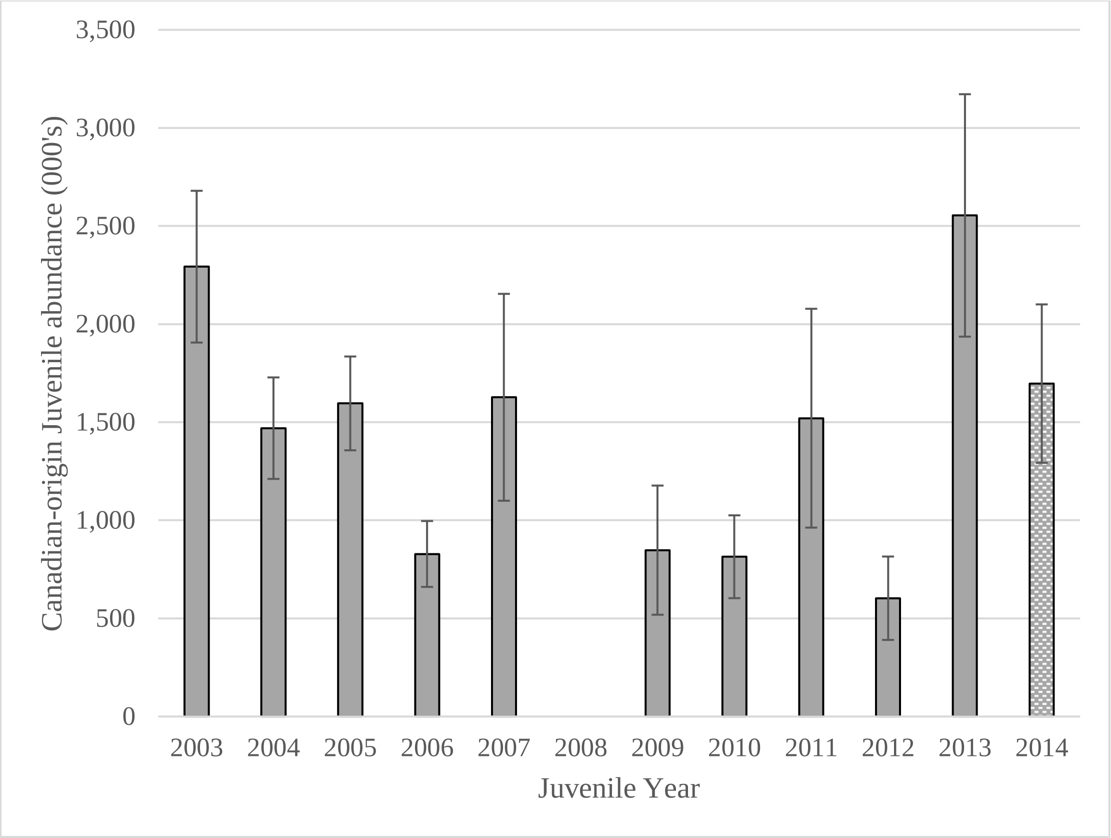

Figure 4. Juvenile abundance estimates for the Canadian-origin stock group of Chinook salmon in Yukon River, 2003 to 2014. Error bar range is two standard deviations in the estimate of juvenile abundance. The 2014 estimate is based on average stock composition and mixed layer depth adjustments.

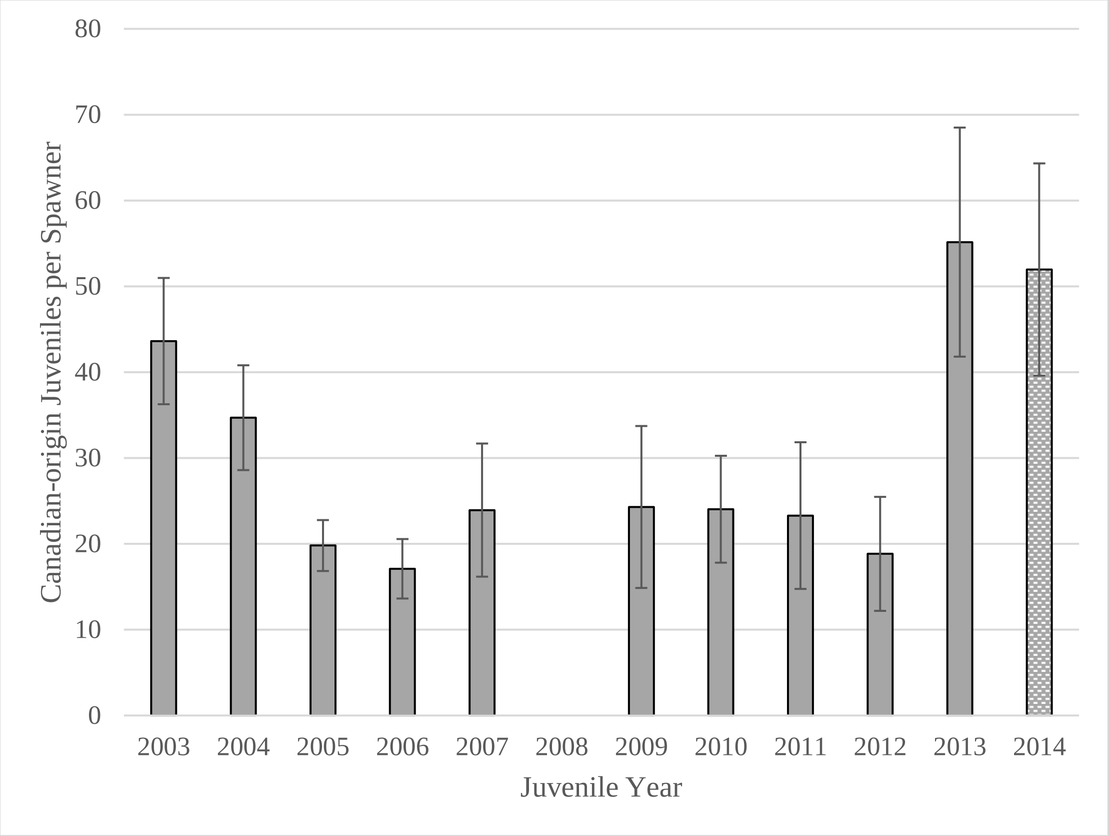

Figure 5. The estimated number of juveniles per spawner for the Canadian-origin stock group of Chinook salmon in the Yukon River, 2003 to 2014. Error bar range is two standard deviations in estimates of juvenile abundance. The 2014 estimate is based on average stock composition and mixed layer depth adjustments.

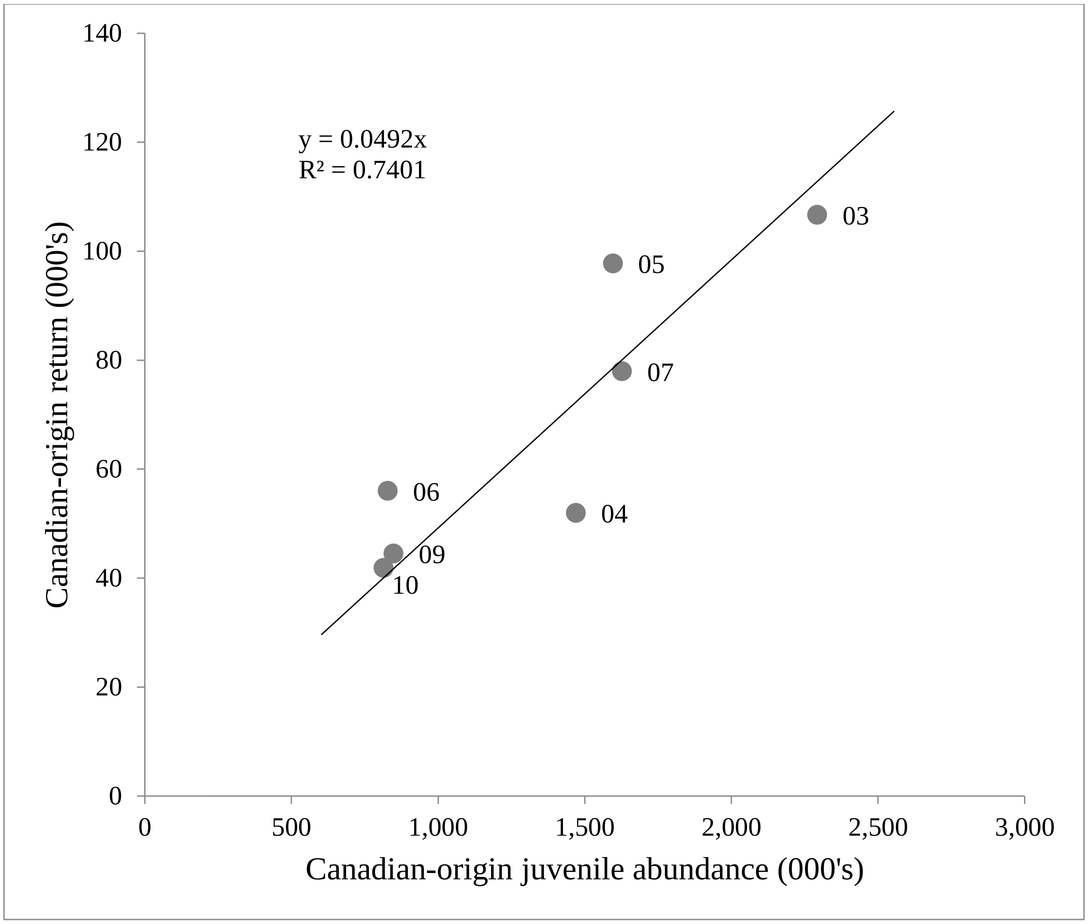

Figure 6. The relationship between juvenile and adult return abundance for the Canadian-origin stock group of Chinook salmon in the Yukon River, 2003 to 2010. Adult abundance is the number of returning adults by juvenile year. Numbers associated with each data point indicate the juvenile year.

Appendix P.

Seabird Distribution and Abundance in the Northeastern Bering Sea and Chukchi Sea

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Athina Catherine Pham, Kathy J. Kuletz

December 30, 2015

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Agencies and Projects	
ADFG	Alaska Department of Fish and Game
AFSC	Alaska Fisheries Science Center
Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
NOAA	National Oceanic and Atmospheric Administration
PMEL	Pacific Marine Environmental Laboratory
SFOS	School of Fisheries and Ocean Sciences
UAF	University of Alaska Fairbanks
USFWS	US Fish and Wildlife Service
Chl a	Chlorophyll-a concentration
CPUE	Catch-per-unit-effort
ISA	Indicator species analysis
MRPP	Multi-response permutation procedure
NMDS	Non-metric multidimensional scaling
RMANOVA	Repeated measures analysis of variance

List of Oral and Poster Presentations

The following presentations included Arctic Eis seabird data, but were not exclusive to the Arctic Eis project:

Pham, Catherine, K. David Hyrenbach, Kathy Kuletz, Ed Farley, Lisa Eisner, and Alexei Pinchuk. Seabird response to interannual variation in oceanographic properties and prey in the northern Bering and Chukchi seas. Accepted for an Oral Presentation at the Pacific Seabird Group meeting, February 2016, Turtle Bay, HI.

Pham, Catherine, K. David Hyrenbach, Kathy Kuletz, Ed Farley, Lisa Eisner, and Alexei Pinchuk. Interannual variability in seabird communities with respect to prey and environmental properties in the northern Bering and Chukchi seas. Accepted for an Oral Presentation at Alaska Marine Science Symposium, January 2016, Anchorage, AK.

Kuletz, Kathy, Adrian Gall, Martin Renner, Elizabeth Labunski, and Tawna Morgan. 2015. North to the Arctic: the late summer and fall migration of seabirds from the Bering Sea into the Chukchi Sea. Oral Presentation, World Seabird Conference, October 2015, Cape Town South Africa.

Poe, Aaron, Melanie Smith, Will Koeppen, Kathy Kuletz, Heather Renner, and Tom Van Pelt. 2015. Exploring climate projections for globally recognized important bird areas in the Bering Sea and Aleutians. Oral presentation at Pacific Seabird Group Annual meeting, February, 2015, San Jose, CA.

Sigler, Mike, Franz Mueter, Bodil Bluhm, Morgan Busby, Ned Cokelet, Seth Danielson, Alex De Robertis, Lisa Eisner, Ed Farley, Katrin Iken, Kathy Kuletz, Bob Lauth, Libby Logerwell, Alexei Pinchuk, Chris Wilson. 2015. Summer zoogeography of the northern Bering and eastern Chukchi Seas. Alaska Marine Science Symposium, January 2015, Anchorage, AK, Poster.

Kuletz, K.J., Megan Ferguson, Adrian Gall, Brendan Hurley, Elizabeth Labunski, Tawna Morgan, Robert Day. 2014. Seasonal and spatial patterns of marine-bird and -mammal distributions in the pacific arctic: a delineation of biologically important marine areas. Oral Presentation, Alaska Marine Science Symposium, January 2014, Anchorage, AK.

Pham, C., K. Kuletz, E. Labunksi, and M. Renner. 2013. Post-breeding distribution of Ancient Murrelets in the Bering and Chukchi seas. Poster presentation at the Pacific Seabird Group annual meeting, Portland OR, February 20-23, 2013.

Kuletz, K., E. Labunski, M. Renner, and M. Bishop. 2013. The murrelet in winter –a review of Marbled Murrelet post-breeding distribution with a focus on Alaska. Presentation at the Pacific Seabird Group annual meeting, Portland OR, February 20-23, 2013.

Publications using Arctic Eis Data

Day, R.H., Gall, A.E., Morgan, T.C., Rose, J.R., Plissner, J.H., Sanzenbacher, P.M., Fenneman, J.D., Kuletz, K.J., Watts, B.A., 2013a. Seabirds new to the Chukchi and Beaufort seas, Alaska: response to a changing climate? *Western Birds* 44, 174–182. . [Note: This article documents the first sighting of the Short-tailed Albatross in the Chukchi Sea during an Arctic Eis cruise, and significant range expansion of the Ancient Murrelet documented during both Arctic Eis seasons].

Gall, Adrian E.l, Tawna C. Morgan, Robert H. Day, and Katherine J Kuletz. *In Review*. Ecological shift from piscivorous to planktivorous seabirds in the Chukchi Sea, 1975–2012. *Polar Biology*.

Kuletz, K., M. Ferguson, A. Gall, B. Hurley, E. Labunski, T. Morgan. 2015. Seasonal Spatial Patterns in Seabird and Marine Mammal Distribution in the Eastern Chukchi and Western Beaufort Seas: Identifying Biologically Important Pelagic Areas. *Progress in Oceanography* 136: 175-200. [Note: The analysis for this publication included data from 2012 Arctic Eis. This publication was part of the SOAR special issue (Synthesis of Arctic Research) funded by BOEM, in collaboration between the USFWS, ABR, Inc. (Industry funded survyes and analysis), and National Marine Mammal Lab, NOAA].

Petersen, Aevar, David B. Irons, H. Grant Gilchrist, Gregory J. Robertson, David Boertmann, Hallvard Strøm, Maria Gavrilo, Yuri Artukhin, Daniel S. Clausen, Kathy J. Kuletz, and Mark L. Mallory. 2015. The Status of Glaucous Gulls *Larus hyperboreus* in the Circumpolar Arctic. *Arctic* 68(1):107 – 120. http://dx.doi.org/10.14430/arctic4462. (Information from Arctic Eis surveys for Glaucous Gulls was included in this overview).

Sigler, Mike, Franz Mueter, Bodil Bluhm, Morgan Busby, Ned Cokelet, Seth Danielson, Alex De Robertis, Lisa Eisner, Ed Farley, Katrin Iken, Kathy Kuletz, Bob Lauth, Libby Logerwell, Alexei Pinchuk, Chris Wilson. *In Review*. Summer zoogeography of the northern Bering and eastern Chukchi Seas. *Deep Sea Research II*.

The U.S. Geological Survey announced the public release of the North Pacific Pelagic Seabird Database, which includes the Arctic Eis seabird data. The user's guide, seabird distribution maps, and access to data can be found at:
http://alaska.usgs.gov/science/biology/nppsd/index.php

The Arctic Eis seabird survey data has been incorporated into the North Pacific Pelagic Seabird Database (USGS) and was included in the PacMARS (Pacific Marine Arctic Regional Synthesis) and uploaded to the Arctic Eis AOOS Workspace.

Proposed Objectives and Study Chronology

The overall purpose of the seabird component of the Arctic Ecosystem Integrated Survey (Arctic Eis) project is to contribute new baseline information on the spatiotemporal dynamics of seabirds in the northern Bering and eastern Chukchi seas. The seabird component was not part of the original Arctic Eis proposal, but was integrated via an interagency agreement (M10PG0050; Project AK-10-10) between the Bureau for Ocean Energy Management (BOEM) and U.S. Fish & Wildlife Service (USFWS). The objectives are to (i) characterize seabird distribution and abundance patterns relative to meso scale oceanographic factors and prey availability, (ii) identify interannual changes in seabird community structure, (iii) identify factors that influence the coarse scale distribution of different seabird foraging guilds, and (iv) identify areas of high and low seabird abundance, and the interannual variance in seabird density within those areas. The results will inform management of the northern Bering and Chukchi seas by providing USFWS and BOEM with information about the abundance and distribution of seabirds across this sensitive region. If there are discrete seabird communities associated with specific oceanographic habitats within this region, characterization of those communities and habitats will guide management strategies.

In August and September of 2012 and 2013, the Arctic Eis project conducted research cruises in the northern Bering Sea and eastern Chukchi Sea. During these cruises, we conducted visual surveys as the ship transited between sample stations.

In 2014, C. Pham was awarded funding from USFWS (via BOEM funds) to assist Dr. Kathy Kuletz with data analysis and reporting on the Arctic Eis seabird component. She began her master's degree studies at Hawai'i Pacific University in Fall 2015. In spring 2015, C. Pham was awarded a Graduate Student Research Award from the North Pacific Research Board to help support her studies thesis research.The goal is to complete all Arctic Eis analyses by September 2016.

Processing of the seabird data began in spring 2015 and was completed during summer 2015. The 2012 and 2013 seabird data was contributed to the North Pacific Pelagic Seabird Database (http://alaska.usgs.gov/science/biology/nppsd/index.php), and is posted on the Arctic Eis AOOS Ocean Workspace. Processing of oceanographic and prey data towards analyses as part of the seabird component began in summer 2015 and will be completed in December 2015. We constructed multivariate statistical models using oceanographic and biological data in conjunction with seabird survey data from the Arctic Eis cruises. Analyses of meso scale seabird community structure were completed during fall 2015. Analyses of coarse scale seabird habitat use will be completed during winter 2015-2016.

The Arctic Eis seabird data has been integrated into several projects that resulted in presentations at professional meetings and in publications (see List of Presentations and Publications). Results from C. Pham's thesis will be presented at the Alaska Marine Science Symposium in January 2016 and the Pacific Seabird Group meeting in February 2016. We plan to submit an abstract to the Western Alaska Interdisciplinary Science Conference & Forum, to be held in March 2016.

1. Abstract

This study seeks to improve our knowledge of arctic seabird ecology by examining distributional and community changes in response to interannual changes in marine habitats and prey. To this end, we used data from the Arctic Eis to examine the prey and oceanographic factors that influenced seabird community structure within and between the two study years. First, we defined seabird communities and their associations with habitats and prey using a nonmetric multidimensional ordination. The ordination identified three habitats based on associated seabird communities. These habitats were most strongly correlated with latitude, longitude, salinity, chlorophyll-a, slope, and fish catch-per-unit-effort. A multi-response permutation procedure grouped by year and geographic region revealed differences between years in seabird community structure. These results suggest that seabird communities are structured by ecotones that may change in location interannually, with oceanographic properties being slightly stronger predictors than prey abundance. We will examine these correlations on a coarse scale by using generalized additive models to determine the most important factors that influence the distribution of seabird foraging guilds and numerically dominant species.

2. Introduction

Arctic marine ecosystems are particularly sensitive to the effects of climate change because they are simpler than other marine ecosystems in terms of biodiversity and number of trophic levels (Grebmeier et al. 2006, Sakshaug et al. 1994), and are experiencing disproportionate warming (ACIA 2004). Climate change is predicted to affect these ecosystems directly via physical changes in water column properties, and indirectly via changes in food web dynamics. However, because these ecosystems are poorly studied, it is unclear how effects cascade through trophic levels to impact marine predators such as seabirds. Thus, integrated ecosystem research is necessary to develop precautionary management measures to monitor and conserve arctic marine ecosystem structure and function (Ruckelshaus et al. 2008, NOAA 2004).

The most conspicuous effect of climate change on arctic marine ecosystems is the loss of seasonal sea ice, which is predicted to increase maritime activities such as shipping and energy exploration. The most recent attempt to conduct offshore drilling in Alaska's Chukchi Sea has heightened concerns about the environmental impacts of increasing energy exploration and shipping in the Arctic (DOI 2013). Maritime activities can affect marine ecosystems through chronic and catastrophic impacts including pollution, chronic disturbance, habitat destruction, and direct mortality. For mid and upper trophic levels, such human impacts can result in long-term decreased reproductive effort, population redistributions, and acute mortality (e.g., Peterson et al. 2003, Schwemmer et al. 2011). A better understanding of the relationships between seabirds and their habitat and prey will help guide policy and management decisions.

Seabirds are important marine ecosystem indicators because they are numerous, conspicuous, and broadly distributed in an environment where most components are hidden from view and difficult to sample (e.g., fish, marine mammals). Furthermore, as mid and upper trophic predators, they integrate information across trophic levels and indicate changes in multiple ecosystem components (Sydeman et al. 2012). In temperate, sub-polar, and polar marine ecosystems, seabirds respond to changes in ocean productivity and prey availability in diverse but predictable manners (Piatt et al. 2007, Sydeman et al. 2012, Ainley et al. 1998). Thus, seabirds can serve as ecosystem indicators, indicating both natural fluctuations due to climate variability and changes caused by human activities.

While seabird studies have historically focused on their breeding biology due to the relatively easy accessibility of their breeding grounds, seabirds spend the vast majority of their lives at sea. Thus, in order to fully realize the role of seabirds as ecosystem indicators, we need to understand their distributions and habitat use patterns. In particular, understanding how the spatiotemporal patterns of their prey and the underlying oceanographic processes influence seabird distribution across space and time is critical to planning for ecosystem changes. Concurrently, future changes in seabird distribution and abundance patterns could be used to infer changes in the underlying biological and physical processes.

To date, a few studies have described seabird communities in the northern Bering and Chukchi seas in relation to their prey and oceanographic habitats (e.g., Sigler et al. 2011, Gall et al. 2013, Kuletz et al. 2015). However, studies that quantified the spatial dynamics of seabirds in relation to prey and physical properties have been generally limited in scope, focusing on a small number of abundant species and rarely examining seasonal or interannual variability (e.g., Russell et al. 1999, Piatt & Springer 2003). The use of seabirds as indicators of spatial changes in arctic marine ecosystems is hampered by the lack of integrated spatiotemporal data; this study attempts to address this information gap.

The ultimate goal of the Arctic Eis project is to improve understanding of the potential effects of climate change, energy exploration, and other human activities on these ecosystems through integrated research (Andrews 2012, Weems 2014). Because of the comprehensive coverage of these cruises (in U.S. waters) over two sampling seasons, Arctic Eis provides enhanced baseline information on various ecosystem components as well as new information on the community structure of pelagic fishes. This coverage allows for a rare opportunity to examine different ecosystem components in relation to each other at both meso and coarse spatial scales. Here, we focus on the spatial patterns of seabird communities with respect to their prey and oceanographic habitats.

2.1. Study region: Oceanography of the Northern Bering Sea and Chukchi Sea

The northern Bering Sea and Chukchi Sea continental shelf ecosystem is influenced by three distinct water masses that are defined primarily by their salinity, and organized east to west—the Anadyr Water, Bering Shelf Water, and Alaska Coastal Water (Coachman et al. 1975, Weingartner et al. 1999, Fig. 1, Appendix A). These water masses advect nutrients, heat, and plankton biomass northward, supporting high productivity in the northern Bering Sea and through the Bering Strait into the Chukchi Sea (Springer & McRoy 1993). Anadyr Water is relatively cold, saline, and rich in nutrients, and Bering Shelf Water has properties similar to Anadyr Water (Coachman & Shigaev 1992, Weingartner 1997). Alaska Coastal Water originates from river input into the eastern Bering Sea and is relatively warm, fresh, and poor in nutrients (Springer et al. 1984, Coachman & Shigaev 1992, Weingartner 1997). North of the Bering Strait, Anadyr Water and Bering Shelf Water merge into Bering Sea Water (Coachman et al. 1975). The properties, extent, and mixing of these water masses can fluctuate greatly due to interannual variability in atmospheric circulation, including regional wind patterns, and in the timing and spatial extent of seasonal sea ice (Weingartner et al. 1999, 2005; Woodgate et al. 2005, 2006).

2.2. A review of seabird spatial ecology

Seabirds respond to changes in bottom-up food web dynamics by shifting their at-sea dispersion (Bennett 1997). However, the specific mechanisms responsible for these responses are poorly understood because seabird distributions, densities, and community structures are influenced by multiple biological and physical processes that operate at hierarchical scales (Hunt & Schneider 1987, Sydeman et al. 2012). At the broadest scales (>1000 km), seabirds are constrained by adaptations to specific oceanographic habitats and to a lesser extent by distribution of prey within those habitats (Hunt & Schneider 1987). Since most seabirds are fairly flexible in their prey selection, physiological adaptations are then probably more important at these scales than the distribution of specific prey species (Hobson et al. 1994, Ainley et al. 1992). At smaller scales (<100 km), seabirds are patchily distributed with the greatest densities found in areas of high prey availability (Hunt & Schneider 1987; Benoit-Bird et al. 2011, 2013). Hunt & Schneider (1987) proposed that combined effects of meso scale physical processes and prey patchiness on seabird distributions occur on meso to large scales of 10 – 500 km, and result in distinct communities associated with particular physical habitats. Prey patchiness likely determines seabird patchiness within coarse to meso scales (Hunt & Schneider 1987; Logerwell et al. 1998; Mehlum et al. 1999; Benoit-Bird et al. 2011, 2013).

2.3. Meso to large scale ecosystem structure

In marine ecosystems, biogeographic domains (also called provinces) are spatially- and temporally-defined regions characterized by the distinctness of their underlying physical environment and their overlying biotic community relative to those of surrounding regions (Hayden et al. 1984). In pelagic marine ecosystems, these domains are dynamic, often shifting in geographic location and changing in community structure as a result of spatial and seasonal variability in the underlying physical dynamics. The long term persistence of their characteristic physical characteristics and biotic communities, independent of absolute geographic location and seasonal changes, may then be the most important defining characteristic of these domains (Hayden et al. 1984, Hunt et al. 2014).

On meso to large scales, the biogeography of the northern Bering and Chukchi seas appears to be tied to water mass properties and latitudinal gradients. Sea ice is the driving factor, and in the late summer and early fall period, affects water masses and the biotic communities indirectly. The extent of sea ice during the preceding winter and the timing of its annual retreat can affect the physical properties of the water masses of the region for the remainder of the year (Weintgartner et al. 2005).

Zooplankton communities in particular are very strongly associated with specific water masses. For example, large copepods dominate high salinity Anadyr Water (Eisner et al. 2013, Hopcroft et al.

2010, Piatt & Springer 2003). Certain small copepods dominate low salinity Alaska Coastal Water, while other small copepod species are relatively evenly distributed across water masses (Eisner et al. 2013, Hopcroft et al. 2010, Piatt & Springer 2003). There is also a latitudinal gradient in zooplankton communities, with sub-arctic species being most abundant in the northern Bering Sea and southern Chukchi Sea, and arctic species being most abundant in the Chukchi Sea (Eisner et al. 2013, Hopcroft et al. 2010, Piatt & Springer 2003). Overall, zooplankton densities are greatest just north of the Bering Strait and in high salinity waters, and their distributions and abundances vary with season, year, and latitude (Eisner et al. 2013, Questel et al. 2013, Hopcroft et al. 2010).

Relatively little is known about community-habitat associations of pelagic fishes in the northern Bering and Chukchi seas, but they appear to be structured primarily along a latitudinal gradient and secondarily with water masses (Eisner et al. 2013). Juvenile saffron cod (*Eleginus gracilis*), juvenile Arctic cod (*Boreogadus glacialis*), and adult Pacific sand lance (*Ammodytes hexapterus*) are most abundant in the central and northern Chukchi Sea, while adult Pacific herring (*Clupea pallasii*), walleye pollock (*Theragra chalcogramma*), and capelin (*Mallotus villosus*) are most abundant in the northern Bering and southern Chukchi seas (Eisner et al. 2013, Piatt & Springer 2003). Both diversity and biomass decrease with latitude, and high diversity and biomass are associated with Alaska Coastal Water (Eisner et al. 2013, Piatt & Springer 2003).

Based on physical oceanography, zooplankton communities, and pelagic fish communities, the northern Bering and eastern Chukchi seas might then be divided into several domains based on latitudinal and water mass differences. Indeed, using zooplankton, fish, and seabird communities, Sigler et al. (2011) identified three latitudinally-structured domains in the Pacific Arctic during the summer—the Eastern Bering Shelf Province, the Chirikov-Chukchi Province, and the Beaufort Sea Province. While the northern Bering and Chukchi seas were grouped into the Chirikov-Chukchi Province, Sigler et al.'s results suggested that there are differences between the northern Bering Sea and the Chukchi Sea; for example, Crested and Least Auklets (*Aethia cristatella* and *A. pusilla*) dominate the northern Bering Sea while Short-Tailed Shearwaters (*Ardenna tenuirostris*) dominate the Chukchi Sea. Furthermore, the authors acknowledged that there is evidence for longitudinal differences though they did not examine those in their study. There may then be at least two and potentially four or more domains within the northern Bering and Chukchi seas.

Water mass properties such as temperature and salinity and their gradients can directly influence seabird community structure by aggregating species that have similar physical habitat preferences. The strength of gradients of these properties within and between water masses is particularly important, both in creating boundaries between oceanographic habitats and in creating habitats for species and communities that are adapted to the conditions found at those boundaries (Hunt et al. 2014, Elphick & Hunt 1993). Sigler et al. (2011) also suggested that the biotic communities and the physical oceanography of the Pacific Arctic are linked, but did not quantify the relationships amongst the biotic components and the underlying oceanographic processes. Our study builds on the Sigler et al. results by examining both longitudinal and latitudinal gradients in physical and biological properties, and by quantifying the links between the biotic components and the oceanographic properties of the region.

2.4. Objectives and hypotheses

Data from the Arctic Eis cruises was used to characterize the spatial patterns of arctic seabirds at meso scales (100s km) in relation to oceanographic properties and prey availability to determine the factors that influenced their community structures and distributions over the two study years. Towards these objectives, we tested the following two hypotheses:

> (1) Distinct seabird communities inhabit specific biogeographic domains of the northeastern Bering Sea and eastern Chukchi Sea as a result of biophysical processes. These domains are generally located in the northern Bering Sea/Bering Strait, nearshore and offshore waters of the Chukchi Sea, and the northern Chukchi Sea.
>
> (2) Interannual differences in seabird community structure track shifts in the extent and location of these domains.

3. Methods

3.1. Oceanographic and prey data collection

Concurrent with our seabird survey data, physical and biological data were collected by Arctic Eis researchers and used for these analyses (see Arctic Eis reports for details on methods). Briefly, conductivity, temperature, depth (CTD) instrument with ancillary sensors was used to obtain vertical profiles of salinity, temperature, density, and chlorophyll-a fluorescence from the surface to near bottom depths at each trawl station. Zooplankton samples were collected at each trawl station from surface to near bottom using a double oblique bongo (60 cm diameter frame with 505 µm mesh nets) and a 150 µm mesh net. Surface trawls were conducted at trawl stations using a Cantrawl midwater rope trawl (model 400/601, Cantrawl Pacific Ltd., Richmond, B.C.) modified to fish at the surface. The Principle Investigators or their graduate students and technicians processed the raw data used in our analyses (Table 1).

Bathymetric data were extracted from ETOPO1, a 1 arc-minute global relief model of the Earth's surface that integrates both land topography and ocean bathymetry (http://www.ngdc.noaa.gov/mgg/global/, National Geophysical Data Center, Boulder, CO).

3.2. Oceanographic and prey variables

The analyses include variables that describe the habitats that those communities inhabit. These are: mixed layer temperature, mixed layer salinity, and their horizontal gradients, bathymetric depth and slope, mixed layer chlorophyll-a concentration (chl a), zooplankton density, and fish catch-per-unit-effort (CPUE) (Table 1).

Vertical water column structure was defined in terms of the mixed layer depth. Calculations were based on those described in Kara et al. (2000), using a density criterion of $\Delta\sigma_t$=0.1 kg/m^3 (Peralta-Ferriz & Woodgate 2015). Water temperature, salinity, and chl a were averaged from the surface to the mixed layer depth.

Zooplankton density was summarized by sample station. Only forage fishes (i.e. herring, gadids) were retained, and were summarized as fish CPUE by sample station.

3.3. At-sea seabird surveys

Seabird surveys were conducted using visual observations and standardized strip transects (Tasker et al. 1984, Kuletz et al. 2008) during daylight hours while transiting between sample stations. The observer recorded all marine bird and mammal sightings within 300m and a 90° arc forward from the ‘center line’ (line of travel). Transect width was occasionally reduced to 200 m or 100 m depending on visibility conditions, and surveys were discontinued if visibility was <100 m (i.e., due to fog or seas), or if seas were > Beaufort Scale 6. Birds and marine mammals on or in the water were recorded continuously, while flying birds were recorded during quick ‘Scans’ of the transect window at intervals of approximately 1 min^{-1} (depending on vessel speed) to avoid overestimating. Birds actively foraging from the air, such as surface plunging or touching the water surface were recorded as if ‘on water’ (i.e., continuously). The observer recorded observations directly into a laptop computer, recording species, number of individuals, behavior (on water or in air), and distance bin (bin 1 = 0-100 m from center line; bin 2 = 101-200 m; bin 3 = 201-300 m). Birds were identified to the lowest taxonomic level possible. Environmental variables such as sea state (Beaufort Scale), glare, weather (Appendix B), and sea ice cover (proportion in tenths) were recorded at first entry and automatically thereafter unless updated as necessary.

All surveying was conducted from the port side of the bridge, with data entered directly into a computer using survey software DLog3 (A.G. Ford, Inc., Portland, OR). Latitude and longitude were continuously recorded using a Garmin 60CSx handheld GPS unit connected to the laptop. Binoculars (10x42) were used to aid in identification, and a digital camera was occasionally used to confirm identification. A geometrically marked wooden dowel was used to verify distance estimates from the line of travel to the sighted birds, and verified when possible with a laser rangefinder.

3.4. Seabird data manipulation and correcting for detectability

Analyses included species (Table 2) within the families Gaviidae (loons), Procellariidae (fulmars, shearwaters), Phalacrocoracidae (cormorants), Alcidae (auks), Laridae (gulls), Sternidae (terns), and Stercorariidae (jaegers), plus the taxa phalaropes (genus *Phalaropus*) and marine species of Anatidae (eiders and other seaducks); species in these taxa feed in marine waters while at sea. We used only sightings that were on transect (within 300 m or within the reduced transect when conditions were poor). To account for actual area covered by the observer, we converted raw counts of birds to densities (birds/km2); however, we first estimated correction factors to adjust for detectability of different species.

Detectability of seabirds is affected by both endogenous and exogenous factors (Buckland et al. 2001, Spear et al. 2004), thus to overcome biases in detectability, correction factors are often used to calculate seabird densities. Endogenous factors are those that are inherent to the birds, and include behavior, shape, size, coloration, and response to the ship (Hyrenbach 2001). Birds that are smaller, forage underwater, and occur individually or in small groups are generally harder to see, while those that are larger, forage aerially, and occur in large groups are generally easier to see (Spear et al. 2004). Furthermore, certain species such as Northern Fulmars are known to be attracted to ships, while others such as loons (*Gavia* spp.) may avoid ships (Camphuysen & Garthe 1997, Schwemmer et al. 2011).

Exogenous factors are those that are not inherent to the birds, and include ship size, observer experience, weather, and sea state. It is generally easier to detect birds that are farther from the ship when observing from a large ship than it is from a small ship, though birds may respond differently to different-sized ships (Agness et al. 2008). Since the Arctic EIS cruises were conducted aboard the same ship both years, ship size was not a factor.

Observers may differ in their ability to detect birds as a result of differences in visual acuity, attentiveness, experience, and the manner in which individuals search for and identify birds (Ronconi & Burger 2009). During Arctic Eis surveys, the same seabird observer (C. Pham) conducted all surveys in 2012, and conducted surveys during the northern Chukchi Sea and northern Bering Sea portions in 2013, while another experienced observer (T. Zeller, USFWS) conducted surveys during the southern Chukchi Sea portion of the cruise in 2013. As a result, observer effect was confounded by year and location and cannot be accurately controlled for here, but we assume it was minimal because of the expertise of both observers and because all but one survey was conducted by the same person.

The effect of changing detectability with increasing distance from the ship integrates both endogenous and exogenous factors. The strip transect survey method assumes that all birds in the first bin (0-100 m from the ship) are sighted, and that detectability decreases as the distance from the ship increases. The number of birds sighted farther from the center line (bins 2 and 3) can be corrected relative to those sighted in bin 1. The detectability relative to the distance to ship changes with species as a result of their physical and behavioral characteristics (Gall et al. 2013, Ronconi & Burger 2009). Furthermore, the effect of weather conditions and sea states vary among types of birds; for example, the detectability of small diving birds may decrease much more with increasing sea state than that of large birds that forage aerially.

Preliminary analyses using uncorrected densities, with zero densities removed, found no significant differences between the mean total bird densities of transects segments with different widths (ANOVA; F=0.98, df=2, p=0.37). Moreover, transects segments with reduced widths (200 m or 100 m) were not significantly different in proportions of identified and unidentified birds compared to segments of 300 m width (200 m: χ^2=0.61, df=1, p=0.43; 100 m: χ^2=0.01, df=1, p=0.93). Therefore, survey transects of all widths were retained for analyses. A preliminary review of the uncorrected seabird data with zero densities removed showed that there were a small number of density values that appeared to be disproportionately high (Table 3). These values may be associated with transects that are shorter in length where numbers that are normal or somewhat higher than average are artificially overinflated when converted into densities. To control for this effect, all survey transects and 3-km transect segments <1 km in length were removed (as per Michael et al. 2014). Additionally, high seabird densities may occur for natural reasons such as proximity to a nesting colony, migrating birds flocking together, or proximity to a food-rich area. Since these high densities contain information about the birds and their environment, they were retained for all analyses.

To identify variables that have significant effects on detectability, bird species were first classified into “detectability groups” based on physical and behavioral similarities: small alcids, large alcids, gulls and terns, Short-Tailed Shearwaters, Northern Fulmars, and phalaropes (Table 4). Less abundant species were not included in these detectability analyses because too few sightings were recorded to calculate correction factors. In our study area, most of the species that were low in abundance were large bodied birds (i.e. loons, sea ducks, jaegers, cormorants), so it was reasonable to assume that all individuals of these species that were on transect were sighted.

A repeated measures analysis of variance (RMANOVA) was performed for each of these detectability groups. Weather categories, sea state (grouped into Beaufort states 0-1, 2-3, and 4-6), behavior (on water, in air), and the interactions of those three factors with bin (1, 2, 3) were included as predictor variables for the number of birds sighted in each bin. If behavior was significant ($\alpha=0.10$), then the data for that detectability group was separated into “on water” and “in air,” and the RMANOVA was performed again on the separate behavioral groups without including behavior or the interaction between behavior and bin as predictors. Any significant weather or sea state effects ($\alpha=0.10$) were presumed to be related to location-specific differences in seabird abundances because a preliminary correlation analysis showed that sea state and weather are significantly correlated with latitude and longitude, and with each other (Table 5). Significant bin effects, and significant interactions between weather and bin or between sea state and bin were presumed to indicate that differences in the number of birds sighted in each bin were results of detectability biases rather than results of location-specific changes in abundance.

Large alcids, gulls and terns, and Short-Tailed Shearwaters showed significant behavior effects (i.e, being on water or in air had a strong effect on detectability), while small alcids, Northern Fulmars, and phalaropes did not. The former three groups were each split into “on water” and “in air” behavioral groups. The subsequent RMANOVAs showed significant effects for small alcids, large alcids “in air,” Short-Tailed Shearwater “on water,” and Northern Fulmars (Table 6). For the “large alcids in air,” bin alone had a significant effect, and for the other three groups, the interaction between weather and bin had a significant effect. For each of these four groups, the mean number of birds sighted in each bin was calculated for each weather condition (for “large alcids in air” only bin means were calculated), and the largest mean value for each for each weather condition was assumed to be the “normal” number of birds (Table 7). This mean value was the basis for correcting the number of birds sighted in the other two bins for the given weather condition (Zar 2010). For “large alcids in air,” since only bin was significant, the same correction was applied across all weather conditions.

After applying the correction factor provided by the results of the RMANOVAs, survey transects were divided into ~3-km segments to calculate seabird densities (birds/km^2). As noted earlier, segments <1 km were not included in these analyses.

3.5. Treatment of unidentified seabirds

Several seabirds were difficult to identify to species level, and were thus identified to a higher taxonomic level (Table 2). Similar species can have different distributions (e.g., Springer et al. 1996), so the probability of an unidentified bird being one species or the other can change depending on the geographic location. For example, an unidentified murre that is sighted far offshore may have a greater probability of being a Thick-Billed Murre, while an unidentified murre that is sighted near shore may have a greater probability of being a Common Murre. To account for this, the seabird survey data was gridded into 50 x 50 km cells, and unidentified birds were pro-rated within each cell. Pro-rating was applied sequentially from the most exclusive taxonomic groups (e.g., unidentified murre) to the most inclusive groups (e.g., unidentified alcid) (Hunt et al. 2014).

We used four seabird groups:

We considered all shearwaters to be Short-tailed Shearwaters, as was done in Gall et al. (2013), Hunt et al. (2014), and Kuletz et al. (2015). Sooty Shearwaters (*Puffinus griseus*) have not been identified north of the Bering Strait and are extremely rare in the northern Bering Sea (Kessel & Gibson 1978). Only one Sooty Shearwater was identified during the Arctic EIS cruises, and this was in the southeastern Bering Sea during a transit to port rather than on the Arctic EIS grid (Weems 2014).

Red Phalaropes (*Phalaropus fulicarius*) and Red-Necked Phalaropes (*P. lobatus*) were treated as Phalaropus spp. In late summer and early fall, these seagoing shorebirds are molting and can be difficult to identify to species. Furthermore, they can occur in mixed-species flocks in these marine areas. Most phalaropes recorded in this region are Red Phalaropes (Piatt et al. 1989).

Two species of murres (*Uria* sp.) occur in the study area and often show similar at-sea ecologies (Decker & Hunt 1996), although Thick-Billed Murres (*Uria lomvia*) are more omnivorous than Common Murres (*U. aalge*) and forage in a greater range of marine habitats (Springer et al. 1996). Thus, unidentified murres were pro-rated into Common and Thick-Billed Murres (Hunt et al. 2014) at the 50 x 50 km grid scale.

Unidentified small dark auks included six species—Least Auklets, Crested Auklets (*Aethia cristatella*), Parakeet Auklets, Cassin's Auklets (*Ptychoramphus aleuticus*), Ancient Murrelets (*Synthliboramphus antiquus*), Marbled Murrelets (*Brachyramphus marmoratus*), and Kittlitz's Murrelets (*B. brevirostris*) (Table 2)—with different ecologies. For example, the auklets are primarily planktivorous while *Brachyramphus* murrelets are primarily piscivorous, although Kittlitz's Murrelets are more omnivorous than Marbled Murrelets (Russell et al. 1991, Day & Nigro 2000). These unidentified small dark auks were therefore pro-rated into their constituent species at the 50 x 50 km scale.

3.6. Meso scale community structure analysis

At the meso scale, both "flying" and "in air" birds were aggregated for analysis because all birds encountered were presumably both commuting and foraging within the spatial scale of these analyses (100 km). Rare species provide little information and may add "noise" that can result in a weaker ordination (McCune & Grace 2002). Species that made up <1% of total seabird abundance across both years were therefore removed for these analyses. The remaining ten species made up approximately 95% of the entire seabird community (Table 2).

Data was gridded into 100 x 100 km cells to capture meso scale (100s km) variability in seabird communities. Then, 3-km transect segments within each grid cell were aggregated by latitudinal line. Each latitudinal line within a grid cell was treated as an independent sample of that grid cell because of temporal separation between latitudinal survey lines. Samples with seabird survey effort (km) more than one standard deviation below the mean survey effort per sample (latitudinal line within a grid cell) were removed. These samples are less likely to be representative of the grid cell with which they are associated because they contain much less information than samples with more effort.

Oceanographic variables (Table 1) were associated with each sample, and any sample that did not contain all variables was discarded. A static geographic location variable was assigned to each sample based on its centroid coordinates. Seabird, fish, and zooplankton data were log-transformed to normalize the data. The seabird data was also relativized so that each species contributes equally to the ordination. A correlation analysis was performed to examine the relationships between the oceanographic and prey variables.

A non-metric multidimensional scaling (NMDS) ordination using the Sorensen distance measure was used to identify seabird communities, and to quantify the relationships between seabird species and environmental variables. NMDS is a multivariate ordination method that is particularly well suited for community analyses because it makes no assumptions about the shape of the underlying relationships between the data (McCune & Grace 2002). This particular method has been successfully used to characterize biotic communities in the Bering and Chukchi seas (e.g., Gall et al. 2013, Siddon et al. 2011).

After the NMDS, a multi-response permutation procedure (MRPP) was used to determine whether seabird communities were significantly different between geographic locations (McCune & Grace 2002). For the MRPP, static geographic locations were used rather than habitats as identified in the NMDS because of a large difference in sample size between habitats from the NMDS. The geographic locations were the northern Bering Sea (latitude <66°N, includes the Bering Strait), southern Chukchi Sea (66 – 69°N), and northern Chukchi Sea (>69°N).

3.7. Interannual variability in community structure

First, an MRPP with year as the grouping variable was used to determine whether there were any significant changes in seabird communities across the entire study area between years. Because seabird communities may have changed between years within smaller areas of the entire study area, samples were grouped by both year and geographic location, for a total of six groups (i.e. northern Bering Sea 2012, northern Bering Sea 2013, southern Chukchi Sea 2012, southern Chukchi Sea 2013, northern Chukchi Sea 2012, northern Chukchi Sea 2013). Another MRPP using this region-year grouping variable was then performed.

Next, an indicator species analysis (ISA) was used to explore the results of these MRPPs by examining how communities differed between geographic regions and years. Monte Carlo randomization tests tested the strength of associations between indicator species and regions (McCune & Grace 2002).

3.8. Data processing and analysis tools

Oceanographic and prey data were processed in R (v.3.1.1, R Development Core Team, Vienna, Austria). Seabird preliminary analyses and detectability analyses were conducted in SAS (v.9.1.3, SAS

Institute Inc., Cary, NC). Correction for detectability and pro-rating of unidentified birds were performed in R. Bathymetric data was processed in ArcGIS (v.10.2.2, Environmental Systems Research Institute, Redlands, CA). All data were imported into ArcGIS for aggregation into samples for analysis. NMDS, MRPP, and ISA analyses were conducted in PC-ORD (v.6.19, MjM Software, Gleneden Beach, OR).

4. Results

4.1. Summary of results

Seabird surveys totaled 6,500 km of effort across both study years. The most abundant species were Least Auklets, Crested Auklets, and Short-Tailed Shearwaters (Table 1). A review of seabird density maps (Fig. 3) show that the Chirikov basin of the northern Bering Sea, the Bering Strait, Cape Lisburne, and Hanna Shoal have the highest total seabird densities. Seabird distributions appeared to change between years. For example, Short-Tailed Shearwaters appeared to shift more north and inshore from 2012 to 2013, while Least Auklets appeared to shift more south and offshore from 2012 to 2013 (Fig. 3).

4.2. Meso scale community structure analysis

Many of the oceanographic and prey variables were cross-correlated (Correlation analysis; Table 15). For example, zooplankton density was positively correlated with latitude, and mixed layer depth was positively correlated with salinity.

The NMDS produced a three-dimensional ordination that explained 79.90% of the variance in the data (Fig. 4, Table 8). The stress, which measures the departure from a perfect monotonic relationship between the original distance matrix and the ordination distances, was 16.89, which is high (Clarke 1993). The three NMDS dimensions suggest three different habitats that are distinct in their geographic location, physical characteristics, and prey abundance (Table 9). Each axis correlated with a different suite of seabird species (Table 10). There may be some overlap between the oceanographic characteristics and communities associated with each axis (Fig. 4, Tables 8 – 11).

To investigate these apparent regional differences, an MRPP was performed using the three static geographic regions as the grouping variable. For each of the three regions, there was a significantly different seabird community (t=-11.21, A=0.13, p<0.0001).

4.3. Interannual variability in community structure

To examine interannual variability, an MRPP was performed using year as the grouping variable. No significant difference in community structure was found between years across the entire study area (t=-1.02, A=0.01, p=0.15).

To determine whether communities changed between years within smaller regions of the study area, a third MRPP using both geographic region and year as the grouping variables was performed. There was a significant difference between all region-year groups (t=-10.11, A=0.19, p<0.0001). Pairwise comparisons (Table 12) found no significant difference between the northern Bering Sea in 2012 and the northern Bering Sea in 2013 (t=-0.76, A=0.015, p=0.19), nor between the northern Chukchi Sea in 2012 and the southern Chukchi Sea in 2013 (t=-1.57, A=0.04, p=0.08). Pairwise comparisons were significantly different for all other region-year pairs (Table 12).

The identification of indicator species for any given group is based on its indicator value, calculated from both its relative abundance and relative frequency within that group. Indicator species are those that have the highest indicator value within a group, and Monte Carlo tests assess the statistical significance of those indicator values. Based on the Monte Carlo tests from the ISA, Ancient Murrelets and Black-Legged Kittiwakes were key indicators describing the northern Bering Sea in 2012 (p=0.002, p=0.006, respectively). Parakeet Auklets were non-significant but important indicators in 2013 (p=0.17). Common Murres, Thick-Billed Murres, and Northern Fulmars were indicators of the southern Chukchi Sea in 2012 (p=0.001, p=0.001, p=0.04, respectively), while Short-Tailed Shearwaters were indicators in 2013 (p=0.01). For the northern Chukchi Sea, Least Auklets were non-significant indicators in 2012 (p=0.30), while Crested Auklets and phalaropes were significant indicators in 2013 (p=0.005, p=0.05, respectively).

5. Discussion

5.1. Seabird community structure

The high stress of the NMDS ordination indicates a useful but potentially misleading result, so the ordination must be interpreted cautiously (Clarke 1993). Furthermore, many variables are cross-correlated on the scale of this analysis (Table 11), which implies overlap between axes, further complicating interpretation. Bathymetry is difficult to interpret as well since the region is relatively bathymetrically uniform.

Axis 1 is positively correlated with chlorophyll-a concentration, and negatively correlated with latitude, depth, and slope (Table 9). We interpret it to represent the northern Bering Sea based on these correlations, since the northern Bering Sea is the most southerly of our geographic regions, and is a very productive area (Springer & McRoy 1993, Springer et al. 1996, Coachman & Shigaev 1992). All seabird species except for Northern Fulmars are positively correlated with this axis (Table 10), lending further support that is it representative of the NBS. Several large, mixed species seabird colonies occur in the northern Bering Sea (Stephensen & Irons 2003), which result in high densities and high species richness in the region (Kuletz et al. 2015).

Axis 2 is negatively correlated with longitude, temperature gradient, and temperature, and is positively correlated with chlorophyll-a, zooplankton density, and depth (Table 9). This combination appears to be representative of the offshore environment because offshore waters (i.e., Anadyr Water, Bering Sea Water) are cooler (Coachman et al. 2975, Coachman & Shigaev 1992, Weingartner 1997), more productive (Springer & McRoy 1993), and have greater zooplankton biomass (Eisner et al. 2013, Hopcroft et al. 2010) than nearshore waters (i.e., Alaska Coastal Water). Common and Thick-Billed murres, Least and Parakeet auklets, Northern Fulmars, and Short-Tailed Shearwaters are positively correlated with this axis while phalaropes are negatively correlated (Table 10). The positive correlation of Common Murres with Axis 2 is surprising because this species is generally found more inshore but the axis is negatively correlated with longitude. This may be due to the presence of a large colony on Cape Lisburne, which is relatively far west in terms of the longitudinal range of the study area.

Axis 3 is negatively correlated with salinity, and is positively correlated with latitude, salinity gradient, chlorophyll-a, fish CPUE, and slope (Table 9), attributes representative of oceanic fronts and the nearshore environment in the Chukchi Sea. Fronts can be identified by sharp gradients in water mass properties especially salinity (Coachman et al. 1975, Coachman & Shigaev 1992), and are often highly productive areas (see Russell et al. 1990). Furthermore, fronts can be associated with bathymetric features (e.g., Levine & White 1983). Nearshore waters (i.e., Alaska Coastal Water) are relatively fresh (Coachman & Shigaev 1992, Weingartner 1997) and high in fish biomass (Eisner et al. 2013, Piatt & Springer 2003). Black-Legged Kittiwakes and Parakeet Auklets are negatively correlated with the third axis, while Crested and Least auklets, Northern Fulmars, and Short-Tailed Shearwaters are positively correlated (Table 10). Crested and Least auklets rely on oceanographic processes to aggregate their zooplankton prey so are generally found near fronts (i.e. Russell et al. 1999). Fulmars are omnivores that appear to prefer offshore waters and possibly fronts (Elphick & Hunt 1993, Renner et al. 2013), and shearwaters are omnivores that may have a slight preference for fronts (Piatt 1989, Elphick & Hunt 1993, Gall et al. 2013).

The results from the MRPP suggest that overall, the seabird community in the northern Bering Sea was stable between the two years. However, the indicator species for this region changed between years, suggesting minor changes within the northern Bering Sea community. These changes may be small changes in relative abundance, relative frequency, or both, of one or multiple species within the region. In contrast, the seabird communities of the southern and northern Chukchi seas changed significantly between years, including changes in indicator species. The significance of Short-Tailed Shearwaters in the southern Chukchi Sea in 2013 may be attributable to the large increase in their overall abundance that year. The lack of significance of Least Auklets in the northern Chukchi Sea in 2013 was likely due to their relative absence in that region that year. The lack of difference in the communities of the northern Chukchi Sea in 2012 and the southern Chukchi Sea in 2013 indicates a southerly shift in the community from 2012 to 2013. Thus, most of the interannual changes in seabird communities between 2012 and 2013 were driven by the two most abundant species in the region, Short-tailed Shearwaters and Least Auklets. Since those two species are so abundant (Table 2), even small changes in their abundance and distribution can affect community structure as a whole.

The NMDS ordination identified an onshore-offshore gradient in the seabird community of the study area. This, in conjunction with the results from the MRPP and ISA, suggests that seabird communities are structured by both latitudinal and longitudinal (i.e., onshore-offshore) gradients in prey distribution and oceanographic properties. By definition, these gradients do not have hard boundaries, and different seabird species can have similar prey or habitat preferences; there is therefore some overlap in seabird communities. These communities appeared to shift in structure and location between 2012 and 2013, possibly as a result of bottom up changes in their habitats and prey.

The timing of the annual spring phytoplankton bloom is affected by changes in seasonal sea ice cover (Hunt & Stabeno 2002), and zooplankton assemblages are vulnerable to changes in the properties and extent of these water masses (Eisner et al. 2013), both of which are related to broad-scale changes in atmospheric circulation. Because pelagic fish distribution is related to latitude, temperature, substrate type, and water mass properties (Eisner et al. 2013, Ciannelli & Bailey 2005), they are susceptible to broad-scale changes in water mass distributions and properties. Changes in water mass properties and structure can therefore affect the availability of zooplankton and fish to their seabird predators.

5.2. Future analyses

Our next step will be to identify specific factors that influence coarse scale seabird distribution patterns on an interannual basis. We intend to examine seabird habitat use on a coarse spatial scale, using the 3 km segments. The objective is to identify key factors that influence the distribution of different seabird foraging guilds and abundant species. Based on a preliminary examination of the data, the working hypotheses are as follows:

> *(1)* Within these domains, seabird foraging guilds differentially track variability in preferred prey and target areas of high prey availability: planktivores are closely tied to oceanographic processes that concentrate zooplankton near the surface, piscivores are loosely tied to forage fish distribution which are related to latitude and water mass properties, benthivores are associated with shallower coastal habitats, and omnivores show no habitat or prey associations.
>
> *(2)* Areas near St. Lawrence Island, the Bering Strait, Cape Lisburne, and Hanna Shoal show persistently high seabird abundances between years; while this is partly driven by the location of breeding colonies, we hypothesize that it is also driven by high prey availability in these areas. At some distance from these colonies (TBD from the data), seabird distributions and abundances will be more variable between years. Each foraging guild and species consistently tracks a particular set of prey and oceanographic processes across years, and changes in these variables drive interannual changes in their distribution.

Kuletz et al. (2015), using data from the 2012 Arctic Eis cruise and other projects, identified several hotspots in the eastern Chukchi Sea and western Beaufort Sea. These hotspots varied in importance between species and seasons. We will focus on interannual variability and identifying the suite of variables that influences the spatial patterns of each seabird foraging guild and abundant species.

To test our hypotheses, we will include the oceanographic variables examined in the community analyses along with more complex variables that seek to identify processes that influence prey availability and therefore seabird distributions. These will include distance to front, sea ice cover, bathymetric indices, water clarity, mixed layer strength and gradient, and colony effect, among other variables.

Multivariate general additive models (GAM) will be constructed for each foraging guild and for numerically dominant species by habitat as identified in the community analyses. These GAMs will be constructed using environmental oceanographic variables as predictors of seabird densities (birds/km^2).

A stepwise procedure will be used to remove nonsignificant variables and produce the most robust models based on the Akaike information criterion (AIC). Year will first be included as a covariate in the GAMs in order to determine whether it is important in structuring foraging guild distributions. If year is significant, then separate models will be constructed for each year, and cross-validation across years will be used to further explore the effect of year on the relative importance of each variable on seabird densities.

6. Acknowledgements

This work presents a small component of the Arctic Eis project. This project was funded by BOEM via an Interagency Agreement with USFWS (K. Kuletz) (IA No. M10PG00050; Project AK-10-10), and by a North Pacific Research Board Graduate Student Research Award to C. Pham (May 2015).

We appreciated the expertise and support of the captain and crew of the F/V *Bristol Explorer*. We thank Elizabeth Labunski for field coordination, data management, and assistance with GIS products. Tamara Zeller conducted a portion of the Arctic Eis seabird surveys, and Migratory Bird Management, USFWS, Anchorage, provided budgetary and logistical support. Catherine Coon offered helpful advice, as did the Arctic Eis Principal Investigators, who were generous in sharing ideas and their data. We thank Dr. K. David Hyrenbach (Hawaiʻi Pacific University, HPU) for his guidance and eternal patience. We also thank Dr. David Field (HPU) for his advice, especially concerning oceanographic matters.

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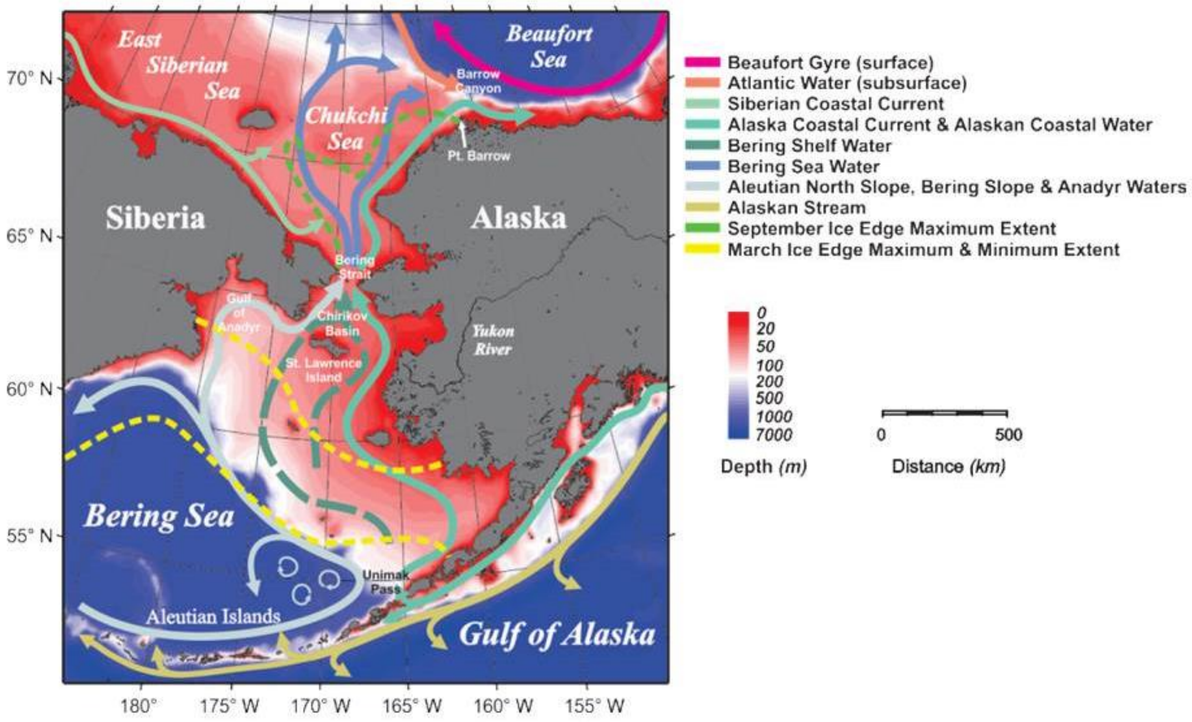
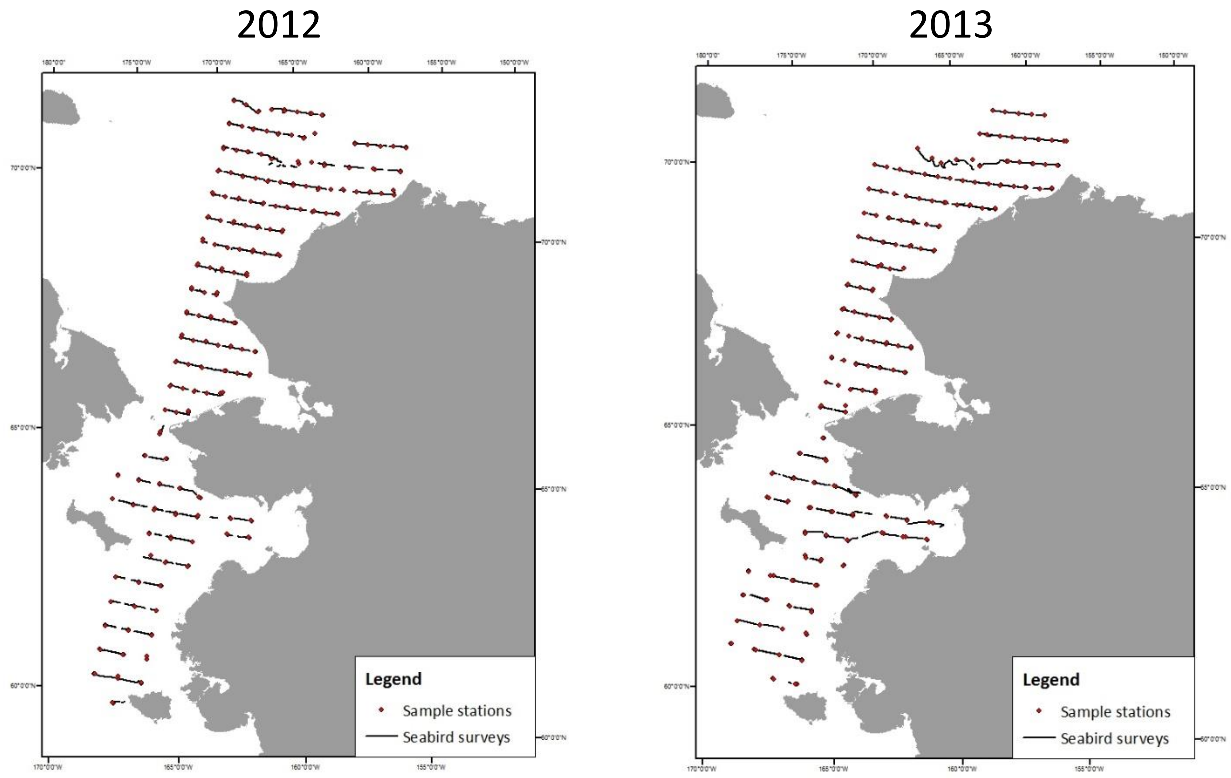


Figure 7. Water circulation in the Pacific Arctic, showing important water masses, currents, and bathymetry (reprinted with permission from The Oceanography Society and Sigler et al. 2011).



2012

2013

Figure 2. Arctic Eis seabird survey transects and sample stations.

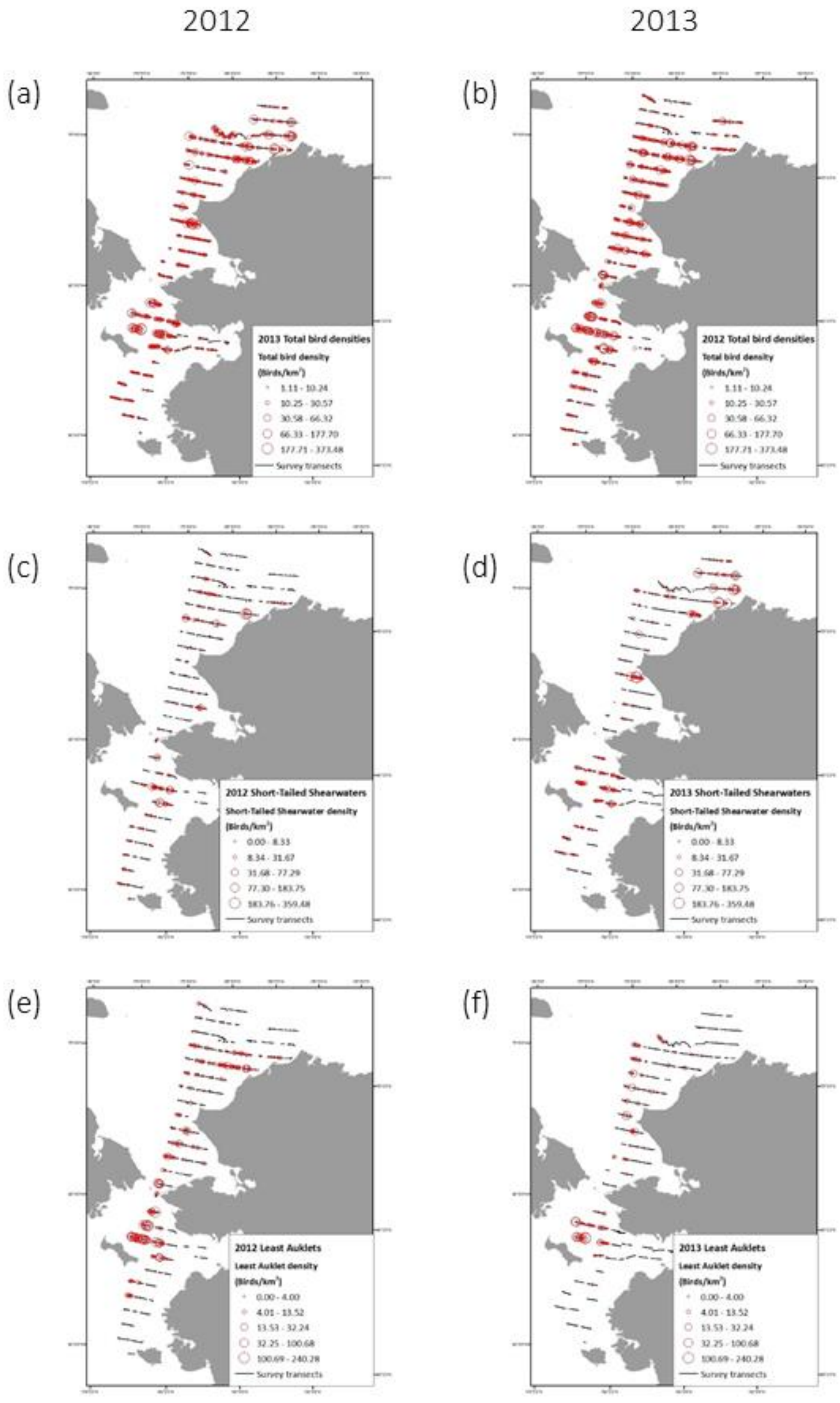


Figure 3. Distribution by year of (a-b) total birds, (c-d) Short-Tailed Shearwaters, and (e-f) Least Auklets.

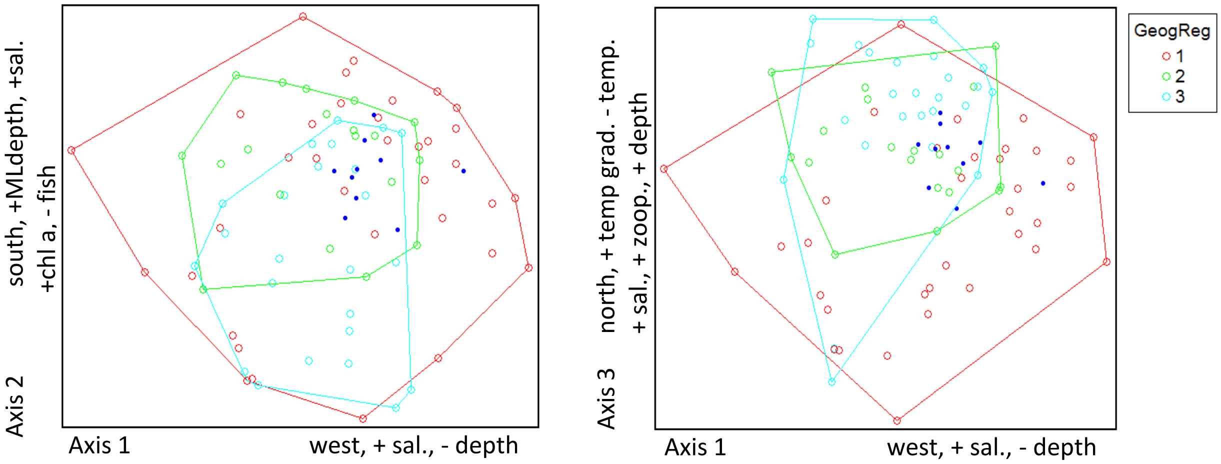


Figure 4. NMDS of seabird community showing two axes on each plot. Region 1=northern Bering Sea, region 2=southern Chukchi Sea, region 3=northern Chukchi Sea. Dark blue dots represent seabird species. Circles represent samples colored according to their geographic region. Lines connect "outermost" samples within each region to help visualize overlap in seabird communities between regions

Table 1. *Definitions and sources for variables used to analyze seabird community structure.*

Variable	Acronym	Unit	Definition	Source
Mixed layer temperature	MLTemp	°C	Water temperature averaged from the surface to the halocline	Arctic Eis
Mixed layer salinity	MLSal	PSU	Water salinity averaged from the surface to the halocline	Arctic Eis
Mixed layer temperature gradient	MLTGrad	°C/km	Change in SST over the distance of the sample	Arctic Eis
Mixed layer salinity gradient	MLSGrad	PSU/km	Change in SSS over the distance of the sample	Arctic Eis
Mixed layer depth	MLDepth	m	Depth of the mixed layer where the maximum density gradient is found	Arctic Eis
Bathymetric depth	Depth	m	Mean depth within an area	ETOPO1
Bathymetric slope	Slope	m/km	Change in depth over the distance of the sample	ETOPO1
Mixed layer chlorophyll a concentration	MLChlA	µg/L	Chlorophyll a concentration averaged across the mixed layer	Arctic Eis
Zooplankton density	Zoop. Dens.	mg/m^3	Large zooplankton density, from Bongo tows	Arctic Eis
Fish catch-per-unit-effort	Fish CPUE	Fish/km^2	Fish abundance interpolated over sample area from surface trawls	Arctic Eis
Latitude	Lat.	Decimal degrees	Midpoint latitude of sample	Arctic Eis
Longitude	Long.	Decimal degrees	Midpoint longitude of sample	Arctic Eis

Table 2. *Species, relative abundance, and foraging guilds of Arctic Eis seabirds, organized taxonomically. Relative abundances are after correcting for detectability and pro-rating of unidentified birds.*

Family	Species	Relative abundance (%)	Foraging guild*
Gaviidae	Pacific Loon	0.055	F
	Red-Throated Loon	0.007	F
Procellariidae	Northern Fulmar	2.213	O
	Short-Tailed Shearwater	16.041	O
	Fork-Tailed Storm Petrel	0.058	P
Phalacrocoracidae	Pelagic Cormorant	0.066	F
Anatidae	Common Eider	0.055	B
	Spectacled Eider	0.175	B
	Steller's Eider	0.009	B
	Harlequin Duck	0.041	B
	Long-Tailed Duck	0.034	B
Scolopacidae	Unidentified phalarope	8.411	P
Stercorariidae	Long-Tailed Jaeger	0.007	F
	Parasitic Jaeger	0.055	F
	Pomarine Jaeger	0.257	F
Sternidae	Arctic Tern	0.014	F
Laridae	Glaucous Gull	0.610	F
	Glaucous-Winged Gull	0.333	F
	Herring Gull	0.048	F
	Slaty-Backed Gull	0.007	F
	Sabine's Gull	0.077	O
	Black-Legged Kittiwake	6.099	F
Alcidae	Common Murre	8.078	F
	Thick-Billed Murre	5.466	F
	Pigeon Guillemot	0.014	F
	Kittlitz's Murrelet	0.306	F
	Ancient Murrelet	1.662	P
	Crested Auklet	20.563	P
	Least Auklet	25.443	P
	Parakeet Auklet	1.999	P
	Cassin's Auklet	0.021	P
	Horned Puffin	0.995	F
	Tufted Puffin	0.730	F

* P = planktivore, F = piscivore, O = omnivore, B = benthivore.

***Table 3**. Frequency distribution of total bird densities using 3-km segments (uncorrected for detectability) with zero densities removed.*

Density	Frequency
0.01-50	1430
50-100	41
100-150	15
150-200	5
200-250	2
300-350	1
400-450	2
1900-1950	1

***Table 4**. Seabird groups used to examine detectability during surveys, and behavior or distance bin or interaction effects for each group's detectability. See Appendix C.3. for species names and codes.*

Groups	Species	Significant behavior	Significant bin or bin interaction effect
Small alcids	PAAU, LEAU, CRAU, CAAU, UNAU, KIMU, BRMU, ANMU, UNML, USDA	None	Weather*bin
Large alcids	COMU, TBMU, UNMU, HOPU, TUPU, PIGU, UNGI, UNAL	Flying	Bin
Gulls and terns	GLGU, GWGU, HERG, SAGU, UNGU, BLKI, ARTE	Both	None
Shearwaters	STSH, UDSH	Water	Weather*bin
Northern Fulmar	NOFU	None	Weather*bin
Phalaropes	REPH, RNPH, UNPH	None	None

***Table 5.** Pearson correlations between weather condition, sea state, latitude, and longitude. Significant p-values at α=0.10 are in bold.*

	Seas	Weather	Latitude	Longitude
Seas	1	r=0.0164	r=-0.114	r=0.071
Weather	**p=0.062**	1	r=0.092	r=0.087
Latitude	**p<0.0001**	**p<0.0001**	1	r=0.491
Longitude	**p<0.0001**	**p<0.0001**	**p<0.0001**	1

Table 6. *RMANOVA by detectability group. Significant p-values at α=0.10 are in bold.*

Detectability group	Behavior	Source	DF	Type III SS	Mean Square	F Value	P
Small alcids	**N/A**	**Bin**	2	4.21	2.11	2.5	**0.08**
		Behavior	1	0.7	0.7	0.82	0.36
		Wx	7	24.19	3.46	4.09	**<0.01**
		SeasGroup	2	2.92	1.46	1.73	0.18
		Behavior*Bin	2	1.75	0.88	1.04	0.35
		Wx*Bin	11	15.85	1.44	1.71	**0.07**
		SeasGroup*Bin	4	4.53	1.13	1.34	0.25
Large alcids	**In air**	**Bin**	2	8.27	4.13	4.62	**0.01**
		Wx	6	8.54	1.42	1.59	0.15
		SeasGroup	2	13.28	6.64	7.42	**<0.01**
		Wx*Bin	8	11.15	1.39	1.56	0.14
		SeasGroup*Bin	4	3.56	0.89	0.99	0.41
Shearwaters	**On water**	**Bin**	2	108.87	54.44	0.56	0.57
		Wx	5	2799.08	559.82	5.77	**<.01**
		SeasGroup	2	279.23	139.61	1.44	0.24
		Wx*Bin	7	3526.03	503.72	5.19	**<.01**
		SeasGroup*Bin	4	317.04	79.26	0.82	0.52
Northern Fulmars	**N/A**	**Bin**	2	0.2	0.1	1.63	0.2
		Behavior	1	0.14	0.14	2.29	0.13
		Wx	6	0.43	0.07	1.18	0.32
		SeasGroup	2	0	0	0	1
		Behavior*Bin	2	0.21	0.11	1.75	0.18
		Wx*Bin	9	1.46	0.16	2.66	**0.01**
		SeasGroup*Bin	4	0.33	0.08	1.37	0.25

Table 7. *Mean number and standard deviation of birds per bin by weather condition for each detectability group. Mean values to be used to correct numbers are in bold.*

				Bin1		Bin2		Bin3	
Detectability group	**Behavior**	**Wx**	**N**	**Mean**	**Std Dev**	**Mean**	**Std Dev**	**Mean**	**Std Dev**
Small alcids	**N/A**	**0**	429	**0.83**	1.39	0.69	1.37	0.5	1.83
		1	1331	**0.71**	1.18	0.59	1.1	0.39	1.22
		2	414	**0.68**	1.03	0.62	1.25	0.44	1.2
		3	14	1.36	1.01	0.14	0.36	0	0
		4	107	**0.69**	1.01	0.48	0.86	0.26	0.57
		5	2	0	0	1	0	0	0
		6	20	**1.45**	2.35	0.3	0.57	0.4	0.99
		7	55	0.51	0.79	**0.76**	1.84	0.67	1.23
Large alcids	**In air**	N/A	369	1.57	1.39	1.37	1.23	**1.81**	2.4
Shearwaters	**On water**	**0**	23	1.39	4.2	1.22	2.32	**7.39**	31.34
		1	115	**2.51**	10.28	2.32	11.02	1.98	8.85
		2	40	1.13	3.38	**2.43**	8.3	0.85	3.95
		4	4	1	0	0	0	0	0
		6	17	7.41	21.2	10.65	19.71	3.82	8.51
		7	3	0.33	0.58	1	1	0	0
Northern Fulmar	**N/A**	**0**	29	0.34	0.48	**0.52**	0.78	0.38	0.68
		1	140	**0.46**	0.55	0.36	0.55	0.27	0.49
		2	15	0.27	0.46	0.33	0.82	0.87	1.19
		3	2	0.5	0.71	0.5	0.71	0	0
		4	17	0.65	1	0.35	0.49	0.24	0.44
		6	1	0	.	0	.	1	.
		7	4	0.5	0.58	0.5	1	0.25	0.5

Table 8. *Variance in real data explained by NMDS axes.*

	r^2	
	Increment	**Cumulative**
Axis 1	0.225	0.225
Axis 2	0.335	0.560
Axis 3	0.239	0.799

Table 9. *Kendall's tau correlations between environmental variables and NMDS axes. Tau is the first number, and p-value is the second number. Significant correlations and p-values at α=0.05 are in bold. For definition of variable acronyms, see Table 2.*

	Axis1	**Axis2**	**Axis3**
Longitude	-0.151	**-0.323**	0.083
	0.051	**<.0001**	0.286
Latitude	**-0.154**	-0.128	**0.435**
	0.047	0.098	**<.0001**
MLTempGrad	-0.003	**-0.150**	0.111
	0.970	**0.050**	0.147
MLSalGrad	0.004	0.033	**0.172**
	0.963	0.669	**0.025**
MLDepth	0.001	0.117	0.022
	0.990	0.127	0.770
MLTemp	-0.096	**-0.167**	-0.025
	0.212	**0.030**	0.744
MLSal	-0.058	0.114	**-0.403**
	0.449	0.137	**<.0001**
MLChlA	**0.197**	**0.344**	**0.213**
	0.010	**<.0001**	**0.005**
ZoopDens	0.083	**0.156**	-0.136
	0.280	**0.042**	0.076
FishCPUE	0.013	0.122	**0.311**
	0.869	0.111	**<.0001**
Depth	**-0.169**	**0.154**	0.146
	0.027	**0.045**	0.057
Slope	**-0.153**	0.002	**0.427**
	0.049	0.980	**<.0001**

Table 10. *Kendall's tau correlations between species and NMDS axes. Tau is the first number, and p-value is the second number. Significant correlations and p-values at α=0.05 are in bold.*

	Axis1	**Axis2**	**Axis3**
Ancient Murrelet	**0.537**	0.112	-0.108
	<.0001	0.209	0.228
Black-Legged Kittiwake	**0.185**	-0.109	**-0.315**
	0.017	0.157	**<.0001**
Common Murre	**0.453**	**0.374**	0.020
	<.0001	**<.0001**	0.801
Crested Auklet	**0.175**	0.023	**0.474**
	0.034	0.779	**<.0001**
Least Auklet	**0.213**	**0.309**	**0.394**
	0.008	**0.0001**	**<.0001**
Northern Fulmar	0.058	**0.305**	**0.193**
	0.468	**0.0001**	**0.016**
Parakeet Auklet	**0.227**	**0.537**	**-0.229**
	0.008	**<.0001**	**0.008**
***Phalaropus* spp.**	**0.523**	**-0.158**	0.139
	<.0001	**0.058**	0.097
Short-Tailed Shearwater	**0.180**	**0.237**	**0.163**
	0.023	**0.003**	**0.040**
Thick-Billed Murre	**0.223**	**0.446**	0.126
	0.008	**<.0001**	0.132

Table 11. *Pearson correlations between environmental variables used in NMDS ordination. Significant correlations and p-values at α=0.05 are in bold. For definition of variable acronyms, see Table 2.*

	Long.	**Lat.**	**Fish CPUE**	**Zoop. dens.**	**Depth**	**Slope**	**MLDepth**	**MLTemp**	**MLSal**	**MLChlA**	**MLTGrad**	**MLSGrad**
Long.	1	**r=0.507**	r=-0.024	r=-0.147	r=0.112	**r=-0.302**	**r=-0.336**	**r=-0.317**	**r=-0.525**	r=-0.189	0.008	0.189
Lat.	**p<.0001**	1	r=-0.273	**r=0.429**	**r=0.688**	**r=-0.337**	**r=-0.247**	**r=-0.553**	r=-0.035	r=0.041	0.188	0.019
Fish CPUE	0.831	0.014	1	r=-0.158	**r=-0.251**	**r=0.223**	r=0.028	r=0.148	r=-0.020	r=-0.034	-0.170	-0.118
Zoop. dens.	0.193	**p <.0001**	0.161	1	**r=0.345**	r=-0.026	r=0.038	r=-0.190	**r=0.335**	r=0.177	0.074	-0.082
Depth	0.325	**p <.0001**	**p=0.025**	**p=0.002**	1	**r=-0.329**	r=-0.012	**r=-0.664**	**r=0.251**	r=0.053	**0.220**	-0.201
Slope	**p=0.007**	**p=0.002**	**p=0.047**	0.820	**p=0.003**	1	r=0.027	r=0.218	r=0.128	**r=-0.300**	**-0.444**	**-0.318**
MLDepth	**p=0.002**	**p=0.027**	0.804	0.741	0.919	0.815	1	r=-0.140	**r=0.509**	r=-0.060	0.196	-0.068
MLTemp	**p=0.004**	**p <.0001**	0.191	0.091	**p <.0001**	0.053	0.215	1	r=-0.102	r=0.204	**-0.315**	0.022
MLSal	**p <.0001**	0.761	0.858	**p=0.002**	**p=0.025**	0.257	**p <.0001**	0.368	1	r=0.185	0.049	**-0.563**
MLChlA	0.092	0.718	0.762	0.117	0.641	**p=0.007**	0.599	0.069	0.100	1	**0.268**	0.028
MLTGrad	0.942	0.096	0.133	0.515	**p=0.050**	**p <.0001**	0.082	**p=0.004**	0.666	**p=0.016**	1.000	**0.483**
MLSGrad	0.093	0.870	0.298	0.469	0.073	**p=0.004**	0.550	0.845	**p <.0001**	0.802	**<.0001**	1.000

Table 12. *Pairwise comparisons for MRPP using region-year groups. NBS = northern Bering Sea, SCS = southern Chukchi Sea, NCS = northern Chukchi Sea. P-values at α=0.05 are in bold*

Pairs	**T**	**A**	**p**
NBS 2012 vs. SCS 2012	-5.72	0.14	**0.0003**
NBS 2012 vs. NCS 2012	-5.46	0.11	**0.001**
NBS 2012 vs. NBS 2013	-0.76	0.01	0.192
NBS 2012 vs. SCS 2013	-3.84	0.10	**0.004**
NBS 2012 vs. NCS 2013	-5.77	0.16	**0.0003**
SCS 2012 vs. NCS 2012	-5.90	0.14	**0.001**
SCS 2012 vs. NBS 2013	-4.41	0.09	**0.001**
SCS 2012 vs. SCS 2013	-3.94	0.14	**0.003**
SCS 2012 vs. NCS 2013	-8.00	0.29	**0.0001**
NCS 2012 vs. NBS 2013	-4.73	0.09	**0.001**
NCS 2012 vs. SCS 2013	-1.57	0.04	0.075
NCS 2012 vs. NCS 2013	-3.72	0.09	**0.004**
NBS 2013 vs. SCS 2013	-3.54	0.08	**0.003**
NBS 2013 vs. NCS 2013	-4.30	0.11	**0.002**
SCS 2013 vs. NCS 2013	-6.68	0.24	**0.0001**

Appendix A. Physical and biological properties of water masses of the northern Bering and Chukchi seas.

Water mass	Salinity (PSU)	Temperature (°C)	Nutrients and chlorophyll a	References
Anadyr Water	< ~ 31.8–32.2	~ 2–13	High	Eisner et al. 2013
Bering Shelf Water	~ 31.8–33	~ 5–9	High	Eisner et al. 2013
Alaska Coastal Water	~ 32.3–33.3	~ 6–11	Low	Eisner et al. 2013
Bering Sea Water	~ 32.2–32.6	~ -1–4	High	Piatt & Springer 2003
Transition Water	~ 31.3–32	~ 4.5–8	Medium	Eisner et al. 2013, Hopcroft et al. 2010
Winter Water	> ~ 32	~ -2–1	High	Weintgartner et al. 2005
Melt Water	< ~ 30	~ -1–2	Low	Weintgartner et al. 2005

Appendix B. Weather categories used for seabird surveys.

Category	Weather condition
0	<50% clouds
1	>50% clouds
2	Patchy fog
3	Solid fog
4	Mist / light rain
5	Medium / heavy rain
6	Fog and rain
7	Snow

Appendix C.1. Raw seabird abundances from the 2012 Arctic Eis cruise. These numbers include birds that were sighted outside of the study area. Leg 1 corresponds mostly to the southern Chukchi Sea, Leg 2 corresponds mostly to the northern Chukchi Sea, and Leg 3 corresponds mostly to the northern Bering Sea. See Appendix C.3. for species names and codes.

	Leg 1		**Leg 2**		**Leg 3**		**Total**	
Species	**On transect**	**%**	**On transect**	**%**	**On transect**	**%**	**On transect**	**%**
COLO	0	0.00	1	0.01	1	0.04	2	0.01
PALO	0	0.00	0	0.00	7	0.31	7	0.04
YBLO	0	0.00	1	0.01	0	0.00	1	0.01
UNLO	0	0.00	0	0.00	1	0.04	1	0.01
NOFU	196	2.49	71	0.99	36	1.57	303	1.75
STSH	1,851	23.51	4,180	58.54	448	19.60	6,479	37.42
UNPR	1	0.00	1	0.00	0	0.00	2	0.01
FTSP	83	1.05	0	0.00	6	0.26	89	0.51
PECO	1	0.01	1	0.01	16	0.70	18	0.10
NOPI	0	0.00	0	0.00	7	0.31	7	0.04
COEI	8	0.10	0	0.00	0	0.00	8	0.05
SPEI	4	0.05	0	0.00	8	0.35	12	0.07
HADU	0	0.00	2	0.03	2	0.09	4	0.02
LTDU	0	0.00	2	0.03	6	0.26	8	0.05
UNDU	1	0.01	4	0.06	1	0.04	6	0.03
UNSC	0	0.00	0	0.00	2	0.09	2	0.01
PESA	2	0.03	0	0.00	0	0.00	2	0.01
RUTU	2	0.03	0	0.00	0	0.00	2	0.01
STSA	0	0.00	0	0.00	1	0.04	1	0.01
REPH	269	3.42	25	0.35	17	0.74	311	1.80
RNPH	14	0.18	3	0.04	16	0.70	33	0.19
UNPH	171	2.17	140	1.96	42	1.84	353	2.04
UNSB	72	0.91	23	0.32	5	0.22	100	0.58
LTJA	4	0.05	0	0.00	0	0.00	4	0.02
PAJA	13	0.17	11	0.15	3	0.13	27	0.16
POJA	35	0.44	10	0.14	11	0.48	56	0.32
ALTE	2	0.03	0	0.00	0	0.00	2	0.01
ARTE	16	0.20	23	0.32	0	0.00	39	0.23
GLGU	50	0.64	40	0.56	11	0.48	101	0.58
GWGU	12	0.15	0	0.00	46	2.01	58	0.34
HEGU	3	0.04	0	0.00	3	0.13	6	0.03
SAGU	9	0.11	3	0.04	0	0.00	12	0.07
BLKI	575	7.30	354	4.96	270	11.81	1199	6.93
UNGU	11	0.14	5	0.07	11	0.48	27	0.16
UNTE	10	0.13	2	0.03	0	0.00	12	0.07
COMU	704	8.94	162	2.27	86	3.76	952	5.50
TBMU	665	8.45	108	1.51	8	0.35	781	4.51
PIGU	2	0.03	0	0.00	0	0.00	2	0.01

KIMU	17	0.22	3	0.04	0	0.00	20	0.12
MAMU	2	0.03	0	0.00	0	0.00	2	0.01
ANMU	6	0.08	11	0.15	119	5.21	136	0.79
CAAU	3	0.04	0	0.00	1	0.04	4	0.02
CRAU	506	6.43	937	13.12	122	5.34	1,565	9.04
LEAU	687	8.72	685	9.59	804	35.17	2,176	12.57
PAAU	75	0.95	30	0.42	9	0.39	114	0.66
HOPU	149	1.89	34	0.48	19	0.83	202	1.17
TUPU	106	1.35	61	0.85	18	0.79	185	1.07
BRMU	28	0.36	3	0.04	3	0.13	34	0.20
UNAL	18	0.23	18	0.25	11	0.48	47	0.27
UNAU	3	0.04	0	0.00	0	0.00	3	0.02
UNGI	0	0.00	1	0.01	0	0.00	1	0.01
UNML	0	0.00	4	0.06	0	0.00	4	0.02
UNMU	1434	18.21	138	1.93	49	2.14	1,621	9.36
USDA	56	0.71	45	0.63	58	2.54	159	0.92
Total	7,876		7,142		2,284		**17,302**	

Appendix C.2. Raw seabird abundances from the 2013 Arctic Eis cruise. These numbers include birds that were sighted outside of the study area. Leg 1 corresponds mostly to the southern Chukchi Sea, Leg 2 corresponds mostly to the northern Chukchi Sea, and Leg 3 corresponds mostly to the northern Bering Sea. See Appendix C.3. for species names and codes.

	Leg 1		Leg 2		Leg 3		Total	
Species	**On transect**	**%**	**On transect**	**%**	**On transect**	**%**	**On transect**	**%**
PALO	1	0.03	28	0.27	5	0.13	34	0.19
RTLO	0	0.00	2	0.02	1	0.03	3	0.02
YBLO	0	0.00	1	0.01	3	0.08	4	0.02
UNLO	0	0.00	9	0.09	0	0.00	9	0.05
NOFU	1,506	38.25	86	0.82	45	1.15	1,637	8.92
SOSH	0	0.00	0	0.00	1	0.03	1	0.01
STSH	315	8	5,756	54.7	1,109	28.4	7,180	39.1
UNDS	80	2.03	3	0.03	5	0.13	88	0.48
FTSP	208	5.28	2	0.02	4	0.1	214	1.17
PECO	2	0.05	10	0.1	6	0.15	18	0.1
RBME	0	0.00	0	0.00	1	0.03	1	0.01
KIEI	0	0.00	0	0.00	3	0.08	3	0.02
COEI	72	1.83	0	0.00	0	0.00	72	0.39
SPEI	0	0.00	0	0.00	7	0.18	7	0.04
STEI	0	0.00	0	0.00	3	0.08	3	0.02
LTDU	0	0.00	9	0.09	5	0.13	14	0.08
UNDU	0	0.00	2	0.02	2	0.05	4	0.02
UNEI	0	0.00	0	0	11	0.28	11	0.06
STSA	0	0.00	1	0.01	0	0.00	1	0.01
REPH	77	1.96	451	4.29	74	1.9	602	3.28
RNPH	0	0.00	36	0.34	5	0.13	41	0.22
UNPH	10	0.25	1,540	14.6	110	2.82	1,660	9.04
UNSB	2	0.05	21	0.2	24	0.62	47	0.26
LTJA	1	0.03	0	0.00	1	0.03	2	0.01
PAJA	3	0.08	5	0.05	3	0.08	11	0.06
POJA	10	0.25	24	0.23	18	0.46	52	0.28
UNJA	5	0.13	0	0	2	0.05	7	0.04
ARTE	16	0.41	3	0.03	1	0.03	20	0.11
GLGU	1	0.03	92	0.87	38	0.97	131	0.71
GWGU	6	0.15	2	0.02	19	0.49	27	0.15
HERG	1	0.03	3	0.03	5	0.13	9	0.05
BLKI	282	7.16	382	3.63	154	3.95	818	4.46
RLKI	4	0.1	0	0.00	0	0.00	4	0.02
SAGU	2	0.05	7	0.07	3	0.08	12	0.07
SBGU	0	0.00	0	0.00	2	0.05	2	0.01
UNGU	3	0.08	3	0.03	5	0.13	11	0.06
COMU	209	5.31	280	2.66	105	2.69	594	3.24
TBMU	315	8	194	1.84	171	4.38	680	3.7

UNMU	207	5.26	215	2.04	68	1.74	490	2.67
PIGU	0	0.00	5	0.05	0	0.00	5	0.03
KIMU	1	0.03	1	0.01	0	0.00	2	0.01
MAMU	3	0.08	0	0.00	1	0.03	4	0.02
UNBR	4	0.1	1	0.01	5	0.13	10	0.05
ANMU	59	1.5	15	0.14	65	1.67	139	0.76
UNML	0	0.00	2	0.02	3	0.08	5	0.03
CRAU	41	1.04	718	6.82	253	6.49	1,012	5.51
LEAU	187	4.75	318	3.02	1,235	31.7	1,740	9.48
PAAU	54	1.37	27	0.26	181	4.64	262	1.43
UNAU	103	2.62	36	0.34	72	1.85	211	1.15
HOPU	64	1.63	59	0.56	17	0.44	140	0.76
TUPU	71	1.8	153	1.45	31	0.79	255	1.39
UNAL	10	0.25	20	0.19	15	0.38	45	0.25
Total	3,935		10,522		3,897		**18,354**	

Appendix C.3. Families, common and scientific names, and species codes for all birds sighted during the Arctic Eis cruises. This table includes species that were sighted off transect or outside the study area (i.e. during transits to and from port).

Family	Common Name	Scientific name / species included	Code
Gaviidae	Pacific Loon	*Gavia pacifica*	PALO
	Red-Throated Loon	*Gavia stellata*	RTLO
	Common Loon	*Gavia immer*	COLO
	Yellow-Billed Loon	*Gavia adamsii*	YBLO
	Unidentified loon	*Gavia* sp.; RTLO, PALO, COLO, YBLO	UNLO
Procellariidae	Northern Fulmar	*Fulmaris glacialis*	NOFU
	Short-Tailed Shearwater	*Ardenna tenuirostris*	STSH
	Sooty Shearwater	*Ardenna grisea*	SOSH
	Unidentified dark shearwater	*Ardenna* sp.; STSH, SOSH	UNDS
	Fork-Tailed Storm Petrel	*Oceanodroma furcata*	FTSP
Phalacrocoracidae	Pelagic Cormorant	*Phalacrocorax pelagicus*	PECO
Anatidae	Common Eider	*Somateria mollissima*	COEI
	Spectacled Eider	*Somateria fischeri*	SPEI
	Steller's Eider	*Polysticta stelleri*	STEI
	King Eider	*Somateria spectabilis*	KIEI
	Unidentified eider	COEI, SPEI, KIEI, STEI	UNEI
	Harlequin Duck	*Histrionicus histrionicus*	HADU
	Long-Tailed Duck	*Clangula hyemalis*	LTDU
	Northern Pintail	*Anas acuta*	NOPI
	Unidentified duck	LTDU, HADU, COEI, SPEI, KIEI, STEI	UNDU
Scolopacidae	Red-Necked Phalarope	*Phalaropus lobatus*	RNPH
	Red Phalarope	*Phalaropus fulicarius*	REPH
	Unidentified phalarope	*Phalaropus* sp.; REPH, RNPH	UNPH
	Pectoral Sandpiper	*Calidris melanotos*	PESA
	Sharp-Tailed Sandpiper	*Calidris acuminata*	STSA
	Ruddy Turnstone	*Arenaria interpres*	RUTU
Scolopacidae, Charadriidae, & Haematopodidae	Unidentified shorebird	Scolopacidae, Charadriidae, & Haematopodidae	UNSB
Stercorariidae	Long-Tailed Jaeger	*Stercorarius longicaudus*	LTJA
	Parasitic Jaeger	*Stercorarius parasiticus*	PAJA
	Pomarine Jaeger	*Stercorarius pomarinus*	POJA
	Unidentified jaeger	*Stercorarius* sp.; POJA, PAJA, LTJA	UNJA
Sternidae	Arctic Tern	*Sterna paradisaea*	ARTE
Laridae	Glaucous Gull	*Larus hyperboreus*	GLGU
	Glaucous-Winged Gull	*Larus glaucescens*	GWGU
	Herring Gull	*Larus argentatus*	HEGU
	Slaty-Backed Gull	*Larus schistisagus*	SBGU
	Unidentified gull	*Larus* sp.; GLGU, GWGU, SBGU, HEGU	UNGU

	Sabine's Gull	*Xema sabini*	SAGU
	Black-Legged Kittiwake	*Rissa tridactyla*	BLKI
	Red-Legged Kittiwake	*Rissa brevirostris*	RLKI
Alcidae	Common Murre	*Uria aalge*	COMU
	Thick-Billed Murre	*Uria lomvia*	TBMU
	Unidentified murre	*Uria* sp.; COMU, TBMU	UNMU
	Pigeon Guillemot	*Cepphus Columba*	PIGU
	Black Guillemot	*Cepphus grille*	BLGU
	Unidentified guillemot	*Cepphus* sp.; PIGU, BLGU	UNGI
	Unidentified alcid	Alcidae; COMU, TBMU, UNMU, PIGU, BLGU, UNGI	UNAL
	Kittlitz's Murrelet	*Brachyramphus brevirostris*	KIMU
	Marbled Murrelet	*Brachyramphus marmoratus*	MAMU
	Unidentified *Brachyramphus* murrelet	*Brachyramphus* sp.; MAMU, KIMU	BRMU
	Ancient Murrelet	*Synthliboramphus antiquus*	ANMU
	Unidentified murrelet	ANMU, KIMU, MAMU	UNML
	Crested Auklet	*Aethia cristatella*	CRAU
	Least Auklet	*Aethia pusilla*	LEAU
	Parakeet Auklet	*Aethia psittacula*	PAAU
	Cassin's Auklet	*Ptychoramphus aleuticus*	CAAU
	Unidentified auklet	CRAI, LEAU, PAAU, CAAU	UNAU
	Unidentified small dark alcid	PAAU, CRAU, LEAU, ANMU, KIMU, CAAU, MAMU	USDA
	Horned Puffin	*Fratercula corniculata*	HOPU
	Tufted Puffin	*Fratercula cirrhata*	TUPU

Appendix Q.

Spatial heterogeneity in zooplankton distribution in the eastern Chukchi Sea and northern Bering Sea as a result of large-scale interactions of water masses.

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15 May 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

List of Oral and Poster Presentations

Pinchuk A.I., Eisner L.B. Spatial heterogeneity in zooplankton distribution in the eastern Chukchi Sea as a result of large-scale interactions of water masses. Ocean Sciences Meeting, New Orleans, Louisiana, USA, February 21-26, 2016. – *Oral presentation*

Pinchuk A.I. Zooplankton Communities near the Alaskan Arctic Coast. Seminar at UAF SFOS Fisheries Division, Juneau, Alaska, USA, March 28, 2016 – *Oral presentation*

Proposed Objectives and Study Chronology

The primary objective of this project was to collect and identify the zooplankton of the Eastern Chukchi and Northern Bering Seas and determine abundances and distribution patterns of major taxa in relation to hydrography. Analyses of assemblage structure were also conducted. Samples were collected in the Chukchi and northern Bering seas between 8 August and 24 September in 2012 and 2013.The sampling design was based on a square grid pattern with stations located 56 km apart, resulting in a total of 139 and 134 sampling locations in 2012 and 2013, respectively. Zooplankters were sampled aboard the *F/V Bristol Explorer* with a 60 cm MARMAP-style bongo frame with a 505 µm mesh net. The net frame was equipped with an SBE 49 CTD transmitting real time tow data. To assess the contribution of small taxa to total zooplankton biomass, a 20 cm PairVET net with 150 µm mesh was attached to the net array according to NOAA standard sampling protocol and deployed simultaneously. The GPS location of the ship during the tow was recorded every 2 s to determine distance towed. Oblique tows from within 5 – 10 m off the bottom to the surface were conducted primarily during daylight hours. Maximal tow depth ranged between 15 m and 98 m depending on bathymetry. Volume filtered was measured with calibrated General Oceanics flowmeters mounted inside the nets. Volumes recorded from the flowmeter were compared with volumes estimated from the distance towed at each station to detect net clogging. All samples were preserved in 5% formalin, buffered with seawater for later processing. In the laboratory, the mesozooplankton samples were sequentially split using a Folsom splitter until the smallest subsample contained approximately 200 specimens of the most abundant taxa. All taxa in the smallest subsamples were identified, staged, enumerated and weighed. Each larger subsample was examined to identify, enumerate and weigh the larger, less abundant taxa. Blotted wet weights for each taxa and stage were also determined. The data were uploaded to a Microsoft Access database, and analysis was done with standard statistics software.

A chronology of activities for each survey year follows:

2012 Survey

August - Prepared *F/V Bristol Explorer* for survey. Departed Dutch Harbor, AK for survey.
September - Completed survey, unloaded gear and samples. Samples shipped to Juneau.
October - Samples arrived in Juneau.
July (2013) – sorting of 505 µm mesh net samples completed.
December (2013) - sorting of 150 µm mesh net samples completed.
January(2014) - Data entry completed and available at the Arctic EIS Ocean Workspace (https://workspace.aoos.org/).
June (2014) – Begin data analysis and mapping distributions and abundances of major species.

2013 Survey

August - Prepared *F/V Bristol Explorer* for survey. Departed Dutch Harbor, AK for Survey survey.
September - Completed survey, unloaded gear and samples. Samples shipped to Juneau.
November- Samples arrived in Juneau.
January (2015) - sorting of 505 µm mesh net samples completed.

April (2015) - Data entry complete and available at the Arctic EIS Ocean Workspace (https://workspace.aoos.org/).
November (2015) - Finished data analysis and mapping distributions and abundances of major species, manuscript submitted to DSRII special issue
May (2016) - Completed and submitted final report.

In 2013 a significant problem occurred during the survey at sea where the factory processing deck that was being used as a laboratory flooded and the data forms that were used to record the flowmeter revolutions lost. The exact volumes filtered by nets were impossible to obtain. To address this deficiency, a VB 2010 code was generated to calculate distances of each net traveled through the water at 2 s time intervals using ship track record and FASTCAT time stamps recorded during each tow. The total tow distance was multiplied by the respective net opening area and the resulted volumes were stored for future calculations. The exact same procedure was applied to 2012 data and the estimates resulting from flowmeter reading were compared to those resulted from the distances traveled. The comparison indicated that Bongo 150 sampling efficiency was not consistent and subjected to severe clogging thus preventing reliable volume estimation rendering zooplankton quantitative processing impossible. Contrary, the performance of Bongo 505 was satisfactory. Based on the analysis, only the Bongo 505 samples collected in 2013 were targeted for processing.

Specimens collected are housed in the collection of UAF Juneau Center Zooplankton Laboratory. Data are stored and available available at the Arctic EIS Ocean Workspace (https://workspace.aoos.org/).

1. Abstract

Interest in the Arctic shelf ecosystems has increased in recent years as the climate has rapidly warmed and sea ice declined. These changing conditions allowed conduct of large scale surveys aimed at systematic, comparative analyses of interannual variability of the shelf ecosystem. In this study, we compared zooplankton composition and geographical distribution in relation to water properties on the eastern Chukchi and Bering Sea shelves during the summer of 2012 and 2013 as a part of the Arctic Ecosystem Integrated Survey (EIS) program. In 2013, shifts in water mass distribution manifested in a stronger influence of Chukchi Winter and Ice Melt waters, markedly affecting the distribution of expatriate and resident zooplankton species. This pattern was apparent not only in the spatial coverage, but also in their relative abundance and biomass, thus demonstrating the importance of the Arctic community on the northeastern Chukchi shelf. In contrast, zooplankton biomass of Pacific origin decreased in 2013 in the northern Chukchi shelf suggesting a change of its advection pathways into the Arctic. The observed interannual variability in distribution of water properties on the Chukchi Sea shelf is in agreement with previously described systematic oceanographic patterns derived from long-term observation time series.

2. Introduction

Interest in the Arctic shelf has increased in recent years as the climate has rapidly warmed and sea ice declined. These changes may lead to potential increases in shipping, resource extraction (e.g. oil and gas) and commercial fishing (Moran and Farrell, 2011) which could affect arctic ecosystems. A greater understanding of lower trophic level functioning including zooplankton ecology is needed to characterize these arctic shelf habitats and monitor future changes relating to climate and/or anthropogenic impacts.

The northern Bering and Chukchi seas connect the Pacific and the Arctic oceans. The majority of the area consists of shallow (< 60 m depth) shelves lacerated with Herald and Barrow underwater canyons in the northwest and northeast respectively, while Herald and Hanna shoals separated by the moderately deep Central Channel dominate the underwater landscape in the north (Fig 1). The Chukchi Sea is not strictly bounded by land and it does not have a gyre-type circulation characteristic of the neighboring Bering and Okhotsk seas (Stabeno et al 1999, Oshima et al 2004). Instead, primarily one-directional currents flow northward due to difference in sea level between the Pacific and the Arctic (Aagaard et al., 2006; Coachman 1975; Stigebrandt, 1984). The bottom topography defines three major pathways of the Pacific water across the Chukchi shelf splitting the incoming flow into Herald, Central and Alaska Coastal outflows (Weingartner et al 1998, Woodgate et al 2005). Because the northern Bering and Chukchi shelves are shallow, local winds play a major role in the redistribution of water properties. Wind can retard the general south to north flow through the Bering Strait, sometimes entirely blocking or reversing it (Panteleev et al 2010). Similarly, westward oriented winds can divert the Bering inflow onto the western Chukchi shelf, and weaken or reverse flow over the northeastern Chukchi shelf (Weingartner et al 1998). As a result, the variability in the pelagic environment can be large and difficult to assess, especially when using datasets collected over short temporal and spatial scales. Recent analyses of Chukchi Sea thermal conditions based on basin-wide observations conducted during the last six decades reveal multi-year fluctuations between two opposite (“cold” vs “warm”) states during summer months (Luchin and Panteleev, 2014). In the eastern Chukchi Sea, the contrast between the thermal states was strongly manifested north of 70°N, where difference in mean temperature amounted to 5°C (Luchin and Panteleev, 2014). Temperature distributions for each state suggested intensified flow of the Pacific water along the Alaskan coast towards Barrow Canyon during “warm” states, while during the “cold” states most of the Pacific water is deflected westward, to be funneled through Herald Canyon (Luchin and Panteleev, 2014). Such shifts in the magnitude and distribution of fundamental physical properties directly affect pelagic communities, including zooplankton.

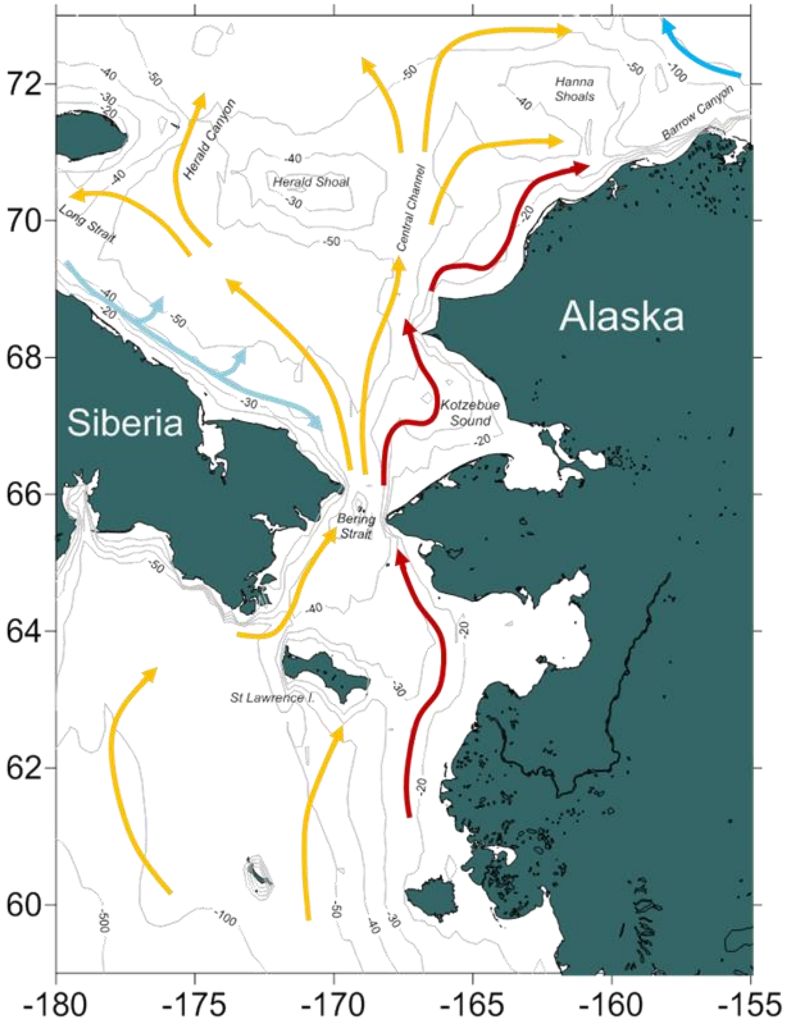

Figure 1. A schematic diagram of water circulation on the Northern Bering – Chukchi shelf (red – Alaska Coastal Current, yellow – Bering Shelf, Anadyr and Chukchi Shelf waters pathways, light blue – Siberian Coastal Current, deep blue – Beaufort Gyre)

Due to geographical proximity, water masses in the northern Bering and Chukchi seas are formed by similar processes (Luchin and Panteleev, 2014) and typically have distinct temperature and salinity characteristics. Water masses entering the Chukchi Sea through the Bering Strait include warmer, fresher Alaska Coastal Water flowing along the eastern shore and Anadyr/Bering Summer Water with moderate temperatures and salinities. Upon entering, the latter eventually transforms into Chukchi Summer Water with similar properties. In contrast, Melt Water is colder fresher water in the surface layer formed by melting of sea ice and is restricted to the northernmost Chukchi Sea during summer. Finally, near-bottom cold and salty

Bering and Chukchi Winter Waters are remnants of the previous winter cooling and considered resident to the corresponding shelves. The contrasting properties of these water masses restrict mixing and promote a tendency for water masses to overlay each other along their boundaries, even in the vicinity of constricted and turbulent Bering Strait (Pinchuk, 1993). These water masses also contain differing nutrient concentrations, phytoplankton biomass and primary productivity (Danielson et al., this issue; Eisner et al., 2012; Springer and McRoy, 1993; Grebmeier et al., 2006) providing diverse habitats for zooplankton and their predators (e.g. fish, marine mammals and seabirds).

Distinct zooplankton taxa assemblages in the Chukchi Sea and their affinity to certain water masses have been reported by multiple studies as early as the 1930s (e.g. Stepanova, 1937; Wirketis, 1952; Brodsky 1956, Pavshtiks, 1984). Those pioneering studies agreed that the Bering Sea Shelf (including Anadyr) waters, while also populated with wide-spread shelf species (e.g. *Calanus glacialis*) among others, are, nevertheless, best characterized by large (> 4 mm) oceanic copepods *Neocalanus* spp., *Eucalanus bungii*, which originate from the Bering Sea outer shelf and are excellent tracers of Pacific intrusion into the high Arctic. In contrast, the large copepods *Calanus hyperboreus, Pareuchaeta glacialis, Metridia longa* originate from the Arctic Basin, and, thus serve as reliable indicators of Arctic-derived waters in the Chukchi Sea (Brodsky, 1956). It has been noted, that spatially these two groups are somewhat distinctive and are likely reflective of complex local interactions between the water masses they inhabit (Wirketis, 1952). The neritic assemblage associated with Alaska Coastal water typically comprise small (<1.5 mm) copepods (e.g. *Centropages abdominals, Epilabidocera amphitrites, Tortanus discaudatus, Acartia clausi*) and the cladocerans *Evadne* spp. and *Podon* spp. (Wirketis, 1952).

Since then, numerous attempts have been made to clarify the taxonomic composition of zooplankton communities and to quantify these distributional patterns at various scales, resulting in one fundamental conclusion – as a whole, the Chukchi Sea zooplankton is a derivative of the Bering Sea zooplankton with only relatively a minor contribution of resident Arctic fauna (Hopcroft et al., 2010; Eisner et al., 2013; Questel et al., 2013; Ershova et al., 2015a, b). However, most of these surveys were restricted to the short ice-free period and were conducted along a handful of transects typically running from nearshore onto the shelf. It comes as no surprise, that high variability and poor reproducibility was observed along discrete sampling locations over the years (Questel et al., 2013, Ershova et al 2015a), thus limiting our understanding of zooplankton dynamics at basin-wide scales. Recent changes in the magnitude and duration of ice cover resulted in a number of surveys covering substantial parts of the Chukchi shelf with sampling grids, allowing comparisons on a synoptic scale (Eisner et al, 2013, Slabinsky and Figurkin, 2014).

The Arctic Ecosystem Integrated Survey (EIS) program launched in 2012 aims at documenting the zooplankton, bottom and pelagic fish and invertebrates, understanding the environmental forcing that impacts northern Bering and Chukchi Sea ecosystems and predicting the future effects of reduced sea ice and warming on these ecosystems. This survey covers most of the northern Bering and Chukchi seas east of the international border and extends as far north as 72.5 °N. The 2012/2013 project was a natural experiment displaying the interplay between two extreme thermal states derived from multi-year observations (Luchin and Panteleev, 2014). We hypothesized that shifts in water mass distribution markedly affected the distribution of expatriate and resident zooplankton taxa both in terms of spatial coverage and relative abundance/biomass, altering the role of Arctic species on the northeast Chukchi shelf. Our study is the first attempt to relate zooplankton variability to systematic oceanographic patterns derived from long-term observation time series.

3. Methods

Samples were collected in the Chukchi and northern Bering seas between 8 August and 24 September in 2012 and 2013.The sampling design was based on a square grid pattern with stations located 56 km apart, resulting in a total of 139 and 134 sampling locations in 2012 and 2013, respectively (Fig. 2). Sampling started in the Bering Strait and continued northward along zonal (east-west) transects up to 72.5 °N latitude. Once the Eastern Chukchi Sea shelf sampling was completed, the ship returned to the Bering Strait and completed the Northern Bering Sea shelf grid in zonal swaths moving southward.

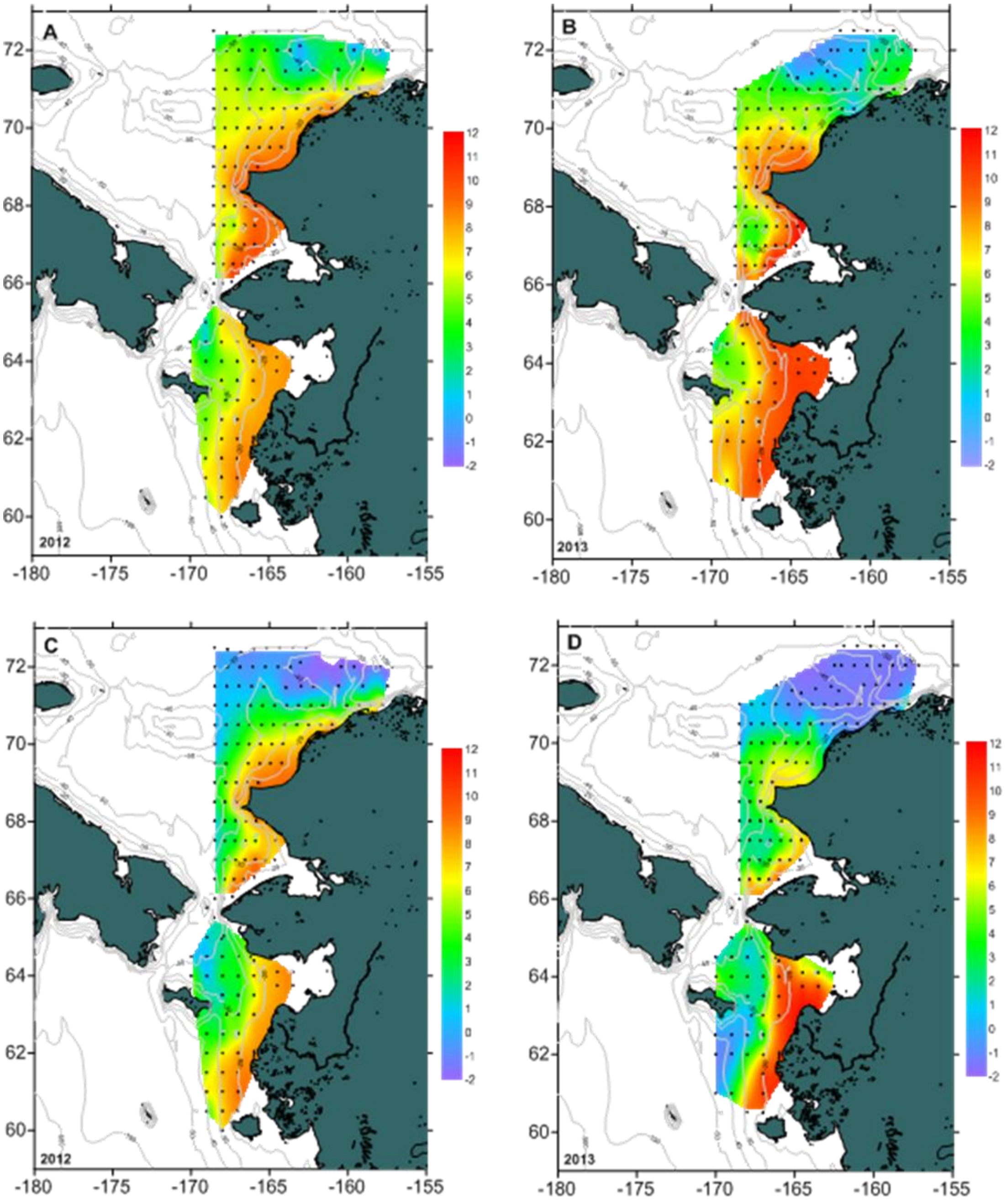

Figure 2. Temperature (°C) above and below the thermocline on the northern Bering and Chukchi Sea shelves in late summer 2012-2013. A, B – above the thermocline in 2012 and 2013 respectively, C, D – below the thermocline in 2012 and 2013 respectively. Black points indicate zooplankton sampling stations.

Conductivity-temperature-depth (CTD) measurements were collected with a Sea-Bird Electronics Inc. (SBE) 911 or SBE 25 CTD to determine surface (above pycnocline) and bottom (below pycnocline) temperature and salinity. Zooplankters were sampled with a 60 cm

MARMAP-style bongo frame with a 505 µm mesh net. The net frame was equipped with an SBE 49 CTD transmitting real time tow data. To assess the contribution of small taxa to total zooplankton biomass, a 20 cm PairVET net with 150 µm mesh was attached to the net array according to NOAA standard sampling protocol (Dougherty et al., 2010), and deployed simultaneously at all stations in 2012. The GPS location of the ship during the tow was recorded every 2 s to determine distance towed. Oblique tows from within 5 – 10 m off the bottom to the surface were conducted primarily during daylight hours. Maximal tow depth ranged between 15 m and 98 m depending on bathymetry. Volume filtered was measured with calibrated General Oceanics flowmeters mounted inside the nets. Volumes recorded from the flowmeter were compared with volumes estimated from the distance towed at each station to detect net clogging. While little clogging occurred in the 505 µm mesh net during sampling, the efficiency of the 150 µm mesh net was inconsistent (Fig. 3), resulting in exclusion of a substantial number of stations from the analysis. Therefore, data on small zooplankton was assumed to be mainly qualitative and should be treated with caution. All samples were preserved in 5% formalin, buffered with seawater for later processing.

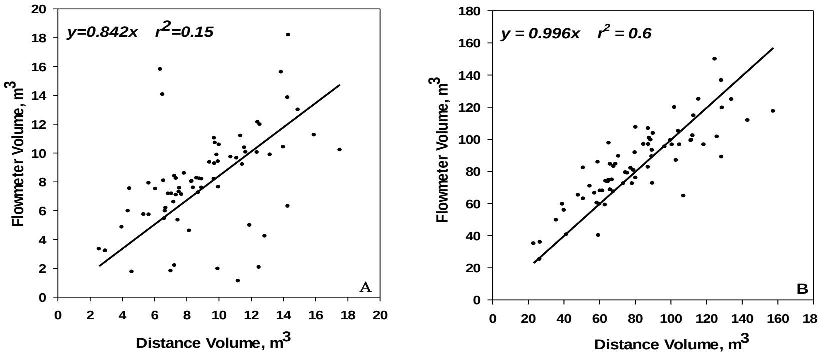

Figure 3. Performance of 505 µm and 150 µm mesh Bongo nets on the northern Bering and Chukchi Sea shelves in late summer 2012 expressed as a relationship between volume estimates derived from the distance towed and those derived from the flowmeter readings. A – 150 µm mesh; B – 505 µm mesh. 100% filtering efficiency achieved when both estimates are equal.

In the laboratory, the mesozooplankton samples were sequentially split using a Folsom splitter until the smallest subsample contained approximately 200 specimens of the most abundant taxa. All taxa in the smallest subsamples were identified, staged, enumerated and weighed. Each larger subsample was examined to identify, enumerate and weigh the larger, less abundant taxa. Blotted wet weights for each taxa and stage were determined as outlined in earlier papers (Coyle et al., 2008, 2011), and the Coefficient of Variation (CV) in average wet weight was computed. If the CV for any given taxa and stage changed by less than 5% when additional weights were taken from subsequent samples, a mean wet weight was calculated and wet weights were no longer measured for that taxa. The wet weight biomass for all subsequent samples was estimated by multiplying the specimen count by the mean wet weight. In practice, only calanoid copepods had consistent wet weights after weighing each taxa and stage in about 10-15 samples. Therefore, wet weights on chaetognaths, shrimp and other larger and soft-bodied taxa were measured and recorded for each sample. Wet weight measurements were done on a Cahn Electrobalance or Mettler top loading balance, depending on the size of the animal. All animals in the samples were identified to the lowest taxonomic category possible. Juveniles of various epibenthic gammarids were not identified to the species level and were grouped in one category Gammaridea. Sibling species *Calanus marshallae* and *C. glacialis* co-occurring in the Bering and Chukchi seas (e.g., Nelson et al., 2009) were not discriminated and are named as *Calanus glacialis* hereafter. Copepodid stages were identified and recorded. Biomass values by station were computed for each species in grams m^{-3}. Many adult euphausiids on the shelves of the Bering and Chukchi seas remain within 1 – 2 m of the bottom during the day (Coyle and Pinchuk, 2002) and those in the water column are difficult to quantitatively capture due to net avoidance (e.g. Sameoto et al., 1993; Wiebe et al., 2004). The latter is also true for larger hyperiids *Themisto libellula*. Therefore, euphausiids and *T. libellula* were not included in the analyses. Large scyphozoan jellyfish (primarily *Cyanea capillata*) and shrimp occasionally captured by the net were excluded from the analysis as well.

The data were uploaded to a Microsoft Access database, and analysis was done with standard statistics software. Physical properties influencing zooplankton distribution were analyzed as follows. The depths of the pycnocline were computed for each station by locating the depth where dst/dZ were maximum (st = sigma-t; Z = depth, m). The mean water-column temperature above and below the pycnocline were then computed. The water mass types were assigned to each station according to Danielson et al (this issue). Two-sided test for difference between proportions of stations occupied by certain water masses was used to estimate changes in the water mass spatial distribution between the years. Due to uneven spatial distribution of zooplankton, the biomass data were ¼ root power transformed to stabilize the variance and reduce heterscedasticity. Analysis of variance (ANOVA) was used to test for significant effects of location (water mass) and year on physical and biological variables, and the distribution of residuals was analyzed. When the residuals satisfied the normality assumption and ANOVA results indicated significant effect, Tukey post-hoc test was applied to identify significant differences ($p<0.05$). Canonical correlation analysis was used to evaluate relationships between the biomass of major zooplankton taxa/groups and temperature and salinity at each station. Canonical correlation looks for linear correlations between two sets of random variables, in this case the physical and biological variables. The physical variables consisted of the mean water temperatures and salinities above and below the pycnocline at each station. The biological variables consisted of the biomass of the major taxa and taxa groups at each station. Output consisted of the correlation level, the probability of obtaining correlation if the data were in fact uncorrelated, and the amount of explained variance.

4. Results

A detailed analysis of physical properties and water mass distribution during the study is reported elsewhere (Danielson et al., this volume). Here, we only briefly describe and contrast physical settings relevant to zooplankton. In 2012, well-mixed warm (>7°C) and low salinity (~30) Alaska Coastal Water (ACW) was found along the Alaskan coast northward to the Beaufort Sea western boundary, while in 2013 ACW did not extend farther than 70°N (Fig. 2). In addition, ACW appeared to be more restricted to the coast in 2012, while in 2013 ACW expanded over denser BCSW or WW further offshore forming well-stratified transition zones, which were found at a larger number of stations (Table 1). The westernmost offshore stations were occupied by weakly stratified, moderately warm (~5°C) and saline (~31) Bering-Chukchi Summer Water (BCSW) which formed a well-stratified transition zones with the denser cold (<2°C) and saline (~33) near-bottom Winter Water (WW), which extended over deeper portions of the shelf and with the less dense ACW above. While BCSW/WW transition occurred at a similar number of stations in both years, ACW/ BCSW transition appeared to be wider in the northern Bering Sea in 2013. Pronounced differences between the years were observed in the northeast where cold (~2°C) and low saline (~29) Ice-Melt Water (MW) displaced BSCW in upper layer at 15 transitional stations in 2012. In contrast, in 2013 twice as many stations in the northeast were occupied by MW which overlaid very cold (<0°C) WW expanding to 70°N southward (Table 1). The test for differences between relative proportions of each group of stations revealed significant ($p<0.05$) increase in the number of MW/WW and ACW/BCSW stations and decrease in the number of ACW and BCSW stations in 2013.

Table 1. Mean temperature (T, °C) and salinity (S, PSU) above (T_{up}, S_{up}) and below (T_{lo}, S_{lo}) the pycnocline in relation to water masses observed at zooplankton stations in the northern Bering and Chukchi shelf in summer 2012 and 2013 (ACW – Alaska Coastal Water, BCSW- Bering Chukchi Summer Water, WW – Winter Water, MW – Melt Water; D – mean depth of pycnocline, m; N – number of stations; SD – Standard Error).

Water Mass	2012						2013					
	N	*D*	$T_{up}\pm SD$	$T_{lo}\pm SD$	$S_{up}\pm SD$	$S_{lo}\pm SD$	*N*	*D*	$T_{up}\pm SD$	$T_{lo}\pm SD$	$S_{up}\pm SD$	$S_{lo}\pm SD$
ACW	34	12	8.7±1.1	8.4±1.1	29.1±0.8	29.8±0.8	17	10	9.8±1.5	9.0±1.6	28.9±1.2	30.1±1.1
ACW/BCSW	20	14	7.3±1.4	5.0±1.5	30.8±1.1	31.8±1.0	39	13	8.6±1.0	4.5±1.1	29.9±0.8	31.6±0.7
ACW/WW	-	-	-	-	-	-	5		7.7±2.8	-0.5±2.9	30.3±2.2	31.4±2.0
BCSW	42	16	5.6±1.0	3.4±1.0	31.2±0.7	32.1±0.7	28	18	5.2±1.2	2.8±1.2	31.5±0.9	32.1±0.8
BCSW/WW	10	16	4.9±2.0	0.4±2.1	30.5±1.5	32.7±1.4	12	17	4.2±1.8	0.3±1.9	31.2±1.4	32.3±1.3
MW/WW	15	14	2.0±1.6	-0.9±1.7	28.8±1.2	32.6±1.1	33	14	2.1±1.6	-1.1±0.7	27.9±1.4	31.9±0.4

A total of 81 unique zooplankton taxa were recorded during the study. The majority (58 taxa) were wide-spread taxa commonly found on Arctic and Subarctic shelves. The large-bodied wide- spread taxa included copepods *Calanus glacialis*, chaetognaths *Parasagitta elegans*, and 15 species of hydrozoan jellyfish with *Aglantha digitale* being most common. The Pacific group comprised 7 large-bodied taxa originated from deep Pacific water, and included copepods *Neocalanus cristatus*, *N. plumchrus*, *N. flemingeri*, *Eucalanus bungii*, *Metridia pacifica*, hyperiids *Themisto pacifica*, and chaetognaths *Eukronia hamata*. The majority of *Neocalanus* copepods were C5 copepodites. The Arctic group included 4 large-bodied taxa originating from the Arctic Basin, and included copepods *Calanus hyperboreus* (mainly C4 copepodites)*, Pareuchaeta glacialis, Metridia longa* and hyperiids *Themisto abyssorum*. Small-size taxa were mainly ubiquitous copepods of Pacific origin belonging to *Pseudocalanus* and *Oithona* genera, as well as neritic copepods *Acartia longiremis*, *A. hudsonica*, and *Centropages abdominalis*, common in nearshore environments. Despite high numerical abundance at some locations, contribution of small taxa to total zooplankton biomass was relatively small (median ~25%).

Canonical analysis revealed significant relationships between the biomass of major zooplankton taxa groups and physical variables. The correlation was 0.82, the explained variance was 73% with $p<0.0001$. Strong positive correlations occurred between the biomass of the Pacific group relative to salinity, indicating an association to the BCSW (Table 2). In contrast, the biomass of the Arctic group showed strong negative correlations to temperature and salinity above the pycnocline, indicating a link to MW. The biomass of shelf species *C. glacialis* and *P. elegans* exhibited strong positive correlations to salinity below the pycnocline, and moderate negative correlations to temperature, indicating their affinity to WW and BCSW. The hydrozoan jellyfish biomass was negatively correlated to salinity and positively, albeit weakly, to temperature, implying a linkage to ACW.

Table 2. Correlation coefficients relating physical properties above (T_{up}, S_{up}) and below (T_{lo}, S_{lo}) the pycnocline to biomass (mg m^{-3}) of major zooplankton taxa groups on the northern Bering and Chukchi sea shelves in summer 2012-2013.

Taxa	T_{up}	T_{lo}	S_{up}	S_{lo}
Calanus glacialis	-0.291	-0.300	0.227	0.481
Parasagitta elegans	-0.245	-0.257	0.154	0.362
Hydrozoan medusa	0.034	0.114	-0.214	-0.239
Larvaceans	-0.498	-0.531	-0.114	0.453
Pacific group	-0.041	-0.092	0.510	0.439
Arctic group	-0.541	-0.468	-0.440	0.080

The total biomass of large zooplankton differed among years and regions occupied by different water masses (ANOVA, F=5.57, $p<0.005$). The interannual difference was driven by changes in BCSW/WW where zooplankton biomass significantly decreased in 2013 (Table 3).

Table 3.Estimates of mean total zooplankton biomass (mg m^{-3}) with 95% confidence intervals (in parentheses) in different water masses on the northern Bering-Chukchi shelf in 2012 and 2013 (ACW – Alaska Coastal Water, BCSW- Bering Chukchi Summer Water, WW – Winter Water, MW – Melt Water). Bold indicates a significant difference between years.

	2012	2013	Tukey (p<0.05)
ACW (1)	111 (74-160)	100 (55-169)	2012=2013
ACW/BCSW (2)	406 (277-574)	205 (149-276)	2012=2013
ACW/WW (3)	-	50 (11-144)	2013
BCSW (4)	448 (348-568)	265 (185-367)	2012=2013
BCSW/WW (5)	**576 (349-898)**	**123 (62-221)**	**2012>2013**
MW/WW (6)	367 (233-553)	236 (168-321)	2012=2013
Tukey (p<0.05)	1<2=4=5=6	1=2=3=4=5=6	

In 2012, the lowest biomass occurred in ACW, while in 2013 no significant differences in biomass content among the water masses were found. In all water masses zooplankton biomass was dominated by *Calanus glacialis*, followed by *Parasagitta elegans*, while hydrozoan jellyfish were especially important in the ACW (Fig. 4); these three taxa/groups on average accounted for over 70% of total biomass in the study area. During both years, the Pacific group was found mainly in BCSW and in the associated transition zones (BCSW/WW and ACW/BCSW), while the Arctic group substantially contributed to zooplankton biomass in MW/WW in 2013. Larvaceans *Oikopleura* spp. were common in MW/WW and BCSW/WW in both years. Hydrozoan jellyfish were a dominant group in ACW in both years; however they also became important in MW/WW in 2013, mainly due to the presence of cold-water *Halitholus cirratus*.

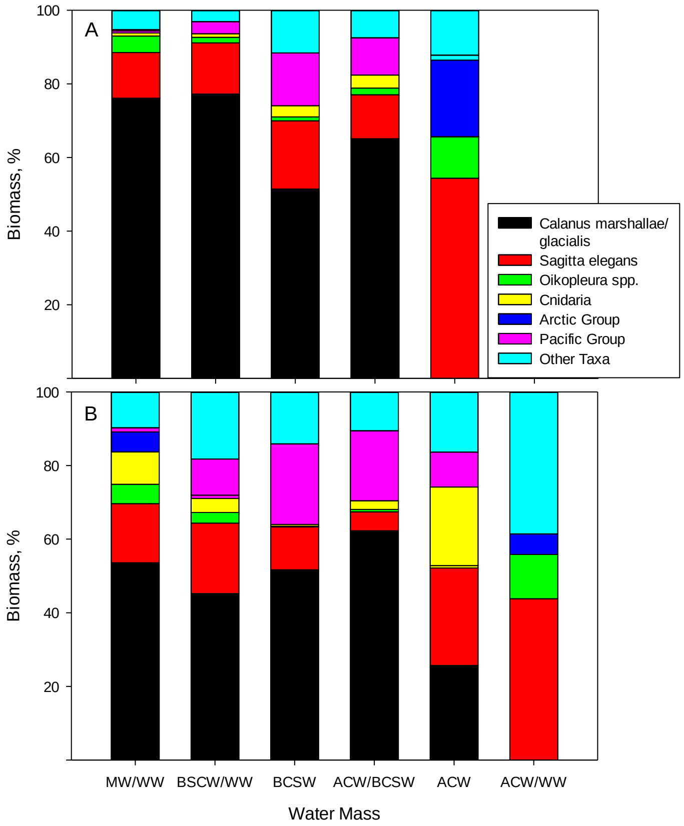

Figure 4. Contribution of major taxa to total large zooplankton biomass in the northern Bering-Chukchi shelf in 2012 (A) and 2013 (B).

Substantial interannual differences were observed in spatial distribution of the zooplankton groups. In 2012, representatives of the Arctic group were found only in small quantities at three stations in the northeast corner of the survey grid, while in 2013 they occurred over a larger area extending from Barrow Canyon to the northern Hanna Shoals (Fig. 5A, 5B). Changes in distribution of the Pacific group showed the opposite trend. In 2012, the range of the Pacific group encompassed the entire stretch of the shelf from St Lawrence Island over the Central Channel to Hanna shoals and the head of Barrow Canyon, while in 2013 it did not extend farther than 70°N (Fig. 5C, 5D).

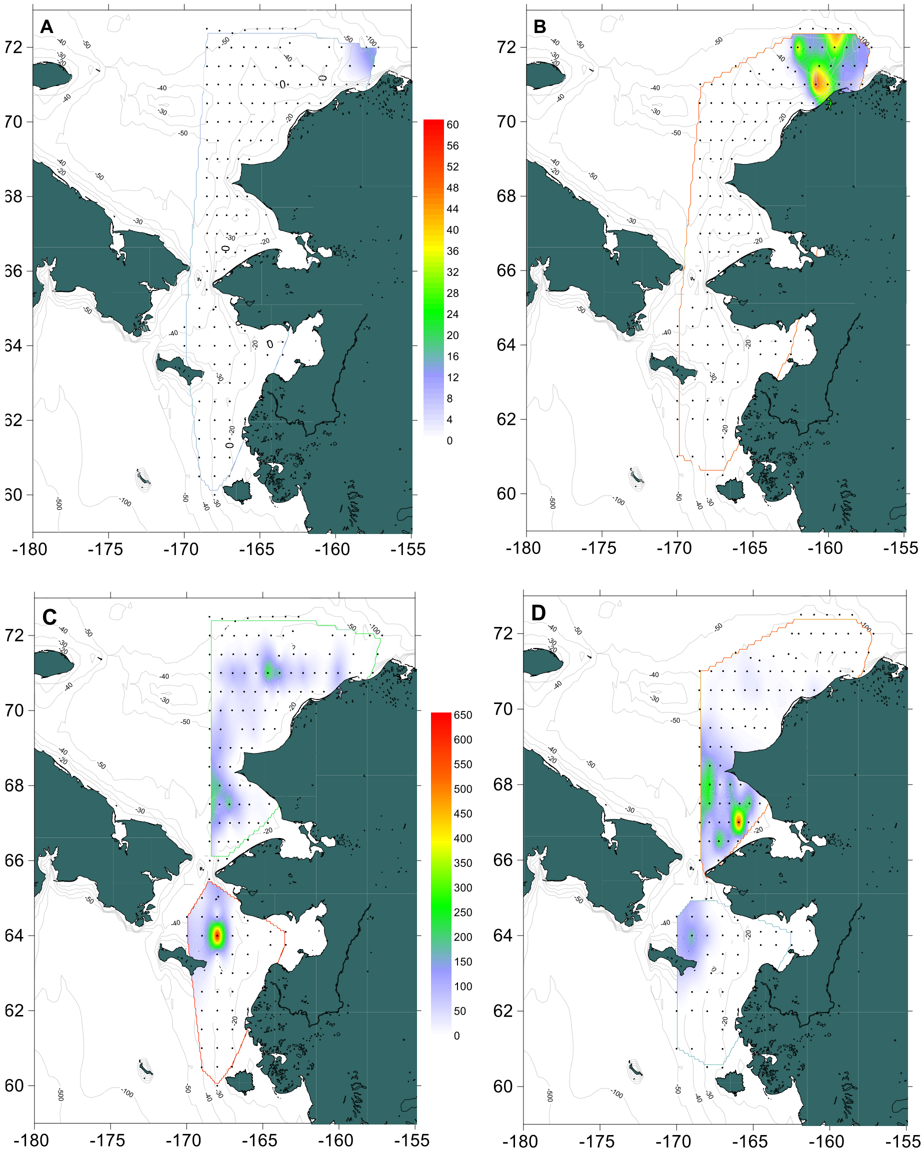

Figure 5. Spatial distribution of the biomass (mg m^{-3}) of Arctic and Pacific zooplankton taxa groups on the northern Bering and Chukchi Sea shelves in late summer 2012-2013. Arctic Group: A – 2012, B – 2013; Pacific Group: C – 2012, D – 2013. Black points indicate zooplankton sampling stations.

The range of *C. glacialis* covered the entire shelf in 2012 with most of the biomass occurring in north of St. Lawrence Island, offshore of Kotzebue Sound, the Central Channel and southern Hanna Shoals (Fig. 6A). In 2013, the distribution of *C. glacialis* on the Chukchi shelf appeared disrupted with most of the biomass occurring to the south and to the north of the Central Channel (Fig. 6B). The spatial distribution of *P. elegans* generally mirrored that of *C. glacialis*.

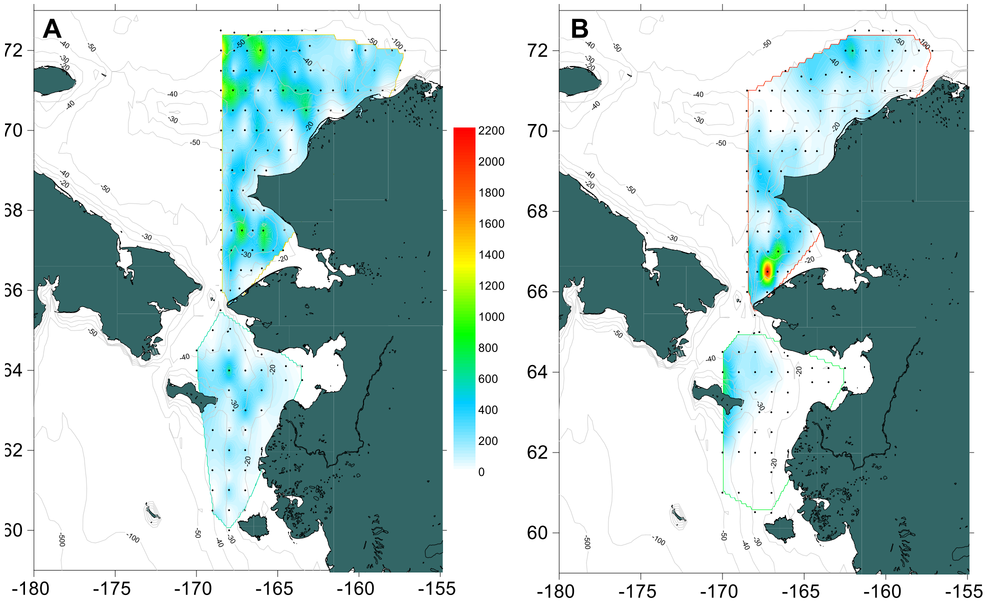

Figure 6. Spatial distribution of the biomass (mg m^{-3}) of *Calanus glacialis* (copepodite stages C3 and older are pooled) on the northern Bering and Chukchi Sea shelves in late summer 2012-2013. A – 2012, B – 2013.

The distribution of *C. glacialis* developmental stages suggested presence of two populations of separate origins (Fig. 7). At the start of the survey in the Bering Strait, the *C. glacialis* population consisted mainly of C4 copepodites. As the surveys progressed northward, C5 copepodites became predominant. However, by the time the ship reached 71°N the *C. glacialis* population structure changed when younger C3 copepodites became prevalent (Figs. 7, 8). During the last phase of the survey south of the Bering Strait, copepodites C5 made up the majority of *C. glacialis* population. Canonical analysis showed significant relationship between the abundance of *C. glacialis* copepodites and physical variables. Strong negative correlations occurred between the abundance of C3 copepodites and both temperature and salinity above the pycnocline, indicating their affinity to MW.

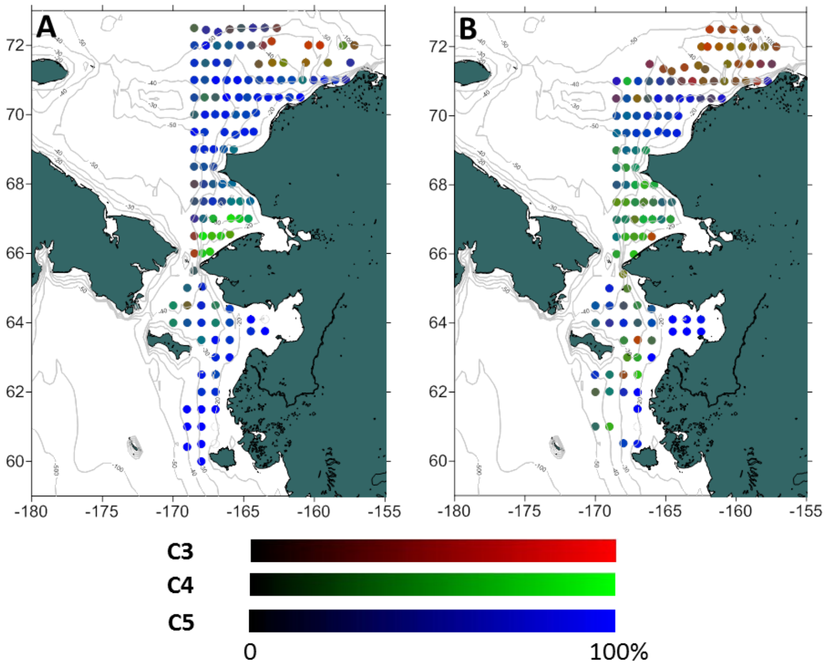

Figure 7. Spatial stage-specific population structure of *Calanus glacialis* (abundance of copepodite stages C3, C4, and C5 normalized to total *C. glacialis* abundance) on the northern Bering and Chukchi Sea shelves in late summer 2012-2013. Data presented as a composite RGB color proportional to each stage contribution at each location. A – 2012, B – 2013. Red – C3, Green – C4 , Blue – C5.

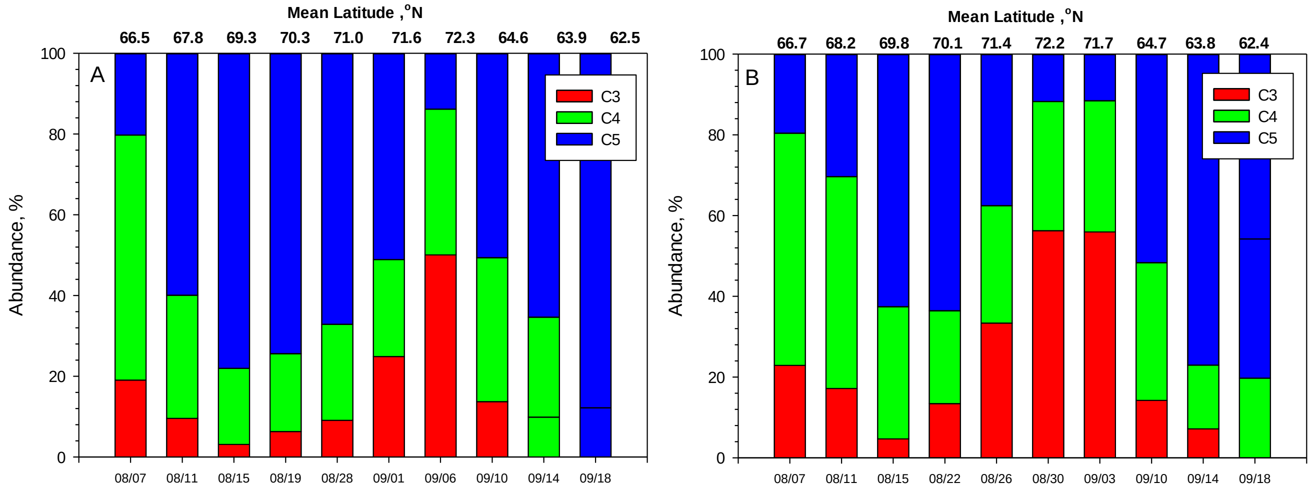

Figure 8. Changes in *C. glacialis* population structure with time (consecutive 5 day bins, mean dates are displayed along the lower axis) and latitude. A – 2012, B – 2013. Mean latitude (°N) for stations sampled during each time bin is shown along the upper axis.

5. Discussion

The zooplankton surveys conducted in 2012 and 2013 indicated a remarkable shift in spatial distribution of the taxon groups of different origins: in 2013, the Pacific group range was reduced to the southern and central Chukchi shelf south of 70°N, while the Arctic group range expanded over the northeastern Chukchi shelf. The population of *C. glacialis*, which comprised the bulk of zooplankton biomass, demonstrated differences in stage-specific distribution with "older" copepodites following the former pattern, and the "younger" copepodites mirroring the latter. The discrepancy is likely due to the presence of two distinct populations of *C. glacialis* in the study area. While *C. glacialis* is typically considered a neritic shelf species inhabiting all Arctic marginal Seas and adjacent North Pacific and North Atlantic waters, it does occur in the Arctic Basin, where it maintains an independent population as evident from observations on reproductive activity, population dynamics and haplotype distributions (Nelson et al 2009, Kosobokova, 2012). In the Arctic Ocean, *C. glacialis* start reproducing in near surface water in late spring, reaching overwintering copepodite stages C3-C4 by the end of the summer. This is consistent with our observations of a younger *C. glacialis* population found in the northeast occupied by MW/WW. Conversely, the *C. glacialis* population recorded from BCSW apparently originates from the northern Bering Sea shelf, where the spawning occurs in early spring and the majority of the population develops to the C5 stage by the end of August (Baier and Napp, 2002, Pinchuk et al, 2014). The gradual change in the population age structure in the southern and central Chukchi Sea as the surveys progressed and the similarity to the age structure in the northern Bering Sea support this suggestion.

The shift in zooplankton distribution appeared to result from a large scale alteration in oceanic circulation, manifested by the advection of MW from the north/northeast over a substantial part of the northeastern shelf, and the apparent shutdown of Alaska Coastal Current north of 70N in 2013 due to persistent south/southwest winds (Danielson et al, in press). The contrasting patterns of the distributions of water temperature above and below the pycnocline correspond well to the distinctive thermal states identified for the Chukchi Sea (Luchin and Panteleev, 2014) and allow the classification of 2012 as a "warm" and 2013 as a "cold" state for the eastern Chukchi shelf. The velocity fields reconstructed for the two thermal states using four-dimensional variational (4Dvar) data assimilation into the Semi-Implicit Ocean Model (Panteleev et al, 2010) suggest intensified northward flows of BCSW through the Central Channel and Herald Canyon during “warm” years, while during “cold” years the northward flow is depressed (Luchin and Panteleev, 2014). An increase in volume transport northward through the Central Channel would result in an elevated biomass of Pacific-origin zooplankton along the pathway of the current. In contrast, the retardation of the flow combined with advection of MW from the north, would result in increased biomass of Pacific zooplankton in the southern (and probably western) Chukchi Sea as well as an expansion of Arctic taxa over the northeastern shelf. The correspondence of these predicted patterns to our observations demonstrates the efficacy of this classification and modeling approach to forecasting of zooplankton the spatial distribution of zooplankton populations on the Chukchi Sea shelf.

The alterations in zooplankton distribution in the Chukchi Sea may have profound effects on the marine trophic web. *Calanus* species are widely distributed in the Arctic Ocean and the northern seas (Mauchline 1998) where they often are a staple food for pelagic predators (Coyle et al 1996). They are a good source of energy due to their high lipid content enriched with wax esters and long-chain fatty alcohols and fatty acids (Kattner et al. 1989; Scott et al. 2000, 2002; Lee et al. 2006, Falk-Petersen et al 2007). In the northern Chukchi Sea, Arctic Cod (*Boreogadus saida*) prey mainly on *C. glacialis*, which amounted to 28% of the diet by mean weight in 2010-2012 with *C. hyperboreus* comprising <5% of the diet, whereas on the Beaufort shelf, the *C. hyperboreus* contribution to Arctic Cod diet amounted to ~24% by mean weight in 2011 (Grey et al, in press). *C. hyperboreus* undergoes a 3-year life cycle in the Arctic Ocean, reproducing at depth during winter using stored lipid reserves and developing to copepodite stage C4 by the second summer (e.g., Dawson, 1978; Conover, 1988; Hirche and Niehoff, 1996). The C4 copepodites accumulate substantial amount of lipids before undergoing seasonal diapause the following winter (Ashjian et al 2003). Like *C. hyperboreus*, *C. glacialis* copepodites (typically C4 and C5) also begin to accumulate lipids before entering seasonal diapause. While the energy content per unit weight of first overwintering stages is similar in both species, the lipid weight per individual *C. hyperboreus* C4 is 5 times as much as that of *C. glacialis* C4 (Falk-Petersen et al, 2009) due to body size differences, making the former a more energetic prey. Thus, it might be expected that Arctic Cod would take advantage of the increased biomass of *C. hyperboreus* on the northeastern Chukchi shelf in 2013. While no diet data from the Arctic EIS 2013 survey are available, preliminary data collected in the vicinity of Barrow Canyon as a part of another project in August 2013 indicated a preference for *C. hyperboreus* by juvenile Arctic Cod, even though *C. glacialis* copepodites occurred in the study area in much higher abundances (Pinchuk et al 2015). Whether the diet shift leads to improved fish body condition remains to be investigated.

The bulk of Pacific taxa was comprised of the subarctic *Neocalanus* copepods that are also rich in lipids (e.g. Evanson et al 2000) and play a key role in pelagic food webs in the North Pacific and central Bering Sea; they are an important prey of pelagic fishes (Burgner, 1991; Odate, 1994, Gordon, Nishida & Nemoto, 1985, Tanimata et al 2008), whales (Kawamura, 1982), and seabirds (Hunt, Harrison & Piatt, 1993). While *Neocalanus* copepods do not seem to contribute substantially to fish diets in the Chukchi Sea at the present, an increasing inflow of BCSW resulting in elevated *Neocalanus* biomass in the central and northern Chukchi Sea during the “warm” state could potentially benefit planktivorous predators. Likewise, shifts of the circulation northwestward during the “cold” state could lead to an increased contribution of Pacific copepods to local food webs enhancing productivity on the western Chukchi shelf (Slabinsky and Figurkin 2014).

Recent evidence shows that the volume of the relatively warm Bering Sea water flowing into the Arctic has increased in the last decade (Woodgate et al. 2015). The increase is partially responsible for warmer temperatures on the Chukchi Sea shelf (Luchin and Panteleev, 2014), and likely contributes to reductions in the extent and duration of seasonal sea ice (Weingartner et al 2013; Thomson and Rogers, 2014), and to increases in primary production (Belanger et al 2013) and biomass of zooplankton of Bering-Pacific origin (Ershova et al 2015). As a result, the Chukchi Sea is at the leading edge of expected changes in ecosystem structure which appear to propagate northward due to climate change. The shifts in climate are expected to impact distribution patterns and life cycles of expatriate species in different ways, which in turn may result not only in their spatial range expansion (Mueter and Litzow, 2008), but also in reorganization of entire food webs as recently observed in the southeastern Bering Sea (Coyle et al 2011, Pinchuk et al 2013). However, very high spatial, seasonal, and interannual variability in the distribution of water properties and associated zooplankton communities (Matsuno et al., 2011; Questel et al., 2013; Ershova et al., 2015, Pisareva et al 2015) makes monitoring of pelagic ecosystems challenging. Interpreting available data from a thermal state oscillation perspective provides a framework for better understanding and prediction of biophysical processes in a changing Chukchi Sea.

6. Acknowledgements

This study was funded in part with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior. It was also funded by the Bureau of Ocean and Energy Management (BOEM) Award # M12PG00018. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of the U.S. Government. Mention of trade names or commercial products does not constitute their endorsement by the U.S. Government.

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Appendix R.

Late summer open water zoogeography of the northern Bering and Chukchi seas

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June 8, 2016
Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)
Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
DIN	dissolved inorganic nitrogen
Chl*a*	water column integrated chlorophyll *a*
TOC	total organic carbon
CTD	conductivity-temperature-depth
GAM	general additive model
CPUE	catch per unit effort
NMDS	nonmetric multidimensional scaling
CA	correspondence analysis

List of Oral and Poster Presentations

Mike Sigler, Franz Mueter, Bodil Bluhm, Morgan Busby, Ned Cokelet, Seth Danielson, Alex De Robertis, Lisa Eisner, Ed Farley, Katrin Iken, Kathy Kuletz, Bob Lauth, Libby Logerwell, Alexei Pinchuk, and Chris Wilson. January 2015. Summer zoogeography of the northern Bering and Chukchi seas. Poster at the Alaska Marine Science Symposium, Anchorage, Alaska.

Mike Sigler, Franz Mueter, Bodil Bluhm, Morgan Busby, Ned Cokelet, Seth Danielson, Alex De Robertis, Lisa Eisner, Ed Farley, Katrin Iken, Kathy Kuletz, Bob Lauth, Libby Logerwell, Alexei Pinchuk, and Chris Wilson. March 2015. Summer zoogeography of the northern Bering and Chukchi seas. Oral presentation at the University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, Juneau, Alaska, weekly seminar.

Mike Sigler, Franz Mueter, Bodil Bluhm, Morgan Busby, Ned Cokelet, Seth Danielson, Alex De Robertis, Lisa Eisner, Ed Farley, Katrin Iken, Kathy Kuletz, Bob Lauth, Libby Logerwell, Alexei Pinchuk, and Chris Wilson. February 2016. Summer zoogeography of the northern Bering and Chukchi seas. Oral presentation at the Alaska Fisheries Science Center (AFSC), Juneau, Alaska, AFSC seminar series.

Proposed Objectives and Study Chronology

Our study objectives were to 1) identify environmental factors that most influence assemblage distributions within the US portions of the Chukchi Sea shelf and northern Bering Sea shelf north of Nunivak Island (~60 °N [Stabeno et al., 2012]); 2) identify spatial gradients in assemblage composition; and 3) identify relationships among assemblages. We focus on four biological assemblages: zooplankton, pelagic fish and jellyfish, epibenthic fish and invertebrates, and seabirds.

This study synthesized data from other projects. Collaborations were developed before and during the Arctic Eis meeting held in Juneau, Alaska during June, 2014. Final versions of most data were received during mid-2014 and some during early 2015 (e.g., 2013 zooplankton, which has one year processing time). Initial analyses were conducted during mid-2014 and finalized during early 2015. The manuscript was submitted July 2015, reviews received October 2015, and revision completed during December 2015-January 2016. Data were submitted to Ocean Workspace during January 2016.

1. Abstract

Ocean currents, water masses, and seasonal sea ice formation contribute to determining relationships among the biotas of the Bering and Chukchi seas. The Bering Sea communicates with the Chukchi Sea via northward advection of water, nutrients, organic matter, and plankton through Bering Strait. We used summer abundance data from zooplankton, pelagic fish and jellyfish, epibenthic fish and invertebrates, and seabird surveys conducted concurrently during 2012 to identify the environmental factors that most influence distributions of biota within the US portions of the Chukchi Sea shelf and Bering Sea shelf north of Nunivak Island. Regional differences in summer distributions of biota largely reflected the underlying hydrography. Depth, temperature, salinity, stratification, and chlorophyll *a*, but not sediment-related or nutrient-related factors, had the largest influence on the distributions of assemblages. The assemblages were principally structured from nearshore to offshore and from south to north. The nearshore to offshore contrast usually is stronger in the south, where the enormous discharge of the Yukon River is more apparent and extends farther offshore, influencing zooplankton, pelagic fish/jellyfish, and seabird assemblages. Some assemblages overlapped spatially, indicating shared influential environmental factors or trophic linkages among assemblages. The gradients in assemblage composition were gradual for epibenthic taxa, abrupt for zooplankton taxa, and intermediate for pelagic fish/jellyfish and seabird taxa, implying that zooplankton assemblage structure is most tied to water mass, epibenthic least, with the other two taxa intermediate. Three cross-assemblage groupings (i.e., communities) emerged based on maps of ordination axes and core use areas by taxa; one associated with Alaska Coastal Water (warmer, fresher, nutrient depauperate), a second associated with Chirikov Basin and the southern Chukchi Sea (colder, saltier, nutrient rich), and a third associated with the northern Chukchi shelf. Gradients in species composition occurred both within and between these communities. The Bering Strait and southern Chukchi Sea community was characterized by distinct zooplankton and seabird taxa, but was not strongly associated with distinct pelagic or epibenthic fish and invertebrate taxa. Although comprehensive data were only available for a single year and annual variation may affect the generality of our results, our comprehensive ecosystem survey approach yielded new insights into the ecological relationships (specifically, on gradients in assemblage composition and identification of communities) of this Arctic region.

Key words: Bering Sea, Chukchi Sea, zoogeography, zooplankton, fish, invertebrates, seabirds

2. Introduction

This paper describes the integrated zoogeography of the northern Bering and Chukchi seas for zooplankton, fish, epifaunal invertebrates, and seabirds during the late summer open water season and identifies the environmental factors structuring these assemblages. The zoogeography of the northern Bering and Chukchi seas has previously been characterized for zooplankton (Hopcroft et al., 2010; Eisner et al., 2013; Ershova et al., 2015), pelagic fish and jellyfish (Eisner et al., 2013), epibenthic fish and invertebrates (Bluhm et al., 2009; Norcross et al., 2010, 2013; Ravelo et al., 2014; Logerwell et al., 2015) and seabirds (Piatt and Springer, 2003; Kuletz et al., 2015), as well as for macrofaunal benthos, which we did not include here (Feder et al., 2007; Petryashov et al., 2013). Our study is novel in that we characterize all four assemblages simultaneously. Another study (Sigler et al., 2011) also characterized these four assemblages simultaneously but used data collected from different, widely scattered years, whereas our study uses data collected in a single year (2012), except for epibenthic fish and invertebrate data for the northern Bering Sea, which was collected in 2010. This approach allows us to infer whether these four assemblages are linked to the same environmental factors or whether and how the influential factors differ among assemblages.

Understanding the environmental factors that influence the structure of these assemblages on a large, regional scale will provide insight into current assemblage structure and information for others to forecast community response to climate change. Changes in climatic conditions as well as biological production and faunal distribution patterns in the region have already been recorded for recent decades (Grebmeier et al., 2006; Mueter and Litzow 2008; Arrigo and vanDijken 2015), and are expected to continue (e.g., Hollowed et al., 2013). The simultaneous surveys of the four assemblages provide a benchmark for assessing climate effects as more surveys are conducted in the future. In the meantime, the simultaneous surveys also provide a space-for-time substitution as a temporary alternative to long-term studies (Pickett, 1989). Space-for-time substitution is one of the most common techniques in ecology and in general, is the extrapolation of a temporal trend from a series of different-aged samples (Pickett, 1989). In our application, latitude substitutes for time, with current states of southerly locations providing information on future states of northerly locations (i.e., as influenced by climate change (Blois et al., 2013)).

The faunal assemblages considered here are directly or indirectly influenced and/or characterized by the following five features. First, ice seasonally covers the northern Bering and Chukchi seas (Fig. 1), with the extent of the seasonal sea ice advance and retreat being the largest of any of the Arctic or subarctic regions, averaging ~1,700 km, while interannual variability has been as great as ~400 km, or ~25% of the seasonal range (Niebauer et al., 1999; Frey et al., 2014). Sea ice covers the northern Bering and Chukchi seas each winter, and by late summer, open water recurs over most or even all of these shelf regions. Second, the northern Bering Sea domain (Grebmeier et al., 2006; Sigler et al., 2011, Stabeno et al., 2012) and Chukchi shelf are strongly connected by Pacific origin waters flowing northward through Bering Strait, including nutrient-rich Anadyr Water near the Siberian coast, Bering Shelf Water, and nutrient-poor Alaska Coastal Water flowing northward along the Alaskan coast (Coachman et al., 1975; Woodgate et al., 2005a, b). Currents generally flow northward through Bering Strait due to differing sea-level heights between the North Pacific and Arctic oceans (Stigebrandt, 1984; Aagaard et al., 2006) and are thence topographically steered across the Chukchi along three primary pathways: Herald Canyon in the west, Barrow Canyon in the east, and the Central Channel in between (e.g., Weingartner et al., 2005). This flow pattern redistributes nutrients and algal production, organic carbon, organisms and hydrographic properties originating along the Bering slope and the central Bering shelf into the northern Bering and Chukchi seas (e.g., Walsh et al., 1989; Grebmeier et al., 2015). Third, while Bering Shelf Waters and Anadyr Waters mix in and downstream of Bering and Anadyr straits, a strong density front typically separates the Alaska Coastal Waters from the offshore waters both in the Bering Sea and farther north (Hunt and Harrison, 1990; Gawarkiewicz et al., 1994; Weingartner et al., 2005). In the northern Chukchi Sea, these two main water bodies encounter and interact with Arctic-origin waters with typically lower temperatures and somewhat different community dominants (e.g., Spall 2007; Petryashev et al., 2013). Fourth, as a result of the seasonal ice cover retreat and its effects on stratification in combination with the nutrient-rich waters over part of the study region, early blooms with relatively little grazing result in large export of *in situ* and advected pelagic production to the seafloor, allowing above-average benthic biomass to become established (e.g., Grebmeier et al., 2006). These are in part responsible for the characteristic feeding aggregations of marine mammal benthivores of the region (e.g., Jay et al., 2012). Fifth, fish populations and individual fish body sizes in the northern Bering and Chukchi Seas are very small compared to the southeastern Bering Sea or the similarly located Barents Sea, which support huge commercial fisheries (Hunt et al., 2013; Norcross et al., 2013). These patterns form the backdrop for biological community structure and their distribution across the study area on the large, regional scale, in addition to biological - such as trophic - interactions, which we focus less on here.

We chose environmental factors for analysis that previously have been shown to influence assemblages in the study region. The selected factors include temperature (Bluhm et al., 2009; Hopcroft et al., 2010; Norcross et al., 2010; Eisner et al., 2013; Ravelo et al., 2014; Ershova et al., 2015), salinity (Hopcroft et al., 2010; Norcross et al., 2010; Eisner et al., 2013), dissolved inorganic nitrogen (DIN) (Piatt and Springer, 2003; Eisner et al., 2013), mean water column stratification (Piatt and Springer, 2003), integrated chlorophyll (Piatt and Springer, 2003), total organic carbon (TOC) in sediments (Bluhm et al., 2009; Ravelo et al., 2014), and percent of silt and clay (% silt/clay) in sediments (Bluhm et al., 2009; Norcross et al., 2010). The physical environmental factors that we use in our analysis (temperature, salinity, and stratification) are known to be structured by regional circulation and wind stress (Danielson et al., 2014; Woodgate et al., 2012, 2005b), air-sea-ice heat fluxes (Drucker et al., 2003), ice retreat (Paquette and Bourke, 1981), water mass mixing (Woodgate et al., 2005a), coastal discharges (Aagaard et al., 2006), and topographic controls (Kinder et al., 1986; Weingartner et al., 2005; Woodgate et al., 2005a; Spall; 2007). The biochemical and geochemical environmental factors (DIN, Chl*a*, TOC, and % silt/clay) depend on the physical environment but also on the phytoplankton blooms, nutrient cycling, and grazing pressures (Walsh et al., 1989). Collectively these factors also characterize major aspects of the environment of the study area including the water column (temperature and salinity), sediment (TOC and % silt/clay), and productivity (DIN, stratification, and chlorophyll).

In our analyses, we first identify spatial gradients in assemblages and then determine the environmental factors most closely linked to these gradients and therefore presumably most influential in structuring these assemblages. This approach, known as indirect gradient analysis, first analyzes patterns in biological assemblages separately from patterns in the environment before examining the influence of environmental factors and has been applied in previous zoogeography analyses of the Chukchi and Bering seas (Bluhm et al., 2009; Ravelo et al., 2014). An alternative approach is to identify spatial gradients or spatial structure in the environment and then determine the associated assemblages. This approach also has been applied in previous zoogeography analyses of the Chukchi and Bering seas, which first identify discrete water masses and then determine the assemblages associated with each water mass (Hopcroft et al., 2010; Norcross et al., 2010; Eisner et al., 2013; Ershova et al., 2015). We chose our approach for two reasons. First, we chose an approach that focuses on spatial patterns in assemblages because these patterns are our primary interest. Second, the alternative approach typically begins with categorizing environmental data into discrete water masses. However water mass boundaries are typically indistinct (e.g., as noted earlier, Bering Shelf Waters and Anadyr Waters mix in and downstream of Bering and Anadyr straits), whereas treating the environmental data as continuous variables, as in our approach, avoids this issue. Thus, we first identify patterns in assemblages independent of water mass structure before quantifying links between these patterns and observed environmental gradients.

Our study objectives were to 1) identify environmental factors that most influence assemblage distributions within the US portions of the Chukchi Sea shelf and northern Bering Sea shelf north of Nunivak Island (~60 °N [Stabeno et al., 2012]); 2) identify spatial gradients in assemblage composition; and 3) identify relationships among assemblages. We focus on four biological assemblages: zooplankton, pelagic fish and jellyfish, epibenthic fish and invertebrates, and seabirds. We, thereby, expect to capture relevant environmental conditions both in the water column and at the seafloor.

3. Methods

The data were collected primarily in August-September 2012 from two vessels, with one vessel focused on conducting a bottom trawl survey and the other vessel focused on conducting zooplankton, surface trawl, and acoustic-midwater trawl surveys. The latter vessel also collected most of the environmental data used herein (physical, chemical and biological oceanographic) and included a seabird biologist to record seabird densities. In addition, a bottom trawl survey of the northern Bering Sea was conducted during August-September 2010 and a repeat set of the 2012 pelagic and environmental surveys was conducted in August-September 2013. As a result, we focus on the comprehensive 2010/2012 survey data and conduct only a limited comparison with the 2013 data.

The sampling design for the Chukchi Sea was based on a 56 km (30 nautical mile (nmi)) square grid pattern, resulting in a total of 73 sampling locations, that was occupied by both vessels. In the northern Bering Sea, the sampling design differed between the two vessels, which followed historical survey patterns established for the southeastern Bering Sea. For the vessel conducting multiple surveys (zooplankton, surface trawl, etc.), the sampling design was based on the same 56 km square grid pattern, resulting in a total of 39 stations. For the bottom trawl survey vessel, 142 sampling stations for the northern Bering Sea survey were selected from a northward extension of the 37 km (20 nmi) survey grid pattern established in 1982 for an annual bottom trawl survey of the eastern Bering Sea shelf (Lauth 2011). The latter vessel sampled more stations because station density was higher and also because a larger area of the northern Bering Sea was sampled (i.e., sampling extended further offshore). When analyzed alone, the full bottom trawl survey data set was included, but when compared to other data sets, only data within the area sampled by both surveys was included.

3.1. Environmental data

Our analyses included ten environmental variables: sea surface temperature, bottom (near-bottom water) temperature, sea surface salinity, bottom salinity, surface dissolved inorganic nitrogen (DIN), bottom DIN, stratification, water column integrated chlorophyll *a* (Chl*a*) concentration, sediment percent silt and clay (% silt/clay), and sediment total organic carbon (TOC) (Fig. 2). Data for the first eight variables were collected during 2010, 2012, and 2013 (Table 1). In contrast, data for the two sediment-related variables were collected during 1970-2012 (Grebmeier and Cooper, 2014). We selected more recent data, starting with 2006, when the annual sample rate increased. The 2006-2012 data were pooled in order to increase sample size, which varied annually (from 34 in 2011 to 154 in 2009). Pooling was reasonable because there was no apparent trend in either % silt/clay or TOC during this time period.

Conductivity-temperature-depth (CTD) measurements were collected with an RD Instruments Citadel CTD-NV during the 2010 bottom trawl survey and Sea-Bird (SBE) 911 or SBE 25 CTD to determine surface and bottom temperature and salinity in 2012 and 2013. The

Sea-Bird CTD was equipped with a Wetlabs Wet-Star fluorometer to estimate in vivo Chl*a* fluorescence. Water samples for nutrients (nitrate, nitrite, and ammonium) and Chl*a* were collected every 10 m during the upcast with Niskin bottles attached to the CTD. Nutrient samples were filtered through 0.45 µm cellulose acetate filters, frozen at -80 °C and analyzed at a shore-based facility using colorometric methods (JGOFS, 1994). Dissolved inorganic nitrogen (DIN) was estimated by summing nitrate, nitrite, and ammonium. Chl*a* samples were filtered through Whatman GF/F filters (nominal pore size 0.7 µm). Filters were stored frozen (-80 °C) and analyzed within 6 months with a Turner Designs (TD-700) bench-top fluorometer following standard methods (Parsons et al., 1984). *In vivo* fluorescence data, calibrated with discrete Chl*a* samples, were used to calculate water column integrated Chl*a*. Stratification (mean water column Brunt-Vaisala frequency) was calculated from the temperature and salinity measurements (Gill, 1982).

Several environmental variables were highly skewed and included a few large outliers. These characteristics could have a strong impact on subsequent correlation and regression analyses. Hence, we examined and, as necessary, transformed environmental variables to approximate normality by determining the best Box-Cox transformation (Box and Cox 1964) and choosing the closest 'natural' transformation (log, fourth-root, square-root). This improved the models substantially and revealed more fine-scale spatial structure, which was otherwise dominated by a few extreme values. The transformed variables were DIN ($\log_e$), stratification (fourth-root), Chl*a* ($\log_e$), and % silt/clay (square-root).

To visually examine environmental variability, we first mapped all environmental measures used in the analyses by predicting values over a regular grid that encompassed the sampling area. Interpolated values were estimated by fitting spatial Gaussian models to the data using ordinary or universal kriging. One very low salinity value at a nearshore station in Norton Sound was eliminated from this analysis to highlight patterns over the main sampling region, which mostly comprised offshore waters (> 20 m depth). Spatial autocorrelation was modeled using a spherical or exponential model with or without a nugget effect. The best fitting model for each variable was determined based on visually examining empirical and theoretical variograms and comparing fitted variograms based on the Akaike information criterion (AIC), following Diggle and Ribeiro (2007). All models were fit using the geoR package (Ribeiro and Diggle, 2001), version 1.7, in the statistical programming language R, version 3.1.2 (R Development Core Team 2014).

Most of these environmental data were collected concurrently at each station with two exceptions. The exceptions resulted in missing data and values were simulated to fill these gaps. Missing data were filled based on transformed values, when necessary. The first exception occurred when individual samples occasionally were missing due to some problem with these samples (e.g., collection equipment failure) (Table 1). Values for these missing data were estimated as follows: a general additive model (GAM) with Gaussian errors was fit to the available data (predicted mean = f(latitude, longitude) + g(depth), where f and g are smoothing splines with the degree of smoothing determined by cross-validation); missing values at a given location were then simulated by adding a random residual to the predicted mean for that location. Random residuals were drawn from a normal distribution with mean zero and variance equal to the estimated residual variance from the GAM. We used this algorithm to generate realistic values for missing observations rather than using predicted means in order to appropriately reflect uncertainty in further analyses (see, e.g., Little and Rubin, 2002). The second exception occurred for sediment samples, which were not collected concurrently with the 2010, 2012, or 2013 cruises. The percent silt/clay and TOC were matched with the other types of environmental data. Each location of concurrently collected environmental data was associated with the nearest sediment sample. If the nearest sample was more than 20 km distant, then the sediment-related values were estimated by the same method as used for missing data estimation. The sediment data had less spatial coverage than the other environmental data (Fig. 2); some extrapolated values may be biased because of the patchiness of the sediment data. Values were estimated for all missing data except for some bottom DIN values for 2010 (Table 1). No bottom DIN samples were collected for the outer shelf of the northern Bering Sea. Although samples were collected for the adjacent middle shelf, no values were estimated to substitute for the missing data for the outer shelf because the oceanographic characteristics of these two regions differ (Coachman 1986).

3.2. Biological assemblages

Zooplankton were sampled with a 60 cm MARMAP-style bongo frame with a 505 µm mesh net. Oblique tows from the surface to within 5 – 10 m of the bottom were conducted primarily during daylight hours. Volume filtered was measured with calibrated General Oceanics flowmeters mounted inside the nets. All samples were preserved in 5% formalin, buffered with seawater for later processing. In the lab, the mesozooplankton samples were processed as follows: each sample was poured into a sorting tray and large organisms, primarily shrimp and jellyfish, were removed and enumerated. The samples were then sequentially split using a Folsom splitter until the smallest subsample contained about 200 specimens of the most abundant taxa. All taxa in the smallest subsamples were identified, staged, enumerated and weighed. Each larger subsample was examined to identify, enumerate and weigh the larger, less abundant taxa. Blotted wet weights of all specimens of each taxa and stage in each sample were taken as outlined in earlier papers (Coyle et al., 2008, 2011) and the coefficient of variation in average wet weight was computed. If the coefficient of variation for any given taxa and stage changed by less than 5% when additional weights were taken from subsequent samples, wet weights were no longer measured for that taxa for that cruise, and the wet weight biomass was estimated by multiplying the specimen count by the mean wet weight. In practice, only calanoid copepods had consistent wet weights after weighing each taxa and stage in about 10-15 samples. Therefore, wet weights on chaetognaths, shrimp and other larger and soft-bodied taxa were measured and recorded for each sample. Wet weight measurements were done on a Cahn Electrobalance or Mettler top loading balance, depending on the size of the animal. All animals in the samples were identified to the lowest taxonomic category possible. Juveniles of various epibenthic gammarids were not identified to the species level and were grouped in one category Gammaridea. Sibling species *Calanus marshallae* and *C. glacialis* co-occurring in the Bering and Chukchi seas (e.g., Nelson et al., 2009) were not discriminated and are named as *C. marshallae* hereafter. Copepodid stages were identified and recorded. Catch per unit effort (CPUE) values by station were computed for each species in grams m^{-3} of filtered volume. Many adult euphausiids on the shelves of the Bering and Chukchi seas remain within 1 – 2 m of the bottom during the day (Coyle and Pinchuk, 2002) and those in the water column are difficult to quantitatively capture due to net avoidance (e.g. Sameoto et al., 1993; Wiebe et al., 2004); therefore, adult euphausiids were not included in the analyses.

Pelagic fish and jellyfish taxa were sampled with a midwater rope trawl with a mean horizontal spread of 55 m, configured to sample the top 15-20 m of the water column (Farley et al., 2007). The net had hexagonal mesh wings and a 1.2-cm mesh codend liner. Trawls were towed at 3.5 – 5 knots (6.5-9.3 km h^{-1}) for 30 min. The whole catch was immediately sorted to species (Mecklenburg et al., 2002) and counted. For large catches, a random subsample was sorted and counted, and results were extrapolated to estimate the total catch by taxon. Individual species were weighed in aggregate and counted, and then these numbers were expanded to the total catch weight. Catch per unit effort (CPUE) values by station were computed for each species (fish and invertebrate) in kilograms per hectare (1 ha = 10,000 m^2) and number of fish per hectare; area swept (ha) was computed as the distance towed multiplied by the mean net width.

Epibenthic fish and invertebrates were sampled with an 83-112 Eastern bottom trawl, which has a 25.3-m (83 ft) headrope and a 34.1-m (112 ft) footrope. Mesh sizes were 10.2 cm (4 in) in the wings and body and 8.9 cm (3.5 in) in the intermediate and codend. The codend also had a liner of 3.2 cm (1.25 in) mesh. Tow durations were 30 min during the northern Bering Sea survey and 15 min during the Chukchi Sea survey. Tow durations were shorter for the Chukchi Sea because this region has a greater biomass of epibenthic invertebrates and small fish compared to the Northern Bering Sea (Stevenson and Lauth, 2012); a longer tow would result in high numerical catches and would require subsampling, which would introduce more uncertainty into the abundance estimates. For both surveys, the tow was conducted near the center of the grid cell of the selected station when possible, and the vessel maintained a single heading during the tow. A bottom contact sensor (inclinometer/accelerometer) was used to assess the bottom tending performance of the net and to determine when the footrope was in contact with the seafloor. Net mensuration sensors were used to assess net performance and to provide net width data used to calculate the area swept by the bottom trawl. Total catches weighing less than 1,150 kg (2,500 lb) were placed directly onto a sorting table and the catch was sorted and enumerated in its entirety. Larger catches were weighed in aggregate and subsampled before sorting. After subsampled catches were sorted, individual species were weighed in aggregate and counted, and then these numbers were expanded to the total catch weight. Catches were sorted to the lowest taxonomic level practicable (Stevenson and Hoff, 2009; Mecklenburg et al., 2002). Mean catch per unit effort (CPUE) values by station were computed for each species (fish and invertebrate) in kilograms per hectare and number of fish per hectare; area swept (hectares) was computed as the distance towed multiplied by the mean net width.

Seabird surveys were conducted by US Fish and Wildlife Service (USFWS) biologists onboard the survey vessel conducting zooplankton and pelagic fish and invertebrate surveys in 2012 and 2013. To obtain estimates of seabird densities, visual surveys were conducted from the inside bridge using USFWS pelagic survey protocol (Kuletz et al., 2008). Surveys were conducted when the ship was underway and conditions were favorable (sufficient daylight to identify species and seas ranging from Beaufort Sea State 0 to 5). Transect width was occasionally truncated to 200 m or 100 m in a given transect if observation conditions (i.e., fog or swells) restricted visibility. The single observer used strip transect methodology, with 10x binoculars for identification, and recorded all birds on one side of the bridge within a 300-m arc, extending 90º from the bow to the beam. Birds were identified to species when possible or to genus, along with number of birds in each observation. Birds on the water were counted continuously, while flying birds were counted in instantaneous scans of the survey window at ~1 min intervals (depending on speed of the vessel) to avoid overestimating the density of flying birds (Tasker et al., 1984; Gould and Forsell, 1989). Observations were entered directly into a laptop computer using DLOG3 (Ford Ecological Consulting, Portland, OR) with a GPS interface. Along with each observation, location (latitude and longitude) was automatically recorded at 20-sec intervals to track survey effort. The surveyed transects were later divided into ~ 3-km segments to calculate bird density (birds km^{-2}), thereby correcting for effort but not for detectability of each species. The centroid of each 3-km segment was used to georeference estimated seabird densities for each segment. Approximately 12,000 km were surveyed over both years (2012 and 2013).

The data were compiled into tables for use in the analyses described in the next section. There was one table for each survey, totaling four tables (zooplankton, pelagic fish and jellyfish, epibenthic fish and invertebrates, and seabirds). Each data table was a station-by-taxon matrix of catch-per-unit-effort (CPUE) data in terms of weight (zooplankton (g m^{-3}), pelagic fish and jellyfish (kg ha^{-1}), epibenthic fish and invertebrates (kg ha^{-1})) or number (seabirds observed (number km^{-2})). Rare species that occurred at less than 5% of the total stations were excluded (McGarigal et al., 2000) as they can have a strong impact on the analysis (Poos and Jackson 2012). Our goal was to focus on broad spatial patterns rather than possible noise or local features that may be associated with rare species. This reduced the number of taxa for each assemblage from 53 to 35 zooplankton taxa, 77 to 29 pelagic fish and jellyfish taxa, 446 to 163 epibenthic fish and invertebrates taxa, and 48 to 23 seabird taxa. In addition, all CPUE data were fourth-root transformed to reduce the influence of a few high abundances.

3.3 Statistical analyses

We used multivariate analysis, regression, and correlation to 1) visualize spatial gradients in species composition; 2) determine which physical habitat characteristics structure the species assemblages; and 3) test if the species composition in a given assemblage was related to that in other assemblages.

3.3.1 Ordination of assemblages

We first conducted a nonmetric multidimensional scaling (NMDS) ordination separately for each of the four assemblages to reduce variability in the abundance of multiple taxa (23 to 163 taxa per assemblage) to two major modes, reflecting the dominant gradients in species composition across stations. Similarities in species composition between each pair of stations were quantified using the Bray-Curtis distance measure computed on the fourth-root transformed CPUEs (Bray and Curtis, 1957). The resulting matrix of Bray-Curtis dissimilarities was used as input for an NMDS ordination and goodness of fit was evaluated using Kruskal's stress criterion (Kruskal 1964). Stress values greater than 0.3 indicate that the configuration is no better than arbitrary and configurations should only be interpreted if stress values are less than 0.2, and ideally less than 0.1 (Clarke, 1993). Regardless of stress, all ordinations were conducted in two dimensions to allow for easy visual examination of the resulting ordination diagram. The computed NMDS scores ($NMDS_1$ along x-axis and $NMDS_2$ along y-axis) were used as indices of species composition in the subsequent analyses. We visualized the spatial patterns of the major gradients in the species composition of each assemblage by mapping the NMDS scores for each ordination axis. A total of 8 maps (4 assemblages x 2 NMDS axes) were constructed by fitting a smooth surface (thin-plate regression spline) to each set of NMDS scores as a function of latitude and longitude. Regression splines were fit using a general additive modeling (GAM) approach to determine the optimum amount of smoothing (Wood, 2006). These NMDS scores reflect the turnover of species along a continuous gradient.

In order to interpret these gradients, we fit linear and Gaussian (dome-shaped) regressions between the CPUEs of individual species and each ordination axis to identify the species that were most strongly associated with each axis, which we termed “indicator species”. The best-fitting model was selected based on the AIC, goodness of fit was quantified using the coefficient of determination (R^2), and the model was compared to the null model (no relationship) using an F-test. Species were selected as “indicator species” if the best-fitting model was significant ($p < 0.05$) and explained at least 20% of the variability in CPUE ($R^2 > 0.2$). The “core use area” of the indicator species was defined by the NMDS scores that encompassed the middle 50% of the area under the fitted curve (i.e., the highest CPUE values); the “core use area” is a measure of niche space for these indicator species.

We applied a second ordination method, correspondence analysis (CA), which provides a measure of the proportion of variability in the underlying CPUE data that is captured by each ordination axis (Greenacre 1984). NMDS based on Bray-Curtis dissimilarities is an appropriate ordination method to summarize the species composition of assemblages consisting of many species, most of which may be absent from the majority of stations (Clarke, 1993), but cannot provide a meaningful measure of the proportion of this variability in the underlying CPUE data that is captured by each ordination axis. CA was performed on each of the station-by-species matrices and the first two CA axes were qualitatively compared to the NMDS results (visual comparison of ordination diagrams and spatial patterns) and were generally found to be very similar. Therefore, we used CA to quantify the proportion of overall variability in the CPUE data that was accounted for by the first two CA axes as a proxy for the proportion of variability that can be captured by two dominant modes of species composition. We note that even if this proportion is low, much of the interpretable information in the station-by-taxon matrices may be contained in the first two axes because CPUE data typically have a low signal to noise ratio.

3.3.2 Environmental factors structuring biological assemblages

We examined relationships between the species composition of each assemblage and relevant environmental variables using several approaches to determine the drivers structuring each biological assemblage. In the analyses, depth, surface water characteristics (temperature, salinity, DIN) and integrated Chl*a* were used to examine relationships with zooplankton, pelagic fish and jellyfish, and seabird assemblages, while depth, bottom water characteristics (temperature, salinity, DIN), and sediment characteristics (TOC, % silt/clay) were included in analyses involving the epibenthic assemblage.

First, we examined relationships visually by constructing biplots depicting the relationship between each environmental variable and the ordination axes. In these biplots, environmental variables are displayed as vectors originating from the center of the ordination diagram and the projection of a given environmental vector on a given ordination axis reflects the correlation between the environmental variable and the NMDS scores. Therefore, the length of a given vector provides a relative measure of the importance of the corresponding variable in structuring the assemblage.

Second, we used a canonical correlation analysis to test the overall significance of the relationship between each biological assemblage and the full set of relevant environmental variables. This test finds the linear combination of environmental variables that maximizes the correlation with a linear combination of the $NMDS_1$ and $NMDS_2$ scores and uses a permutation test to assess its significance (Legendre 2005). The analysis also provides a measure of the proportion of variability in species composition that is accounted for by the full set of explanatory variables, known as the canonical coefficient of determination or canonical R^2. We used the bias-adjusted version of the canonical R^2 recommended by Peres-Neto et al. (2006). The correspondence analysis also was used as a proxy for the proportion of variability captured by the two dominant modes of species composition in NMDS.

Third, if we found an overall significant relationship between environmental variables and NMDS scores, we determined which variables were most strongly related to the observed differences in species composition among stations using the BIO-ENV procedure (Clarke and Ainsworth, 1993). For this procedure, we computed rank-based correlations between all pairwise station dissimilarities based on environmental variables (Euclidean distances) and all pairwise station dissimilarities based on species abundances (Bray-Curtis distances), also known as Mantel correlations. We then identified the subset of variables that maximized these Mantel correlations using the BIO-ENV procedure as implemented in the ‘vegan’ package for R (Oksanen et al., 2015). For each biological assemblage, we present the subsets of the “best” 1, 2, 3, etc., environmental variables that resulted in the highest correlation with the pairwise biological dissimilarities. This procedure was considered exploratory (no significance test is available) and was used to identify potentially useful explanatory variables to consider in more detailed analyses.

Finally, we examined and quantified relationships between the two NMDS scores and selected environmental variables using a multiple regression approach. We modeled the $NMDS_1$ and $NMDS_2$ scores as a function of the explanatory variables identified in the BIO-ENV procedure. We used GAM regressions with a cubic spline smoother to allow for potential nonlinearities in the relationships, but constrained the smooth functions to biologically realistic forms (maximum of three degrees of freedom allowing for linear, dome-shaped, asymptotic and sigmoidal relationships). We fit models using all and selected subsets of the explanatory variables and determined the best model using a generalized cross-validation criterion (Wood, 2006) to determine the degree of smoothing and using the AIC to determine the subset of variables to include.

3.3.3 Relationships among biological assemblages

To identify relationships among the four biological assemblages, we used canonical correlation analyses as described above. Canonical correlations were computed between the NMDS scores of a given assemblage and those of each of the other three assemblages. We estimated the proportion of variability in one assemblage (the “response” assemblage) that can be explained by variability in another assemblage (the “explanatory” assemblage) using the adjusted canonical R^2 as described above and assessed the significance of the relationship between their respective species compositions using a permutation test (Legendre 2005). We only considered relationships that reflect “bottom-up” processes (e.g., seabirds responding to zooplankton variability), with the exception of the relationship between the pelagic fish and jellyfish and epibenthic fish and invertebrates assemblages, which was quantified in two ways with either assemblage explaining variability in the other.

4. Results

We focus on the results of the 2012 surveys combined with the 2010 survey of epibenthic taxa for the northern Bering Sea, which were not sampled in 2012. For brevity, we refer to these samples as the “2012 surveys”. The results of the 2013 surveys are compared with the 2012 surveys in the last section of the results, section 3.5, and are not presented elsewhere in this paper.

4.1. Environmental data

Water mass analysis (Danielson et al., this volume) identified five distinct temperature-salinity modes that encompassed all observed water types in the survey. These included 1) cool and low-salinity waters influenced by ice melt, 2) warm and low-salinity waters influenced by coastal discharges and heating in shallow water depths, 3) cold waters remnant from the previous winter, 4) salty waters influenced by Atlantic water in the Arctic basin, and 5) waters with intermediate temperatures and salinities that encompass Anadyr, Bering, and Chukchi shelf summer waters. Temperatures were higher and salinities were lower in the shallow, nearshore zone (Fig. 2), reflecting the influence of coastal discharges and other freshwater in the Alaska Coastal Current and the ability of solar radiation to induce greater warming in shallow waters. Bottom DIN also was lower nearshore, reflecting the presence of the nutrient-depleted Alaska Coastal Waters. Over the northeastern Chukchi shelf, this pattern changed and bottom and surface temperatures were colder and bottom salinity and DIN were higher everywhere except immediately adjacent to the Alaska coast, reflecting the presence of Chukchi Winter Water (Weingartner 1997). In this region, cool temperatures and low surface salinities indicate the influence of ice melt. Stratification generally was highest where surface salinities were low, likely due to runoff in the coastal waters of Norton Sound and eastern Bering Strait and due to ice melt water on the northern Chukchi shelf. Surface DIN and integrated Chl*a* concentration were highest north of St. Lawrence Island and within Bering Strait, particularly on the less stratified western side. These elevated values likely were due to vertical mixing of nutrient-rich Anadyr water created by water funneling between land masses (e.g., Bering and Anadyr straits separating Russia and Alaska).

4*.2. Ordination of assemblages*

The two major NMDS axes captured much of the variability in the underlying CPUE data for the four assemblages. These two axes accounted for 23-38% of the variability (Table 2), based on correspondence analysis (CA), which was used as a proxy for the proportion of variability captured by the two NMDS axes. Based on this result, we conclude that the NMDS ordination is a suitable tool for examining the structure of these four assemblages. Overall, the spatial patterns of the two major modes of species composition (NMDS axes) indicated that the assemblages were principally structured from nearshore to offshore and from south to north (Fig. 3).

For the zooplankton assemblage, $NMDS_1$ scores were higher associated with Alaska Coastal Water and were lower in the Chirikov Basin and Chukchi Sea (Fig. 3). $NMDS_1$ showed strong relationships with 17 species (termed indicator species, as defined in the methods), with two distinct groupings of species (Fig. 4a). Twelve indicator species were related to negative $NMDS_1$ scores and were associated with the Chirikov Basin and Chukchi Sea. This first grouping was clearly separated from five indicator species which were related to the highest positive values and were associated with the Alaska Coastal Water (see Appendix for species distribution maps of indicator species). $NMDS_2$ scores showed strong relationships with seven species, again with two distinct groupings of species. Five indicator species were related to negative $NMDS_2$ scores and were associated with the Chirikov Basin and southern Chukchi Sea. This first grouping was clearly separated from two taxa which were related to positive values (Fig. 4a) and were associated with the northern Chukchi Sea. Together these results (Fig. 3 and 4a, Appendix) imply an assemblage affiliated with the Alaska Coastal Water, a Chirikov Basin and southern Chukchi Sea assemblage, and a northern Chukchi Sea assemblage (parsed from the Chirikov Basin and Chukchi Sea grouping for $NMDS_1$).

For the pelagic fish and jellyfish assemblage, $NMDS_1$ values were higher northward and $NMDS_2$ values were higher offshore, except in Norton Sound where $NMDS_2$ values also were higher nearshore (Fig. 3). $NMDS_1$ showed strong relationships with nine species (Fig. 4a). The $NMDS_1$ scores reached the lowest negative values for three indicator species, intermediate negative values for four indicator species and positive values for two indicator species. The first group of indicator species is associated with Alaska Coastal Water as is the second group which occurs somewhat farther from shore. In the third group, *Chrysaora melanaster* is widespread. $NMDS_2$ also showed strong relationships with seven species and some grouping of species. The $NMDS_2$ scores were negative for six indicator species which were associated with the eastern Bering Sea. The $NMDS_2$ were positive for one indicator species (the jellyfish *Cyanea capillata*) which was widespread. Arctic cod (*Boreogadus saida*) commonly was caught but was not selected as one of the indicator species because the best-fitting model explained less than 20% of the variability in CPUE ($R^2 < 0.2$). Together these results imply an assemblage associated with the Alaska Coastal Water, and a eastern Bering Sea assemblage (Fig. 3 and 4a, Appendix). The jellyfish species, except for *Aurelia* sp., which is associated with the Alaska Coastal Water, exhibited the widest core use areas (Fig. 4a).

For the epibenthic fish and invertebrate assemblage, $NMDS_1$ values were higher offshore and $NMDS_2$ values were higher southward (Fig. 3). $NMDS_1$ showed strong relationships with 54 species, but unlike the previous assemblage types (zooplankton, pelagic fish and jellyfish), which showed comparatively clear grouping of species, the epibenthic taxa were characterized by a gradual turnover along a gradient of $NMDS_1$ values (Fig. 4b), implying a lack of distinct assemblages or at least strong species overlap between them. The only grouping of numerous species sharing a common core use area was at the highest positive values with about 20 indicator species falling into this group. $NMDS_2$ showed strong relationships with 45 species, with a gradual turnover along the $NMDS_2$ gradient like for $NMDS_1$, but with some grouping of species for the highest positive values (a group of about 20 species) and for the lowest negative values (a group of about 10 species). For the epibenthic taxa, examining the species distribution maps (which are ordered by NMDS axes values) revealed some striking patterns (Appendix). The negative $NMDS_1$ values were associated Alaska Coastal Water. The positive $NMDS_1$ values were associated with an offshore assemblage in both the northern Bering and Chukchi seas (e.g., the crab species *Chionoecetes opilio*) or exclusive to the northern Bering Sea (e.g., Greenland halibut (*Reinhardtius hippoglossoides*)). These Greenland halibut were juveniles and adults whereas the Greenland halibut found nearshore during pelagic sampling were larvae. The negative $NMDS_2$ values were associated with a typically Chukchi Sea assemblage (e.g., the anemone *Urticina crassicornis*) but also found on the northern Bering Sea (e.g., the sea star *Crossaster papposus*). The positive $NMDS_2$ values were associated with a northern Bering Sea assemblage, which most often is exclusive to the northern Bering Sea (e.g., arrowtooth flounder), but not always (e.g., the sea star *Ctenodiscus crispatus*). As for the pelagic fish and jellyfish assemblage, Arctic cod commonly was caught but was not selected as one of the indicator species because the best-fitting model explained less than 20% of the variability in CPUE ($R^2 < 0.2$). Together these results imply a nearshore assemblage affiliated with the Alaska Coastal

Water, a northern Bering Sea assemblage, and a Chukchi Sea assemblage (Fig. 3 and 4b, Appendix).

For the seabird assemblage, $NMDS_1$ values were higher near the Chukchi shelf break as well as nearshore in Norton Sound and southward, whereas these values were lower in Chirikov Basin and the southern and central Chukchi Sea; $NMDS_2$ values generally were lower associated with Alaska Coastal Water (Fig. 3). $NMDS_1$ showed strong relationships with eight species but only with negative $NMDS_1$ values (Fig. 4c). The positive values in both Norton Sound and the northern Chukchi were not strongly associated with any particular species, thus $NMDS_1$ primarily defines a Chirikov Basin and southern Chukchi Sea assemblage. The core use areas mostly overlapped except that short-tailed shearwater (*Puffinus tenuirostris*) was shifted towards less negative values indicating limited overlap with the other indicator species. $NMDS_2$ values showed strong relationships with only two species, with black-legged kittiwake (*Rissa tridactyla*) abundant at the most negative values of the $NMDS_2$ gradient and crested auklet (*Aethia cristatella*) most abundant at positive $NMDS_2$ values. The black-legged kittiwake were associated with the nearshore. Together these results imply an assemblage affiliated with the Alaska Coastal Water and a Chirikov Basin and southern Chukchi Sea assemblage (Fig. 3 and 4c, Appendix).

4.*3. Environmental factors structuring biological assemblages*

The NMDS axes for each of the four assemblages were significantly related to the full set of environmental variables, based on canonical correlation analysis ($p < 0.0001$, Table 3), indicating that these environmental variables substantially influence the structure of the four assemblages. The environmental variables explained from 41% to 59% of the variability in species composition as captured by the NMDS ordination, depending on the assemblage, based on the adjusted canonical R^2.

For the zooplankton assemblage, depth, sea surface temperature, sea surface salinity, and stratification were strongly correlated with the NMDS axes (Fig. 5). However, because depth and temperature are fairly strongly correlated (Pearson's correlation = -0.579), the combination of environmental variables that resulted in the highest rank-based Mantel correlation with the zooplankton assemblage were depth, surface water salinity, and stratification (Mantel's r =

0.536, Table 4). Substituting temperature for depth resulted in a similar correlation (Mantel's *r* = 0.504), but the zooplankton assemblage varied more strongly along the depth gradient (Mantel's *r* = 0.414 when only depth is included) than along the surface water temperature gradient (Mantel's *r* = 0.213 when only temperature is included). The best GAMs of NMDS scores confirmed that the zooplankton assemblage varied strongly and in nonlinear ways along gradients of depth, sea surface salinity, and stratification, which accounted for 71% and 15% of the variability in NMDS axes 1 and 2, respectively (Fig. 6 and 7).

For the pelagic fish/jellyfish assemblage depth, sea surface temperature, DIN, and stratification were strongly correlated with one or both NMDS axes (Fig. 5), while depth, stratification, and Chl*a* resulted in the highest Mantel correlation (Table 4). The best GAMs of NMDS scores confirmed that the pelagic assemblage varied strongly and in nonlinear ways along gradients of depth, stratification, and Chl*a*, which accounted for 66% and 15% of the variability in NMDS axes 1 and 2, respectively (Fig. 6 and 7).

For the epibenthic assemblage depth, bottom temperature and salinity, and % silt/clay were most strongly correlated with the NMDS axes (Fig. 5). Similarly, the same variables had the highest Mantel correlations with the assemblage metrics (Mantel's *r* = 0.573, Table 4). However, only bottom water temperature entered the best GAMs and accounted for 66% and 16% of the variability in NMDS 1 and 2, respectively (Fig. 6 and 7).

For the seabird assemblage depth, sea surface temperature, sea surface salinity, and integrated Chl*a*, were most strongly correlated with the NMDS axes (Fig. 5), while depth, sea surface temperature, sea surface salinity, and stratification had the highest Mantel correlation (Mantel's *r* = 0.337, Table 4). Of these, the best GAMs of NMDS scores confirmed that the seabird assemblage varied strongly and in nonlinear ways along gradients of sea surface temperature, sea surface salinity, and mean stratification, but not depth or integrated Chl*a*, which accounted for 17% and 49% of the variability in NMDS axes 1 and 2, respectively (Fig. 6 and 7).

Overall, six environmental variables demonstrated a substantial influence on the structure of the four assemblages, based on the best GAM models (Fig. 6 and 7). These six were bottom depth, sea surface temperature, bottom temperature, sea surface salinity (but not bottom salinity), stratification, and integrated Chl*a* (Fig. 8). The relationships are correlative; possible mechanisms are described in the discussion. The sediment-related environmental variables (TOC, % silt/clay) and surface and bottom DIN were excluded from the best GAM models. In addition, environmental variables accounted for less of the variability in the seabird assemblage metrics than in the other assemblages (smaller Mantel's r, smaller R^2 of GAMs).

4.4. Relationships among biological assemblages

There was significant and substantial shared variability among the zooplankton, pelagic fish/jellyfish, and epibenthic assemblages (adjusted canonical $R^2 > 0.46$, Table 5). In contrast, the seabird assemblage was significantly but weakly linked to the other assemblages (adjusted canonical $R^2 < 0.26$, Table 5). This analysis suggests that the zooplankton assemblage substantially influences the pelagic fish/jellyfish and epibenthic assemblages, and that the pelagic fish/jellyfish assemblage substantially influences the epibenthic assemblage, and vice versa (Fig. 8). Thus, for example, the environmental factors of bottom depth, stratification, and Chl*a* and the biological assemblages of zooplankton and epibenthic fish and invertebrates demonstrated a substantial influence on the pelagic fish/jellyfish assemblage. Because these relationships are correlative (i.e., not necessarily mechanistic), the two-way relationship between the pelagic and epibenthic assemblages may be due to shared effects of environmental factors and the zooplankton assemblage, rather than direct interactions of these two biological assemblages, or a combination of the two.

4.5. Comparison with 2013

We tested whether the same environmental factors influenced distributions of biota and whether the same same relationships among assemblages occurred in 2013 (excluding the epibenthic assemblage that was not sampled in 2013). In 2013, as in 2012, the NMDS scores for each of the three assemblages had a statistically significant relationship with the full set of environmental variables, based on canonical correlation analysis ($p < 0.0001$). In 2013, the environmental variables explained from 29% to 57% of the variability in NMDS scores, depending on the assemblage, based on the adjusted canonical R^2 (Table 3). More of the variability in NMDS scores was explained in 2012 than 2013 for pelagic (41% vs. 30%) and seabird (49% vs. 34%) taxa whereas explained variability for zooplankton taxa was the same in 2012 and 2013 (57%).

More variability was explained by the combination of environmental variables that resulted in the highest rank-based Mantel correlation in 2012 than 2013 (Mantel's $r = 0.536$ in 2012 and 0.406 in 2013 for zooplankton taxa, 0.434 vs 0.307 for pelagic fish / jellyfish taxa, and 0.335 vs. 0.222 for seabird taxa, Table 4). The best set of explanatory variables, while not identical in 2012 and 2013, shared one to three variables. Zooplankton taxa shared three of the best set variables in 2012 and 2013 (depth, mean stratification, and surface salinity), as did seabird taxa (surface temperature, surface salinity, and mean stratification). While the pelagic fish / jellyfish assemblage shared only one variable in 2012 and 2013 (Chl*a*), the Mantel's *r* value for the best set of explanatory variables identified for 2012 (0.254) was only slightly less than the Mantel's *r* value for the best set of explanatory variables identified for 2013 (0.307). In 2013, as in 2012, there was significant shared variability among the zooplankton, pelagic fish / jellyfish, and seabird assemblages, based on the adjusted canonical R^2 ($p < 0.0001$, Table 5). Explained variability ranged from 11% to 51% in 2012, and 26% to 34% in 2013, for the relationships among these three assemblages (Table 5). We conclude that these environmental and trophic relationships held in 2013 as in 2012, but often less variability was explained in 2013.

5. Discussion

5.1. Influential environmental factors

The environmental factors that most influenced distributions of zooplankton, pelagic fish/jellyfish, epibenthic, and seabird assemblages included water depth, sea surface and bottom water temperature, sea surface salinity, stratification, and Chl*a* (Fig. 8). Not all six factors influenced each assemblage; from one to three factors of these six influenced each assemblage, with connections based on the best GAM models. Depth influenced the zooplankton and pelagic fish/jellyfish assemblages, but not the epibenthic or seabird assemblages. Temperature and salinity together characterize water mass and one or both influenced three of four assemblages (except pelagic) in the Mantel correlations and the GAM models. The strength of stratification or Chl*a* influenced three of four assemblages (all except epibenthic). Only the epibenthic assemblage was strongly influenced by sediment grain size, but only in the Mantel correlations and not the GAM models.

The factors of temperature, salinity, and/or water mass have been cited commonly as structuring factors for zooplankton (Hopcroft et al., 2010; Eisner et al., 2013; Ershova et al., 2015), epibenthic fish and invertebrates (Bluhm et al., 2009; Norcross et al., 2010; Blanchard et al., 2013a, b), and seabird (Piatt and Springer, 2003; Gall et al., 2013) assemblages. Some water mass-zooplankton associations reflect populations transported from elsewhere, such as the transport of Bering Slope-Anadyr Water into Bering Strait (Piatt and Springer, 2003; Hopcroft et al., 2010; Eisner et al., 2013). When large zooplankton are transported, seabirds also may concentrate and forage at these locations (Piatt and Springer, 2003; Gall et al., 2013; Kuletz et al., 2015). Zooplankton species composition and population size also may reflect annual effects of temperature variation on primary and secondary productivity (Ershova et al., 2015). Although temperature or salinity were not classified as influential for the pelagic fish and jellyfish assemblage, Eisner et al. (2013) also found that the best correlation between pelagic fish assemblage structure and several environmental variables excluded temperature and salinity. Instead we found that Chl*a* and stratification were more influential and Eisner et al. (2013) found that latitude was more influential. Assemblages of small epibenthic fishes in the Chukchi Sea, however, are influenced by bottom salinity and bottom temperature as well as by sediment type (Norcross et al., 2010), which may arise from the effects of topography on northward-flowing water, that create regions of slower currents, and consequently, higher organic deposition (Blanchard et al., 2013a, b).

Salinity appeared as a major structuring force for the zooplankton assemblage. The best-fitting GAM models included salinity for both axes 1 and 2; in particular, the GAM for salinity varied particularly strongly along $NMDS_1$ (Fig. 6), reflecting a strong contrast between nearshore, neritic species and typical shelf or oceanic species (Fig 4a). $NMDS_2$ values also strongly decreased at salinities over about 29 (Fig. 7), reflecting the contrast between a assemblage associated with low-salinity meltwater in the northern Chukchi Sea (characterized by *Clione limacina* and Gammaridea) and more saline Pacific waters associated with *Neocalanus* spp., Euphausiacea and *Eucalanus bungii* (Fig. 3 and 4a). Salinity (bottom salinity, in particular) also was a strong structuring variable for zooplankton assemblage composition in September 2007 in the Chirikov Basin and eastern Chukchi Sea (Eisner et al., 2013) and across the Chukchi Sea between 2004-2012 (Ershova et al., 2015). The influence of salinity on the zooplankton assemblage structure is based on the tight linkage between salinity and macronutrients in the productive Anadyr Waters (and the associated Anadyr flow field), in comparison to the less productive Alaska Coastal Waters (Springer and McRoy, 1993). The high macronutrient concentration in turn results in high Chl*a* concentrations that represent the standing crop of phytoplankton and thus reflect the difference between primary production and grazing (correlations for the Arctic in Matrai et al., 2013).

The strength of stratification or Chl*a* influenced three of four assemblages (all except epibenthic). Stratification often influences primary production; early in the year some initial level of stratification is necessary to increase production in the surface layer and trigger the spring phytoplankton bloom. When (or where) nutrients are depleted from the upper water column, strong stratification can reduce production by limiting the vertical fluxes of nutrients into the euphotic zone (Li et al., 2009). Chl*a* (a measure of phytoplankton standing stock) reflects production mediated by stratification; this standing stock influences zooplankton distribution, as we found. Stratification also may influence higher trophic levels, such as the seabird assemblage, by concentrating prey near the surface or just below the pycnocline, as well as through the physical forcing and accumulation of plankton (and fish that prey on them) at the layer boundaries or fronts (Hunt et al., 1990; Decker and Hunt 1996; Mehlum et al., 1998; Gall et al., 2013). Nutrients (DIN) also influence primary production but no statistically significant effect was found for any assemblage in either the GAMs or the Mantel correlations. This likely occurred because the influence of DIN is indirect and thus masked by the more direct influence of Chl*a*.

The depth range in the study area is very small in absolute terms yet highly influential on both the assemblage structure and the flow field. A change in seafloor depth of only 10 m represents 20% to 50% of the total water depth over most of the survey area. Vorticity and continuity constraints associated with such large relative changes in water column depth are sufficient to exert dominant control over the low frequency circulation field (Spall, 2007) and influence the distribution of water masses, sediment grain size, and organic carbon content in the region, thereby playing a leading role in at least epibenthic assemblage structure (Blanchard et al., 2013 a, b).

Bottom substrate type as characterized by silt fraction and organic content did not enter the GAM models, but was an influential environmental variable for the epibenthic assemblage in the maximum rank-based Mantel correlations. Distributions of sediment-related factors did not directly match the distribution of water masses as characterized by the temperature and salinity distribution; rather the distributions of sediment-related factors are more closely linked to the current velocity field (Grebmeier et al., 2015), although the latter was not included in this study. TOC and % silt/clay were higher southwest of St. Lawrence Island and on the south-central and northeastern Chukchi shelf than in the Chirikov Basin and southeast of St. Lawrence Island (Fig. 2). Sediment grain size was also generally coarse nearshore (Grebmeier et al., 2006; see also region-wide trend in source data: Grebmeier and Cooper, 2014). This characterizes the south-central and (part of the) northeastern Chukchi shelf as depositional areas. This finding confirms previous studies in the northern Bering and Chukchi seas that also found substrate type to be moderately influential (Bluhm et al., 2009; Cui et al., 2010; Norcross et al., 2010; Blanchard et al., 2013a, b; Ravelo et al., 2014).

This relationship can be explained through at least two mechanistic connections. One functional connection is a trophic one whereby the distribution of macrofaunal prey of demersal fish and epifauna are in part structured by grain size and sediment organic content (Feder et al., 1994). Extensive diet analysis of demersal fishes from the 2012 survey showed, for example, that the common Arctic staghorn sculpin primarily consumed epibenthic amphipods (Gray, 2015), and snow crab prey commonly included infaunal bivalves, amphipods and polychaetes (Divine et al., this issue). The sediment-association tends to be less strong for non-sedentary epifauna and demersal fish than for sedentary infauna because of the higher mobility of the former epibenthic component. The second connection between substrate and epibenthic assemblage structure is strong for certain invertebrate taxa and is habitat-related in that large-grained sediment such as gravel and boulders provide substrate for taxa that need attachment, in particular filter-feeders such as sponges and ascidians. Such hard bottom habitat tends to be available in areas of high current flow such as Bering Strait, in Barrow Canyon, and under sections of the Alaska Coastal Current, and increases epibenthic species richness in areas where hard substrate is available (Mayer et al., 1996; Bluhm et al., 2009). This large grain size fraction of the substrate, however, was not included in the environmental variables considered in the present study and may be part of the reason sediment grain size was excluded in the best-fitting GAM models. It should also be noted that the spatial coverage of sediment data did not match the survey grid and was less extensive than the assemblage sampling, and as a result, part of the sediment values were extrapolated over sometimes large distances, possibly missing small-scale variability and thereby leading to errors.

Thus, the six influential environmental factors that most influenced distributions of zooplankton, pelagic fish/jellyfish, epibenthic fish and invertebrate, and seabird assemblages likely can be simplified to three factors reflecting bottom depth, water mass and their stratification and productivity (which are tightly linked in the study region). Combined, these factors influence prey availability to the ecosystem components analyzed here. Their influence can be explained by mechanistic connections. Water mass transports organisms from elsewhere (e.g., transport of Bering Slope-Anadyr Water into Chirikov Basin) and also reflects *in situ* processes such as temperature-metabolism effects and temperature preferences (e.g., Laurel et al., 2015). Depth also influences temperature (deeper typically colder) and thus the same temperature-related effects. The influence of Alaska Coastal Water, which is warmer, fresher, and nutrient-poor (Springer and McRoy, 1993), also is expressed as a depth effect (i.e., coastal thus shallower water). Stratification influences productivity, in spring to trigger the spring bloom and later to limit vertical nutrient fluxes, and thus food availability for zooplankton and in turn for planktivorous fish and seabirds. The implication for future studies is that these three environmental factors should be a focal point for system-level evaluations.

5.2. Zoogeographic Gradients

The ordination of assemblages was principally structured from nearshore to offshore and from south to north (Fig. 3). This pattern is most obvious for the epibenthic assemblage, with $NMDS_1$ values consistently increasing from nearshore to offshore and $NMDS_2$ values consistently decreasing from south to north. $NMDS_1$ values also exhibit an obvious north-south gradient for the zooplankton and pelagic fish/jellyfish assemblages. The nearshore to offshore contrast usually is stronger in the south, where the enormous discharge of the Yukon River is more apparent and extends farther offshore (e.g., Danielson et al., this volume); for example $NMDS_1$ values are higher nearshore and south for the zooplankton, pelagic fish/jellyfish, and seabird assemblages. For the seabird assemblage, $NMDS_1$ values are also high near the Chukchi shelf break, which is consistent with identified ‘hotspots’ in this area for some seabird species, particularly shearwaters, black-legged kittiwakes and other surface feeding birds (Kuletz et al., 2015). Surface feeding seabirds are known to aggregate near shelf breaks, where upwelling concentrates prey (Yen et al., 2006; Hunt et al., 2014).

Zooplankton assemblage structure was strongly tied to water masses, whereas epibenthic assemblage structure was much less so; seabird and pelagic fish/jellyfish assemblages were intermediate. This conclusion is based on the gradients in assemblage composition, which were gradual for epibenthic taxa, abrupt for zooplankton taxa, and intermediate for pelagic fish/jellyfish and seabird taxa (Fig. 4). These patterns are logical consequences of differences in lifestyle, motility and degree of water mass-association of the four assemblages. The turnover of epibenthic indicator species (as evident in core use area) was very gradual, especially for $NMDS_1$ (Fig. 4b), which implies epibenthic assemblages with broad distribution ranges and transitions, facilitated by the advective character of the study area that transports meroplanktonic stages across the northern Bering and Chukchi seas. Adult epibenthic invertebrate assemblages are relatively stable in their spatial distribution and do not get carried with water masses, so compared with zooplankton and other pelagic assemblages, these assemblages are unable to adjust to short-term (e.g., seasonal) or medium-term (interannual) variations in water mass characteristics and instead reflect the long-term integration of water mass spatial distributions. epibenthic invertebrates are also typically quite long lived and as such they can integrate over these multiple years of environmental variation (Carroll et al., 2011). While epibenthic (especially infaunal) biomass strongly reflects water mass properties and processes (e.g., Grebmeier et al., 2006), the connection between water mass and epibenthic assemblage structure is less tight (Bluhm et al., 2009).

Species composition for all assemblages gradually transitioned from nearshore to offshore and from boreal and boreal-Arctic to Arctic species. This pattern agrees with previous ecological, taxonomic and biogeographic studies that found large overlap of epibenthic fish and invertebrate species occurrence across the Pacific Arctic, though with different proportions within the assemblages (Sirenko 2001; Feder et al., 2005; Grebmeier et al., 2006; Bluhm et al., 2009; Mecklenburg et al., 2012; Eisner et al., 2013). Within the study region, the northern Bering and southern Chukchi seas have higher proportions of boreal taxa, in part of Pacific origin, while the northern Chukchi Sea has large proportions of Arctic and boreal-Arctic fauna with exact boundaries debated and probably variable over time and between taxa (Mironov 2013; Petryashov et al., 2013).

In contrast to the other assemblages, zooplankton indicator species were distinctly grouped along both axes (Fig. 4a). This implies that zooplankton taxa form assemblages, at least within core use areas, that are more distinct than those of epibenthic taxa. We identified three distinct communities: a nearshore community affiliated with the Alaska Coastal Water, a southern Chukchi community corresponding to Bering Sea Shelf and Anadyr waters, and a northern Chukchi shelf community associated with the near-bottom Winter Water and surface ice melt water separated by a pycnocline. In addition, our analysis discriminated an assemblage of species (e.g., *Calanus marshallae, Themisto libellula*) abundant in the two latter communities, but generally scarce in the neritic community. The latter two species inhabit continental shelves of the Arctic and sub-Arctic seas and appear to be tied to the specific shelf environment (two layered vertical water column structure) rather than to a specific water mass. In terms of zoogeography, the neritic and southern Chukchi communities comprise Bering Sea expatriates advected into the Chukchi Sea, while the northern Chukchi community is reflective of the resident Chukchi Sea fauna of Pacific origin.

The distinct zooplankton assemblages in the Chukchi Sea and their linkages to certain water masses have been reported by multiple studies as early as the 1930s (e.g. Stepanova, 1937; Wirketis, 1952; Pavshtiks, 1984) and these earlier findings have been corroborated by later studies (Hopcroft et al., 2010; Eisner et al., 2013; Questel et al., 2013; Ershova et al., 2015). The studies agreed that Bering Sea Shelf (including Anadyr) waters, while also populated with wide-spread shelf species (e.g., *Calanus marshallae*), are best characterized by large oceanic copepods *Neocalanus* spp., *Eucalanus bungii*. These copepods originate from the Bering Sea outer shelf and are excellent tracers of Pacific intrusion even in the high Arctic. *Neocalanus* spp. can be especially abundant in the vicinity of the Bering Strait (Pinchuk, 1993) in early and mid-summer. In Bering Strait, turbulent upwelling of nutrient-rich Anadyr water at Anadyr and Bering straits further enhances high levels of primary production (Eisner et al., 2013; Lee et al., 2013) and helps sustain the zooplankton entrained in the Anadyr Current, and concomitantly an abundant and diverse seabird assemblage (Piatt and Springer, 2003). The neritic community associated with Alaska Coastal water typically comprises small (<1.5 mm) copepods *Acartia hudsonica*, *Eurytemora* spp. and the cladocerans *Evadne* spp. and *Podon* spp., which can be abundant in the nearshore areas (e.g., Ershova et al 2015). Zooplankton for our study was collected with coarser mesh nets, which allowed quantification of only larger neritic copepods *Epilabidocera amphitrites* and *Centropages abdominalis* in addition to hydrozoan jellyfish *Proboscydactila flavicerrata* and *Eutonina indicans*, and crangonid zoea as characteristic species of the community.

While our analysis identified a northern Chukchi zooplankton assemblage, the discrimination of two character species appeared somewhat superficial. Pteropod *Clione limacina* are widely distributed in boreal waters, including the North Pacific, and hardly characteristic of the Arctic Ocean. Perhaps, using biomass instead of numerical abundance as a quantitative measure biased our estimates of the significance of these large mollusks in zooplankton assemblage. Epibenthic juvenile Gammaridea is also a poor indicator group due to uncertainty in both their taxonomic status and ecological preferences. While epibenthic Gammaridea are often found in zooplankton collections, they are typically not considered true planktonic species, as opposed to some holoplanktonic Gammaridea (e.g., *Cyphocaris chalengerii*) which complete their entire life cycle in the pelagic realm. Hence, their elevated biomass in our samples could have resulted from occasional tows conducted too close to the bottom, near-bottom turbulence or episodic life cycle events such as intensive spawning or swarming behavior (Kim and Oliver, 1989).

The seabird assemblage identified for the Bering Strait and southern Chukchi Sea matches a region with a well-defined zooplankton assemblage. This region has previously been noted for high seabird densities, particularly the planktivorous *Aethia* auklets and larger, piscivorous common and thick-billed murres (although the latter also consumes euphausiids and *Themisto libuella*) (Piatt and Springer, 2003; Gall et al., 2013; Wong et al., 2014; Kuletz et al., 2015). Hence, an overlap of seabird and zooplankton assemblages would be expected. Throughout the study area, the most abundant species is the least auklet (Gall et al., 2013; Kuletz et al., 2015), which consumes small to medium-sized copepods (*C. marshallae* and *N. plumchrus*), whereas the larger-bodied crested auklet consumes large copepods (*N. cristatus*) and *Thysanoessa* euphausiids (Gall et al., 2006; Sheffield Guy et al., 2009).

The summer distribution of seabirds at sea is strongly influenced by location of their breeding colonies, and large seabird colonies exist in summer on St. Lawrence Island, King Island, the Diomede Islands in Bering Strait, and immediately north and south of Point Hope (Stephensen and Irons 2003; Piatt and Springer, 2003; Kuletz et al., 2015). However, few auklets (small numbers of parakeet auklets) nest north of Bering Strait. Since auklets are estimated to forage approximately 50 km from their colonies (Obst et al., 1995), the high numbers of crested auklets found in the central and northern Chukchi Sea must be non- or post-breeding birds (Kuletz et al., 2015); this may be one reason this seabird indicator species shows a different relationship with $NMDS_2$, compared to most seabirds. Similarly, the short-tailed shearwater is a summer visitor that breeds in the southern hemisphere, and the limited overlap between shearwaters and other seabird indicator species may be partly due to its non-restricted foraging range, as well as its more omnivorous diet (Armstrong 1995).

Arctic cod were an abundant epibenthic fish in previous Chukchi Sea surveys (Barber et al., 1997; Norcross et al., 2010, 2013) and the most abundant epibenthic fish during the Chukchi Sea portion of the 2012 bottom trawl survey (Goddard et al., 2014). However in our analyses, Arctic cod were not identified as an indicator species because they fell below the threshold for inclusion (association with an NMDS axis, R^2 <20%) even though Arctic cod were commonly occurring (e.g., 92% of bottom trawl survey stations). Logerwell et al. (2015) also found that Arctic cod use multiple habitats. Arctic cod were widely distributed throughout the study area and their CPUE was highly variable (e.g., bottom trawl survey, mean = 1.6, SD = 5.3). Arctic cod CPUE was most strongly associated with epibenthic $NMDS_2$ (R^2 = 12.5%), followed by epibenthic $NMDS_1$ (7.3%), pelagic $NMDS_2$ (4.4%), and pelagic $NMDS_1$ (1.5%), implying that the strongest gradient in Arctic cod distribution was north-south, as in epibenthic axes 1 and 2.

5.3. Relationships among assemblages

The advective character of the study area results in the generally high faunistic and biogeographic connectivity of the northern Bering and Chukchi seas, in particular the southern Chukchi Sea. Three cross-assemblage geographical groupings (i.e., communities) emerged, with one community associated with the Alaska Coastal Water, a second community associated with the Chirikov Basin and southern Chukchi Sea, and a third community associated with the northern Chukchi shelf (Fig. 9). Both of the first two community groupings connect the northern

Bering and southern Chukchi seas. The Alaska Coastal Water community group is characterized by certain zooplankton, fish, invertebrate and seabird taxa; the northern Bering and southern Chukchi community group is characterized by large crustacean zooplankton and certain seabird taxa; and the northern Chukchi shelf community group is characterized by several epibenthic and pelagic invertebrate species. The Alaska Coastal Water is warmer, fresher, and nutrient depauperate; the Bering Strait and southern Chukchi Sea is colder, saltier, and nutrient rich; and the northern Chukchi shelf is colder and saltier but not as nutrient rich (Coachman et al., 1975). The narrow range of $NMDS_1$ values across much of the Chukchi shelf for the zooplankton, pelagic, and epibenthic assemblages implies that these assemblages are fairly homogeneous across this region. Likewise, either $NMDS_1$ values or $NMDS_2$ values, depending on the taxa, are consistent nearshore and south, implying fairly homogeneous assemblages associated with the Alaska Coastal Water, which extends further offshore in the south. In addition to these three assemblages, a northern Bering, offshore (fourth) community group includes species characteristic of the southeastern Bering Sea such as walleye pollock and is associated with Bering Shelf Water.

The Bering Strait and southern Chukchi Sea community group was different in that it was characterized by distinct zooplankton and seabird taxa, but was not strongly associated with distinct pelagic or epibenthic fish and invertebrate taxa. This region is considered an extension of the Bering Sea greenbelt and Anadyr Current (Piatt and Springer, 2003), which are rich with nutrients and zooplankton, including a number of oceanic and outer shelf/slope species advected onto the northern Bering Sea shelf and through Bering Strait via extensions of the Bering slope and Anadyr currents (Piatt and Springer, 2003; Gibson et al., 2013). This richness is enhanced by turbulent upwelling of this nutrient-rich water at Anadyr and Bering straits (Piatt and Springer, 2003). The location of these nutrient-rich waters flowing past the Bering Sea islands accounts for the exceptionally large seabird colonies in the region (Piatt and Springer, 2003; Stephensen and Irons 2003). We found no evidence that distinct pelagic or epibenthic fish taxa are associated with this water mass. Rather, the fish community throughout the northern Bering Sea and the southern Chukchi Sea is an extension of the Bering shelf community, although both biomass and species diversity of fishes decline rapidly from south to north (Stevenson and Lauth 2012; Mueter et al., 2013).

The zooplankton assemblage was related to the distributions of both the pelagic fish/jellyfish and epibenthic assemblages (Fig. 8). These relationships may reflect both direct connections through trophic relationships and indirect connections through shared environmental influences. In contrast, the relationship between the zooplankton assemblage and the distribution of the seabird assemblage was statistically significant but weak. The weak relationship was surprising given the obvious spatial overlap of the zooplankton and seabird assemblages in Bering Strait and southern Chukchi Sea and the prominence of planktivorous birds in the region (Piatt et al., 1991; Gall et al., 2013; Kuletz et al., 2015). Two of the most abundant seabirds found in the area, least auklets and short-tailed shearwaters, can be highly variable in abundance and distribution, apparently in response to changes in stratification and salinity (Hunt and Harrison, 1990; Gall et al., 2013), which might contribute to the weak associations between seabirds and other biota or factors. The relationship also may be diluted by a 'colony effect' for seabirds; for example, $NMDS_1$ values for seabirds decreased approaching Point Hope (the northernmost seabird colonies), whereas $NMDS_1$ values for zooplankton did not (Fig. 3). Seabirds often were abundant near Point Hope (e.g., common murre, thick billed murre, horned puffin [Kuletz et al., 2015]), whereas zooplankton generally were not (Appendix). Additionally, within the seabird assemblage, prey selection is variable and changes interannually. For example, the least auklet will feed its chicks the smaller copepod *C. marshallae*, but its breeding success increases when the larger *N. flemingeri* is predominate in its diet. The larger-bodied crested auklet will also feed its chicks *N. flemingeri*, but has higher reproductive success when even larger zooplankton (*N. cristatus* and euphausiids) are available (Gall et al., 2006; Sheffield-Guy et al., 2009). The largest diving birds, thick-billed murres and short-tailed shearwaters, also consume euphausiids, but often eat a variety of pelagic fish (Piatt et al., 1991). Thus, the variety and flexibility of seabird diets might further dilute the overall relationship between seabirds and zooplankton.

Commonly zoogeography is examined for one (e.g., epibenthic fish and invertebrates; Bluhm et al., 2009) or two taxa (e.g., zooplankton and pelagic fish/jellyfish; Eisner et al., 2013), whereas our study is novel in examining the zoogeography of several taxa (zooplankton, pelagic fish and invertebrates, epibenthic fish and invertebrates, and seabirds) at once. This approach yielded new insights into how gradients in assemblage composition differed among assemblages (e.g., more abrupt for zooplankton taxa) and allowed us to identify the cross-assemblage geographic groupings (communities) of this Arctic region (Alaska Coastal Water, Chirikov Basin and southern Chukchi Sea, and northern Chukchi Sea) and the environmental factors influencing them. We also can speculate on how climate change will affect these communities based on space-for-time substitution (Pickett, 1989). The most likely (and obvious) effect will be for the northern Chukchi Sea community to retreat northward as the Alaska Coastal Water and Chirikov Basin/southern Chukchi Sea communities advance. The magnitude of advance will be affected by conditions for water sources upstream of these areas (i.e., frequency of ice-free winters in the southeastern Bering Sea) and will be tempered by anticipated ice-covered conditions of the northern Bering and Chukchi seas in the future (Stabeno et al., 2012; Hermann et al., 2013).

6. Acknowledgements

We gratefully acknowledge Jackie Grebmeier, University of Maryland Center for Environmental Science, who provided the sediment data.

This project was funded through the Coastal Impact Assistance Program (U.S. Fish and Wildlife Service) and the University of Alaska Fairbanks (10-CIAP-010 F12AF00188), the Bureau of Ocean Energy Management and the University of Alaska Fairbanks (Agreement Number M12AC00009), the Bureau of Ocean Energy Management and the Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration (Agreement Number M12PG00018), and the Bureau of Ocean Energy Management and the Division of Migratory Bird Management, U.S. Fish and Wildlife Service (Agreement Number M10PG00050). The seabird density estimates are archived in the North Pacific Pelagic Seabird Database (http://alaska.usgs.gov/science/biology/nppsd/index.php).

The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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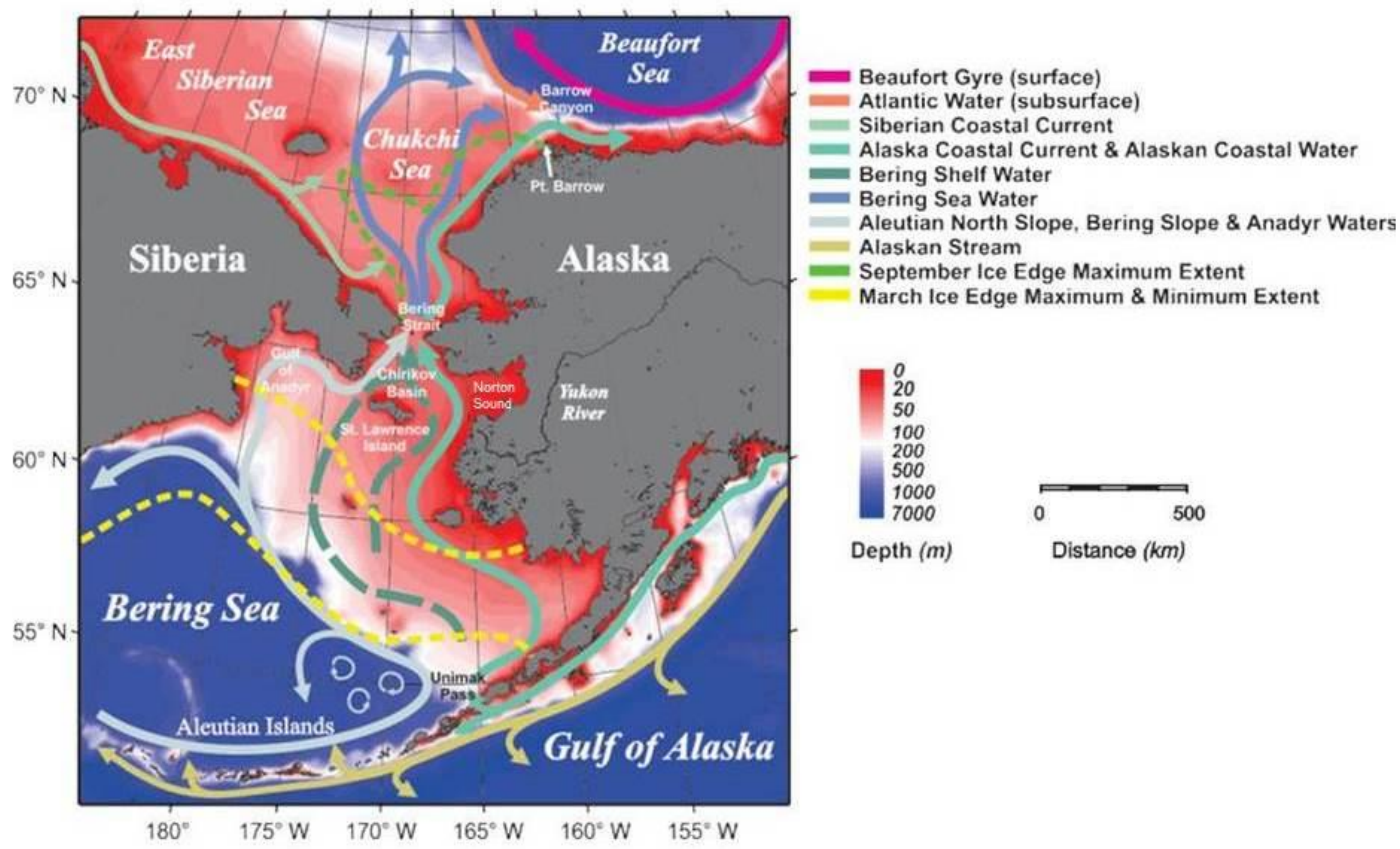


Fig. 1. The Bering, Chukchi, and Beaufort Seas form a continuum between the North Pacific Ocean and the Arctic Ocean. This idealized schematic denotes some of the important water masses and currents that impact regional differences in physical habitat characteristics. Figure courtesy of S. Danielson and T. Weingartner, University of Alaska Fairbanks.

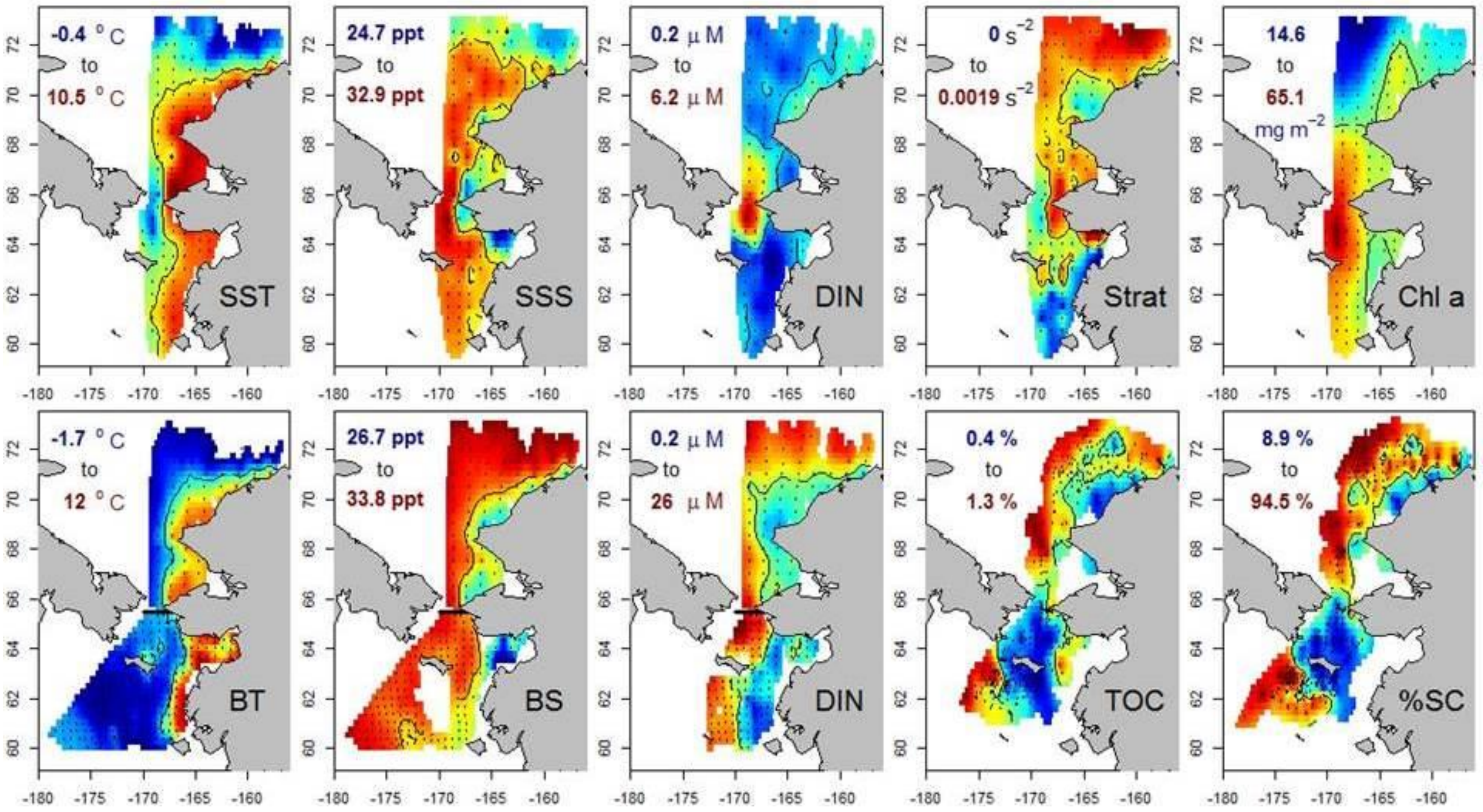


Fig. 2. Environmental conditions in surface waters (top) and bottom waters (bottom), including surface and bottom temperature (SST, BT), surface and bottom salinity (SSS, BS), dissolved inorganic nitrogen (DIN) (surface upper row, bottom lower row), mean stratification (Strat), integrated chlorophyll (Chl a), total organic carbon in sediments (TOC), and percent of silt and clay in the sediment (%SC). All surface values are based on 2012 samples. Bottom temperatures, salinity and DIN are based on 2012 samples in the Chukchi Sea and 2010 samples in the northern Bering Sea, resulting in a discontinuity in Bering Strait (horizontal black bars). Values for TOC and %SC are based on samples obtained between 1970 and 2012. Color scale in each panel ranges from minimum (dark blue) to maximum (dark red) of predicted values from geospatial models (on transformed scale where applicable, see text). Single contour in each panel corresponds to mean isoline (on transformed scale where applicable).

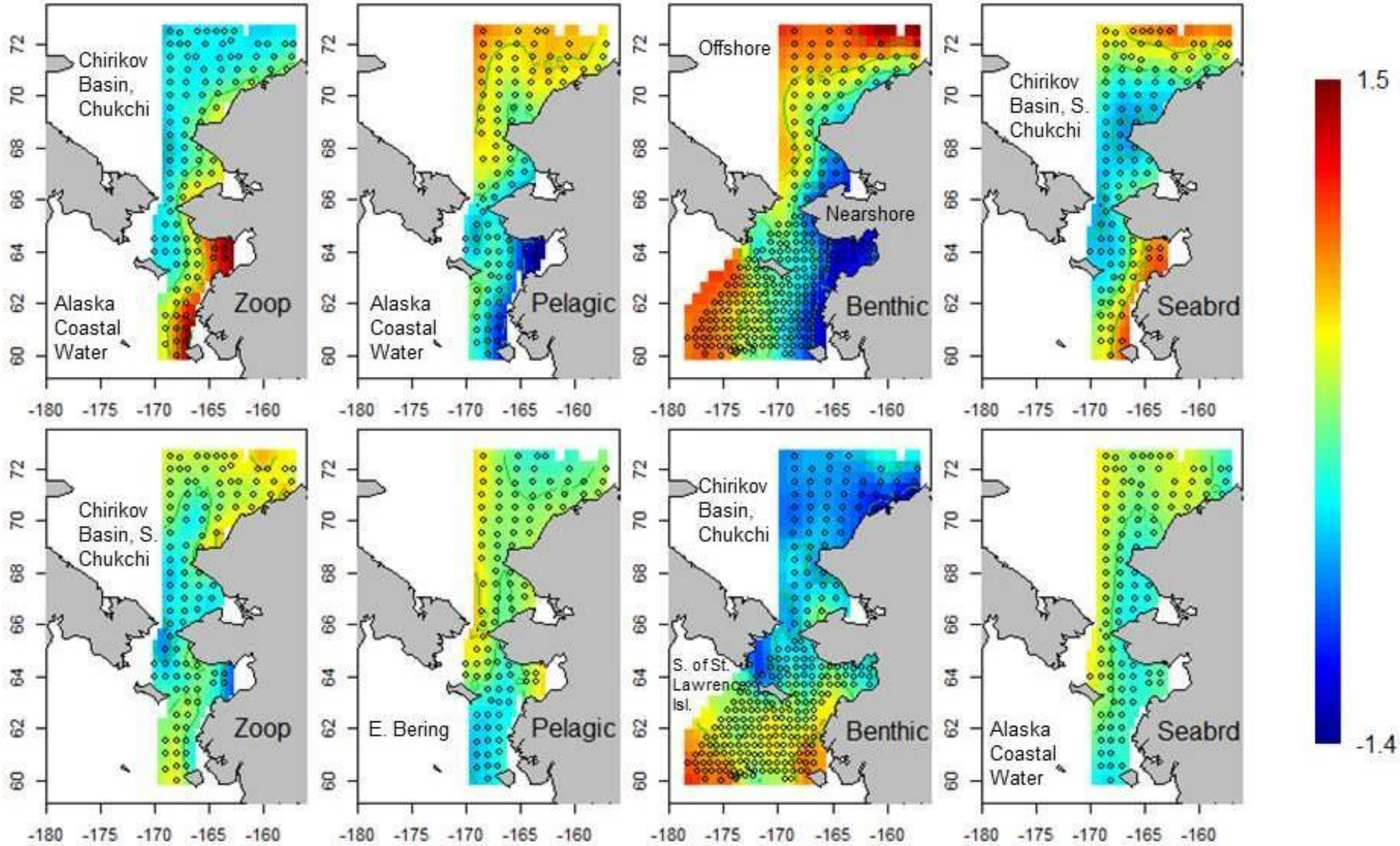


Fig. 3. NMDS plots by taxa. Spatial patterns of first mode of species composition (NMDS axis 1) plotted in upper row and second mode (NMDS axis 2) plotted in lower row. Red values are positive and blue values are negative. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea. The text labels (e.g., Chirikov Basin, Chukchi) lie near areas of similar NMDS values and match the labels in Figure 4.

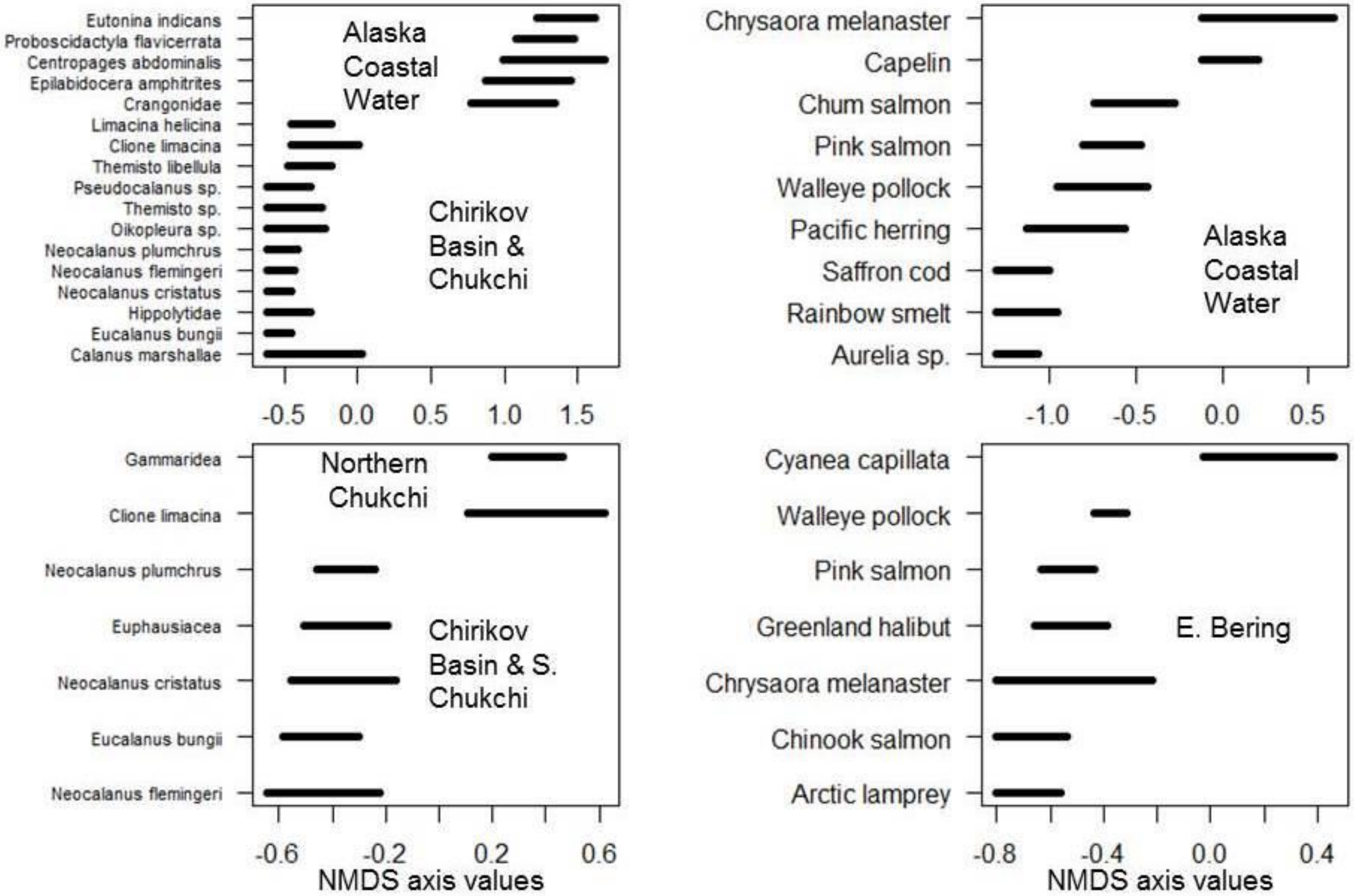


Fig. 4a. Zooplankton (left column) and pelagic (right column) taxa for indicator species (defined in methods). Bar graphs of core use area (defined in methods). The related geographic plots of NMDS axis values are shown in Figure 3. Axis 1 values in upper row and axis 2 values in lower row. Names of identified assemblages are shown beside the bars, as described in the results. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

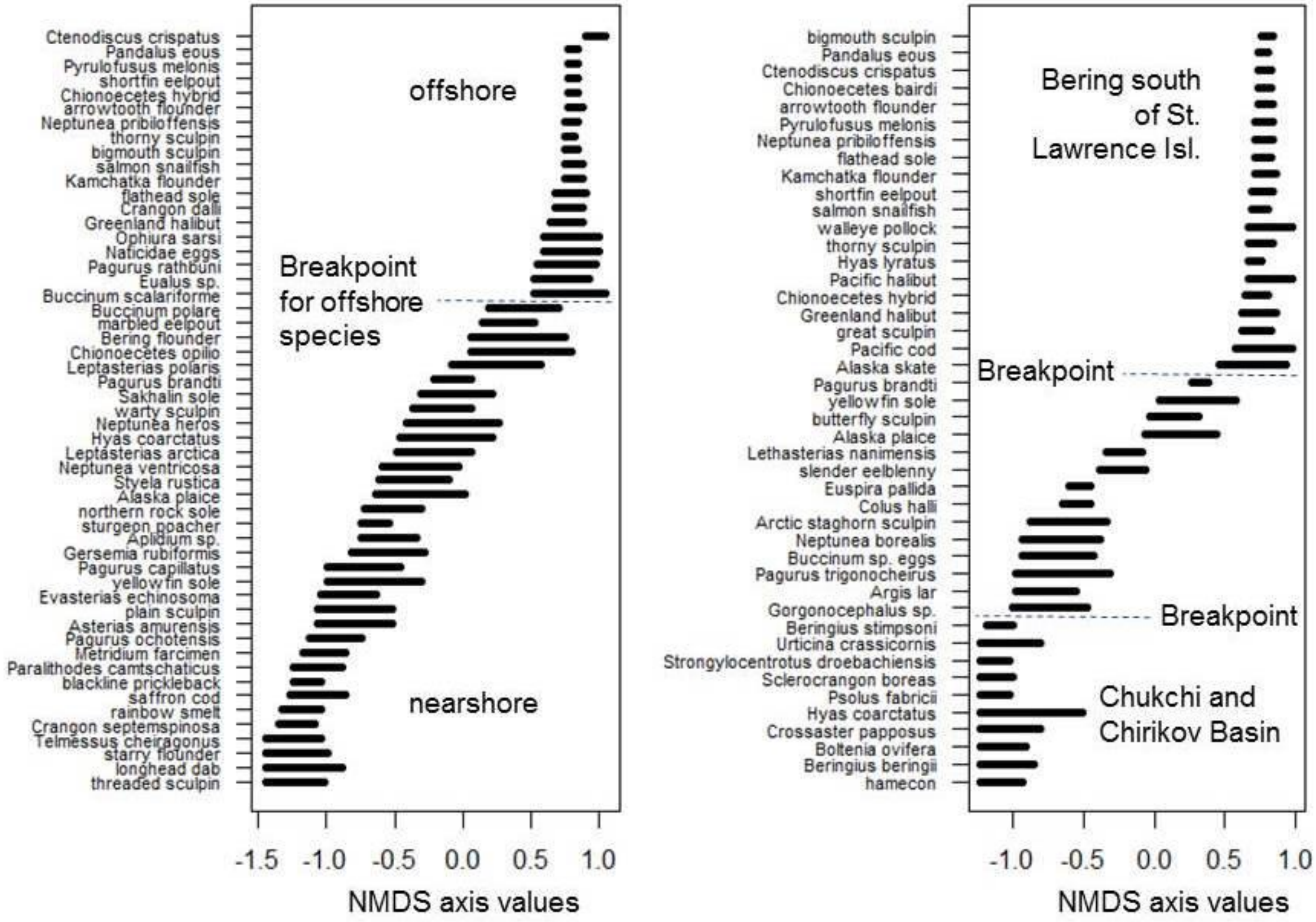


Fig. 4b. Epibenthic taxa for indicator species (defined in methods). At left, Bar graphs of core use area (defined in methods). The related geographic plots of NMDS axis values are shown in Figure 3. Axis 1 values in left column and axis 2 values in right column. Names of identified assemblages are shown beside the bars, as described in the results. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

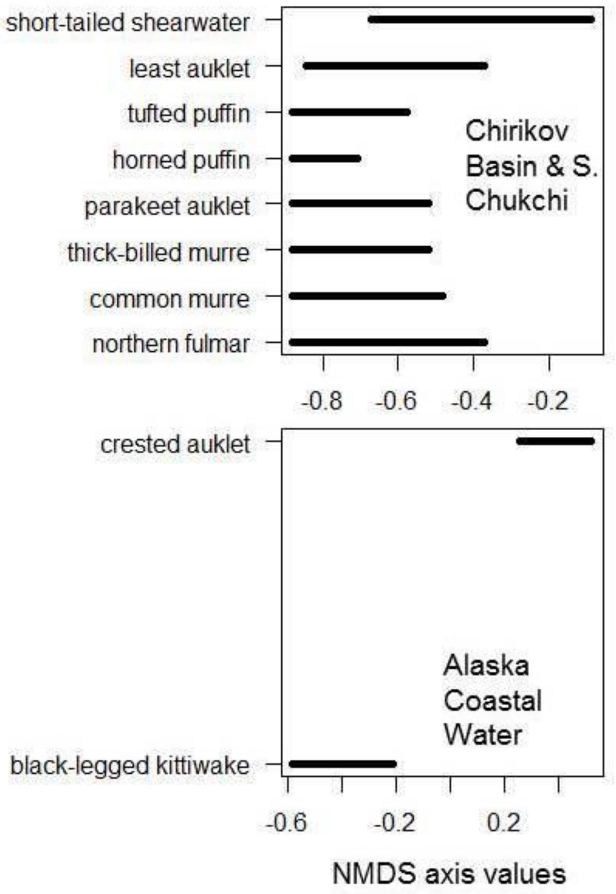


Fig. 4c. Seabird taxa for indicator species (defined in methods). Bar graphs of core use area (defined in methods). The related geographic plots of NMDS axis values are shown in Figure 3. Axis 1 values in upper row and axis 2 values in lower row. Names of identified assemblages are shown beside the bars, as described in the results. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

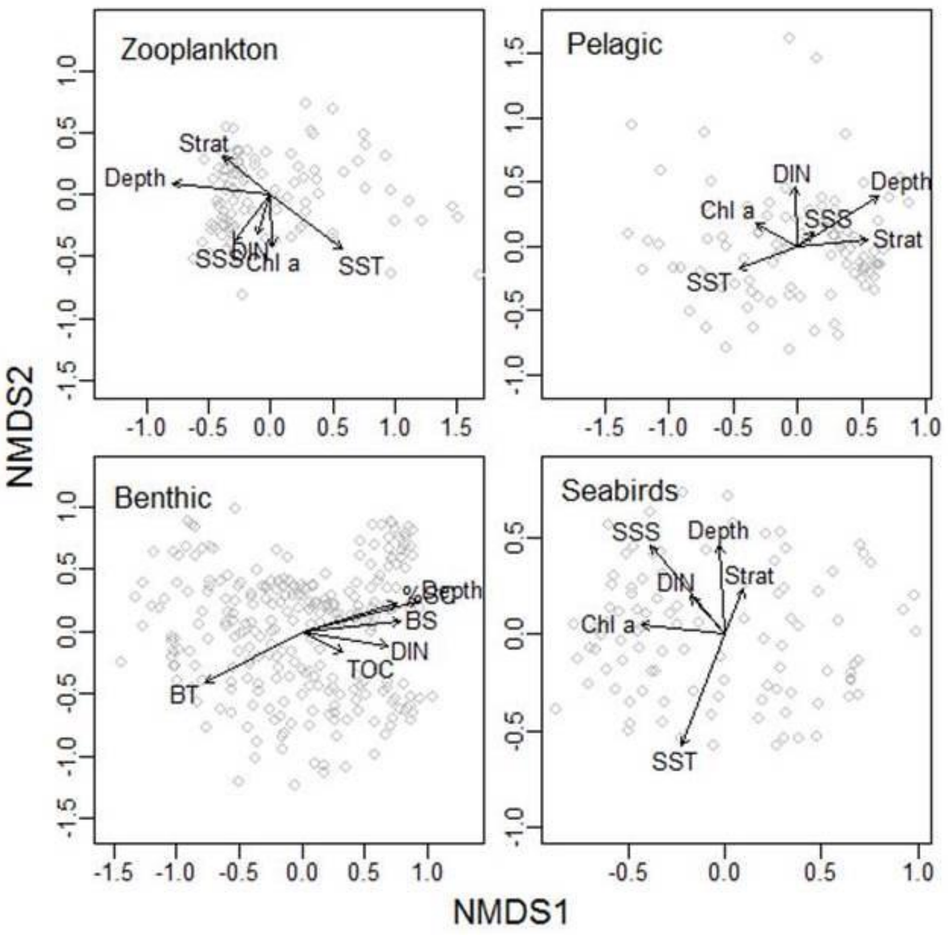


Fig. 5. Bi-plots by taxa and environmental variables including bottom depth (Depth), sea surface and bottom temperature (SST, BT), sea surface and bottom salinity (SSS, BS), dissolved inorganic nitrogen (DIN) (surface values for zooplankton, pelagic, and seabirds; bottom values for epibenthic, mean stratification (Strat), integrated chlorophyll (Chl a), total organic carbon in sediments (TOC), and percent of silt and clay in the sediment (%SC). Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

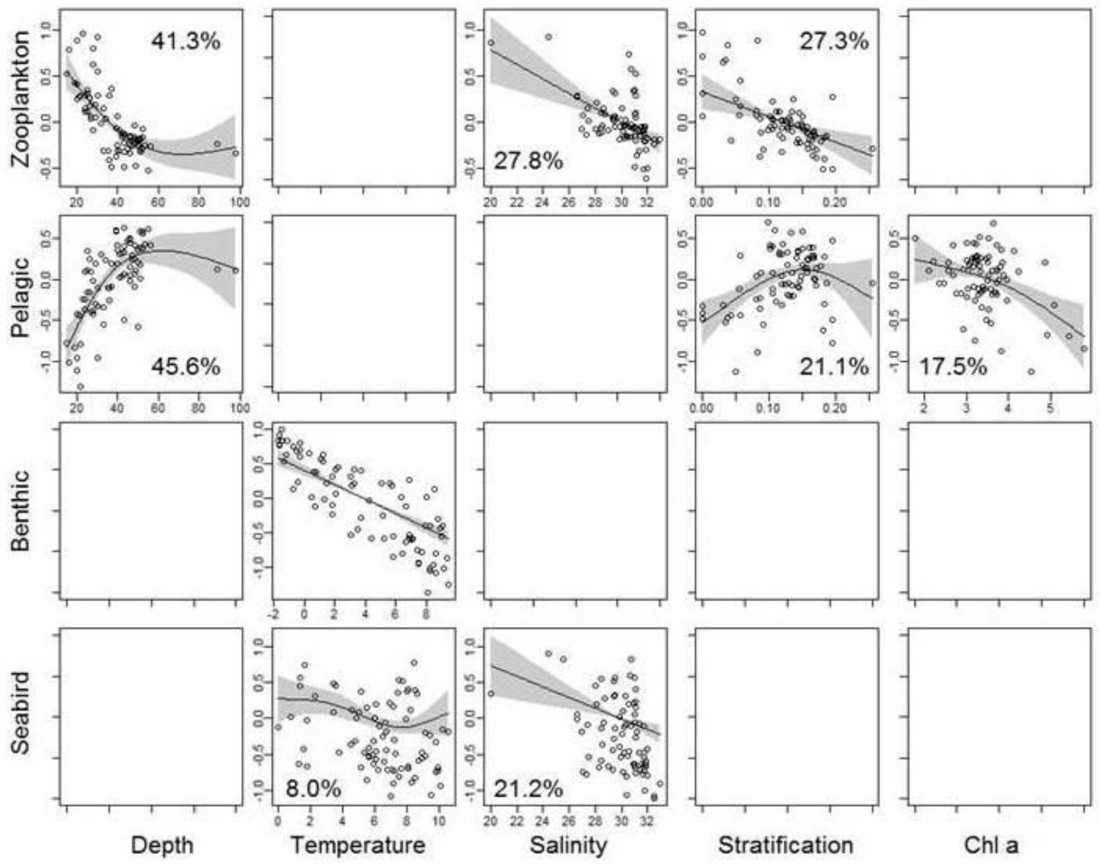


Fig. 6. Relationships (best model: plots and R^2) between indices of species composition (NMDS1) and environmental variables. The R^2 values are 0.732 (zooplankton), 0.707 (pelagic), 0.656 (benthic), and 0.168 (seabird). The sediment-related environmental variables did not enter the best model. Temperature and salinity are surface values for all taxa except epibenthic, which are bottom values. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea. Percentages listed in panels denote partial R^2 values, defined as the proportional reduction in residual sum of squares achieved by adding a given term to a reduced model without that term. There is no percentage listed in panels for taxa with only a single explanatory variable, which simply is the overall R^2 (i.e., 0.656 for benthic).

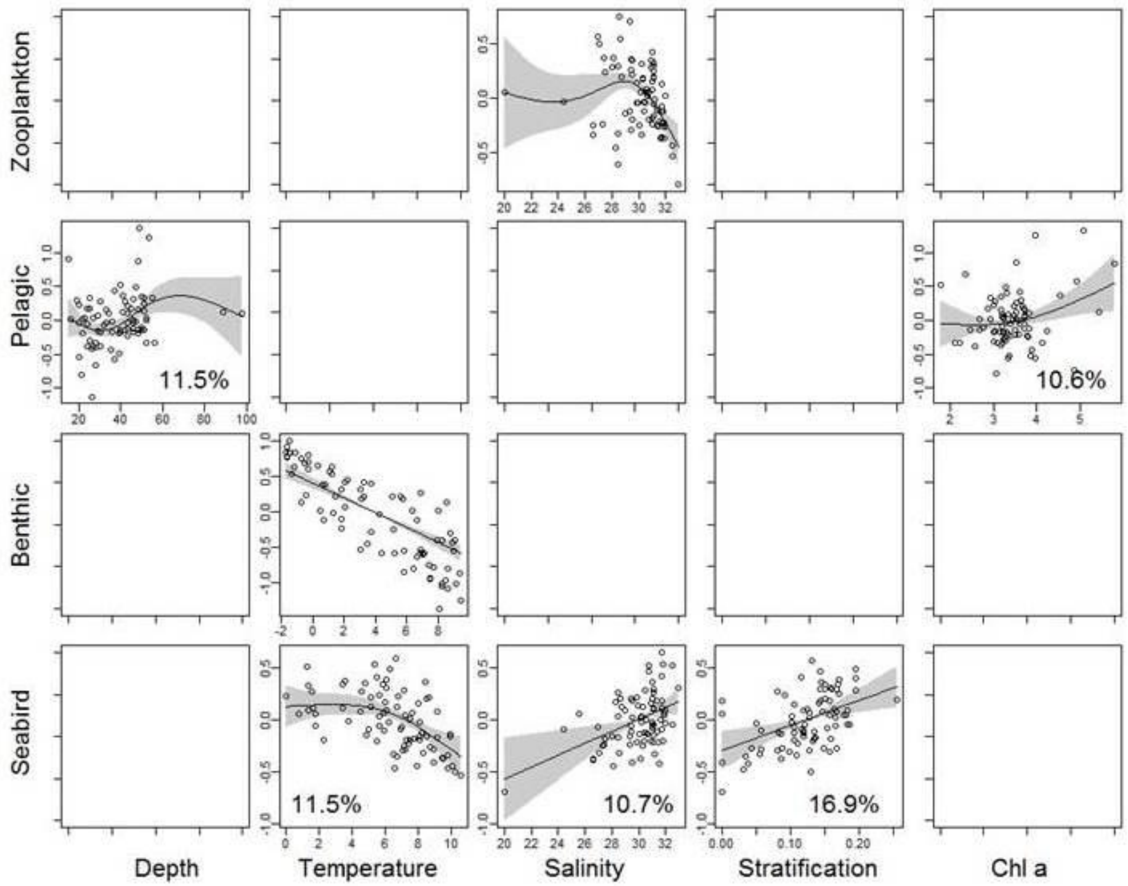


Fig. 7. Relationships (best model: plots and R^2) between indices of species composition (NMDS2) and environmental variables. The R^2 values are 0.199 (zooplankton), 0.150 (pelagic), 0.157 (benthic), and 0.490 (seabird). The sediment-related environmental variables were not statistically significant. Temperature and salinity are surface values for all assemblages except epibenthic, which are bottom values. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea. Percentages denote partial R^2 values, defined as the proportional reduction in residual sum of squares achieved by adding a given term to a reduced model without that term. There is no percentage listed in panels for taxa with only a single explanatory variable, which simply is the overall R^2 (e.g., 0.199 for zooplankton).

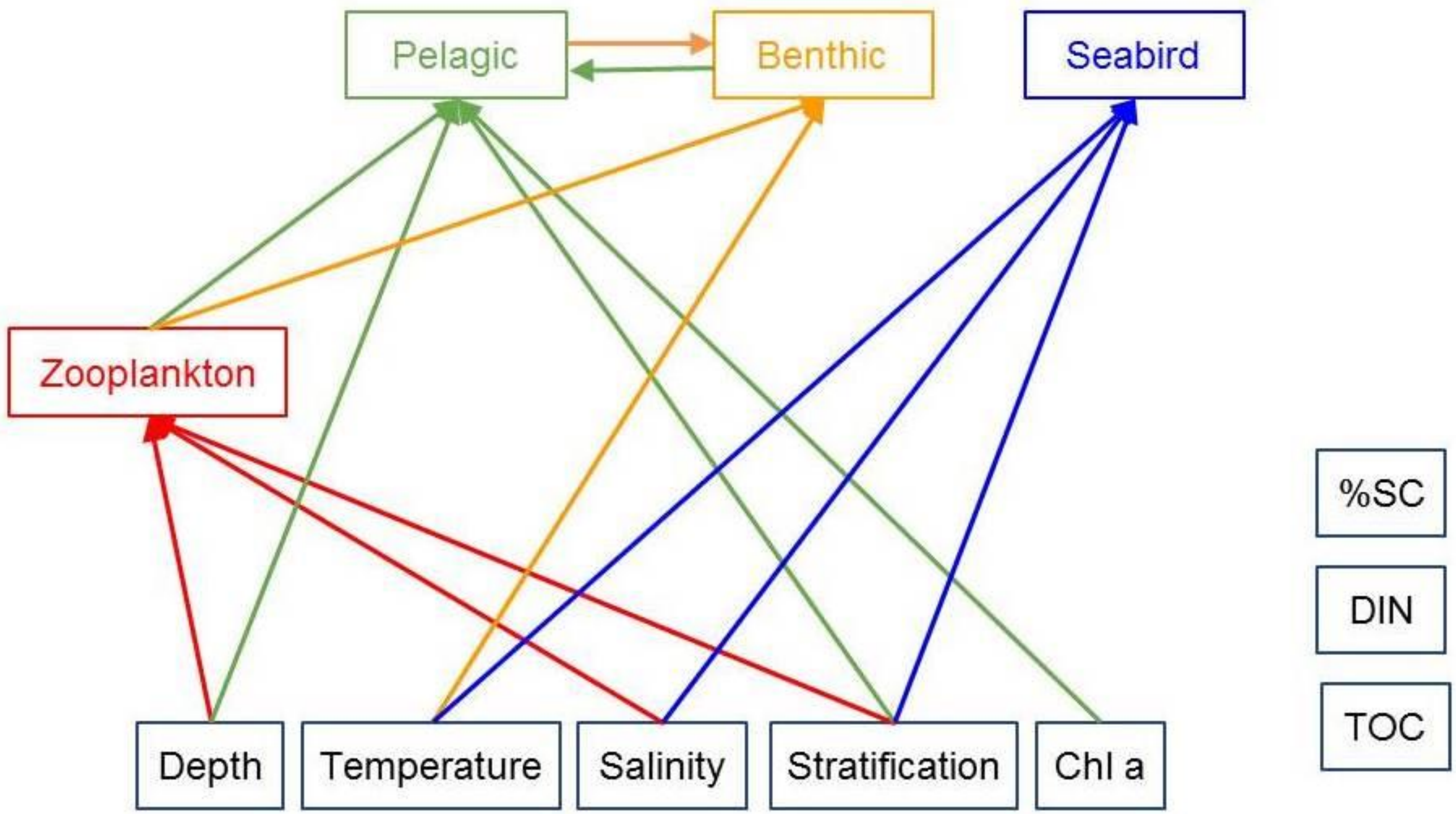


Fig. 8. Diagram linking taxa, based on indices of species composition (NMDS scores) and environmental variables, with connections based on best GAM models (Figures 6 and 7). The diagram also links among taxa, with connections based on adjusted canonical $R^2 > 0.4$ (Table 5). Connectivity between pelagic and epibenthic assemblages was quantified and tested for significance because they may influence each other. Other connections are assumed to be one-way. Total organic carbon (TOC), % silt/clay (%SC), and dissolved inorganic nitrogen (DIN) were included in the analyses but are not significantly related. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

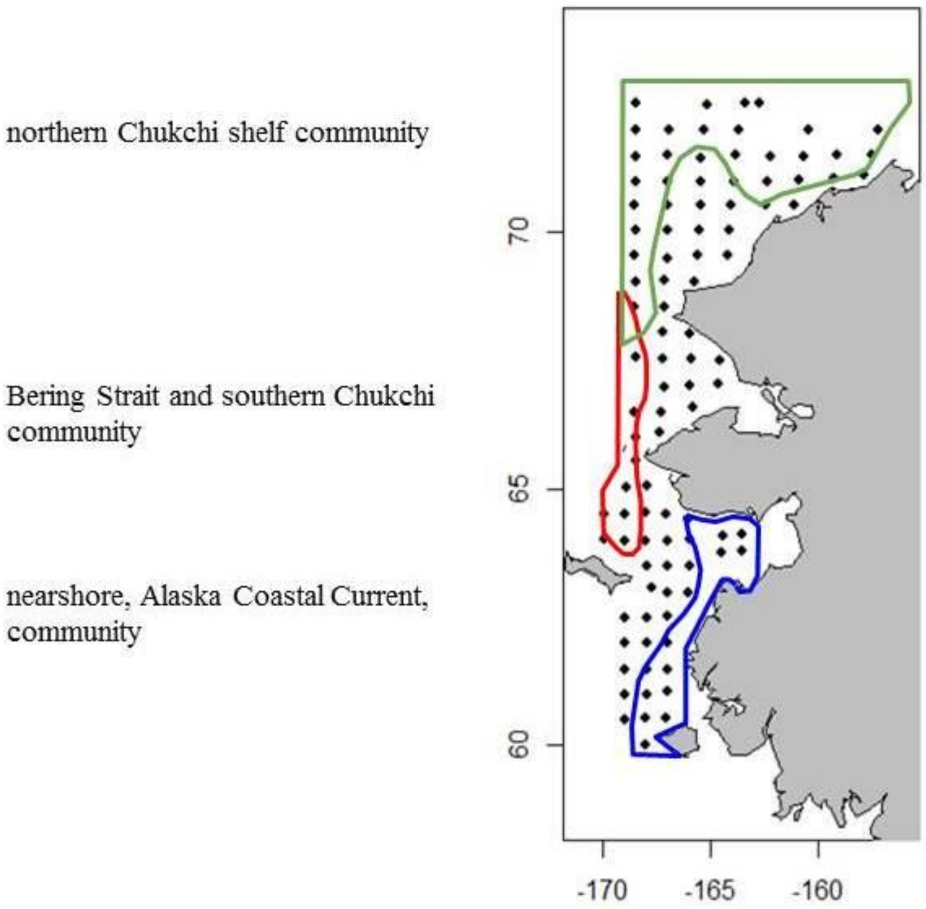


Fig. 9. Map showing polygons outlining regions of three cross-taxa assemblages with selected indicator species listed. The three regions are Chukchi shelf (green), Bering Strait and northward (red), and Alaska Coastal Current (blue). The regions are approximate and based on NMDS axes maps (Figure 3) and core use areas (Figure 4), as explained in the results section “Ordination of assemblages”. A northern Bering shelf community located offshore (e.g., walleye pollock) is not shown because it is based only on epibenthic data. The dots represent station locations in 2012. Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

Table 1. Sample sizes for environmental data, including the number of observations (obs.), missing values (miss.) and, for the missing values, the number that were estimated (est.). For example for surface temperature in 2012, there were 106 observations and 3 missing values and values were estimated for all 3 missing values. The year indicates collection year except for sediment samples, which were collected during 2006-2012. Only bottom-related data were included for 2010 because the only recent bottom trawl survey of the northern Bering Sea occurred in 2010. DIN abbreviates dissolved inorganic nitrogen.

Environmental variable	Year								
	2010			2012			2013		
Surface-related	obs.	miss.	est.	obs.	miss.	est.	obs.	miss.	est.
Surface temperature				106	3	3	94	6	6
Surface salinity				106	3	3	94	6	6
Surface DIN				99	10	10	99	1	1
Stratification				106	3	3	94	6	6
Integrated chlorophyll *a*				109	0	0	100	0	0
Bottom-related									
Bottom temperature	202	0	0	106	3	3	94	6	6
Bottom salinity	145	57	57	106	3	3	94	6	6
Bottom DIN	111	91	30	199	10	10	99	1	1
% silt/clay	68	134	134	50	59	59	42	58	58
Total organic carbon	74	128	128	54	55	55	47	53	53

Table 2. Cumulative proportion of the overall variability in 4th root transformed abundances (station-by-species matrix, after eliminating rare species) that can be explained by the first two axes from a correspondence analysis (CA). Based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea.

Response variables (assemblage)	CA1	CA2
zooplankton	0.255	0.379
pelagic	0.192	0.328
benthic	0.133	0.228
seabirds	0.135	0.233

Table 3. Relationships between indices of species composition (NMDS scores) and six explanatory variables (see text) measured at 79 stations based on canonical correlation analysis. In addition to canonical correlations for the first and second canonical axes, adjusted canonical coefficient of determination (R^2) value and permutation-based significance level (*p*-value) for each analysis are shown. One station with several unusual values for environmental variables was removed prior to analysis (*n*=79). Results in columns 1-4 are based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea; results in column 5 are based on 2013 samples.

Response variables (assemblage)	Canonical correlations	adjusted canonical R^2	*p*-value	2013 adj R^2
zooplankton	0.869, 0.533	0.571	< 0.0001	0.571
pelagic	0.774, 0.458	0.408	< 0.0001	0.296
benthic	0.891, 0.299	0.588	< 0.0001	
seabirds	0.768, 0.679	0.489	< 0.0001	0.343

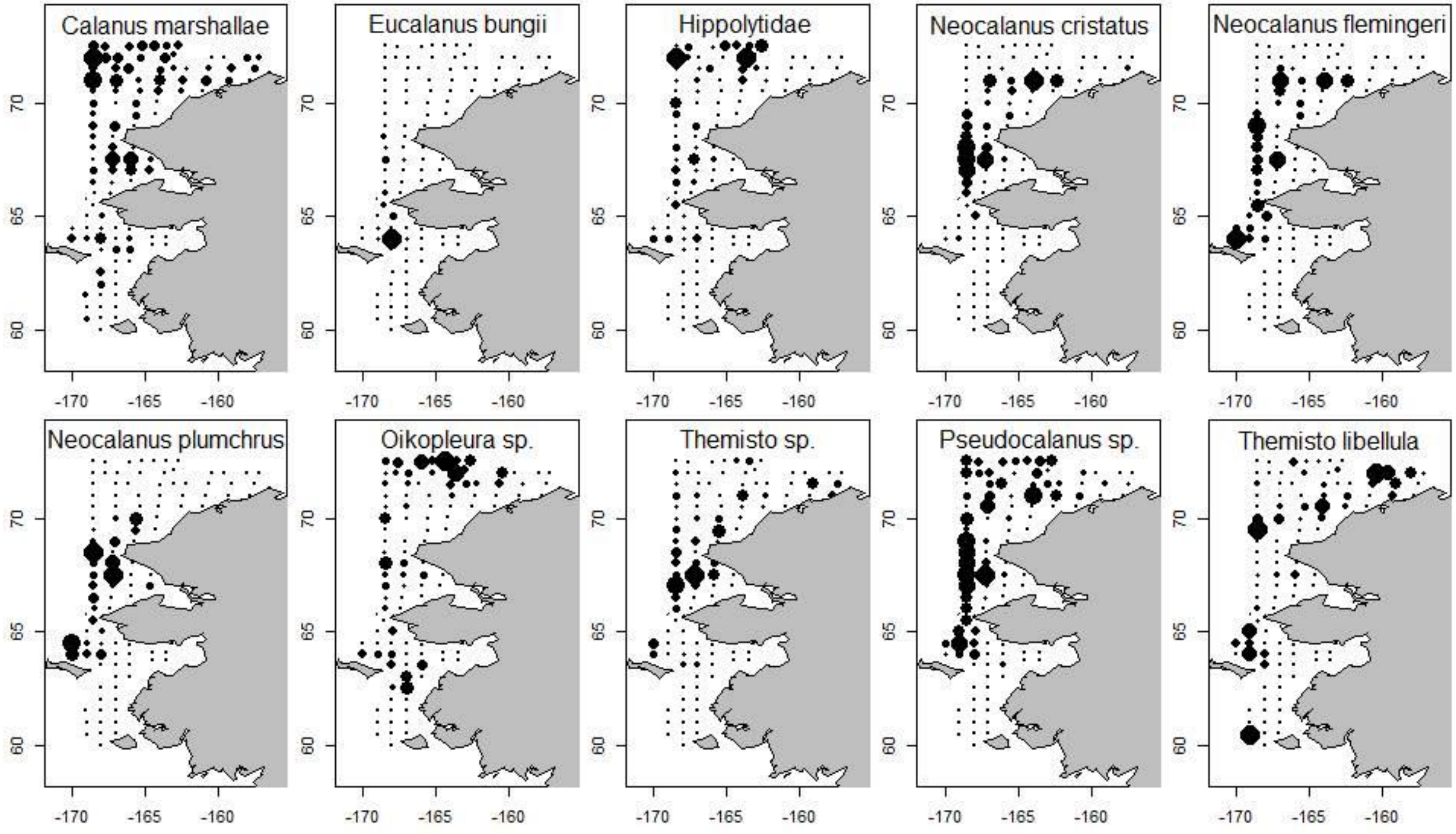
Table 4. Best sets of 1, 2, 3, etc., explanatory variables and maximum rank-based Mantel correlations (in parentheses) between each set of variables and indices of species composition (NMDS scores) for four biological assemblages. Highest overall Mantel correlations for each assemblage are highlighted in bold. Abbreviations are bottom depth (Depth), surface and bottom temperature (SST, BT), surface and bottom salinity (SSS, BS), mean stratification (Strat), integrated chlorophyll (Chl*a*), and percent of silt and clay in the sediment (%SC). Results in rows 1-6 are based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea; results in rows 7-8 are based on 2013 samples. The alternate set for 2013 (row 8) shows Mantel correlations for variables that were best for the 2012 data.

# of variables	zooplankton	pelagic	benthic	seabird
1	Strat (0.427)	Strat (0.346)	Depth (0.545)	Strat (0.240)
2	Depth + Strat (0.527)	Strat + Chl*a* (0.400)	Depth + BS (0.563)	Strat + SST (0.316)
3	**Depth + Strat + SSS (0.536)**	**Depth + Strat + Chla (0.434)**	Depth + BT + %SC (0.563)	Strat + SST + SSS (0.335)
4	Depth + Strat + SSS + SST (0.516)	Strat + Chl*a* **+** Depth + DIN (0.433)	**Depth + BT + %SC + BS (0.573)**	**Strat + SST + SSS + Depth (0.337)**
5	Depth + Strat + SSS + SST + DIN (0.477)	Strat + Chl*a* **+** Depth + DIN+ SSS (0.427)	Depth + BT + %SC + BS + DIN (0.576)	Strat + SST + SSS + Depth + Chl*a* (0.305)
6	All (0.409)	All (0.393)	All (0.551)	All (0.257)
Best set 2013	Depth + SSS + DIN + Strat (0.406)	SST + SSS + Chl*a* (0.307)		SST + SSS + Strat (0.222)
Alternate set 2013	Depth + Strat + SSS (0.394)	Depth + Strat + Chl*a* (0.254)		Strat + SST + SSS + Depth (0.209)

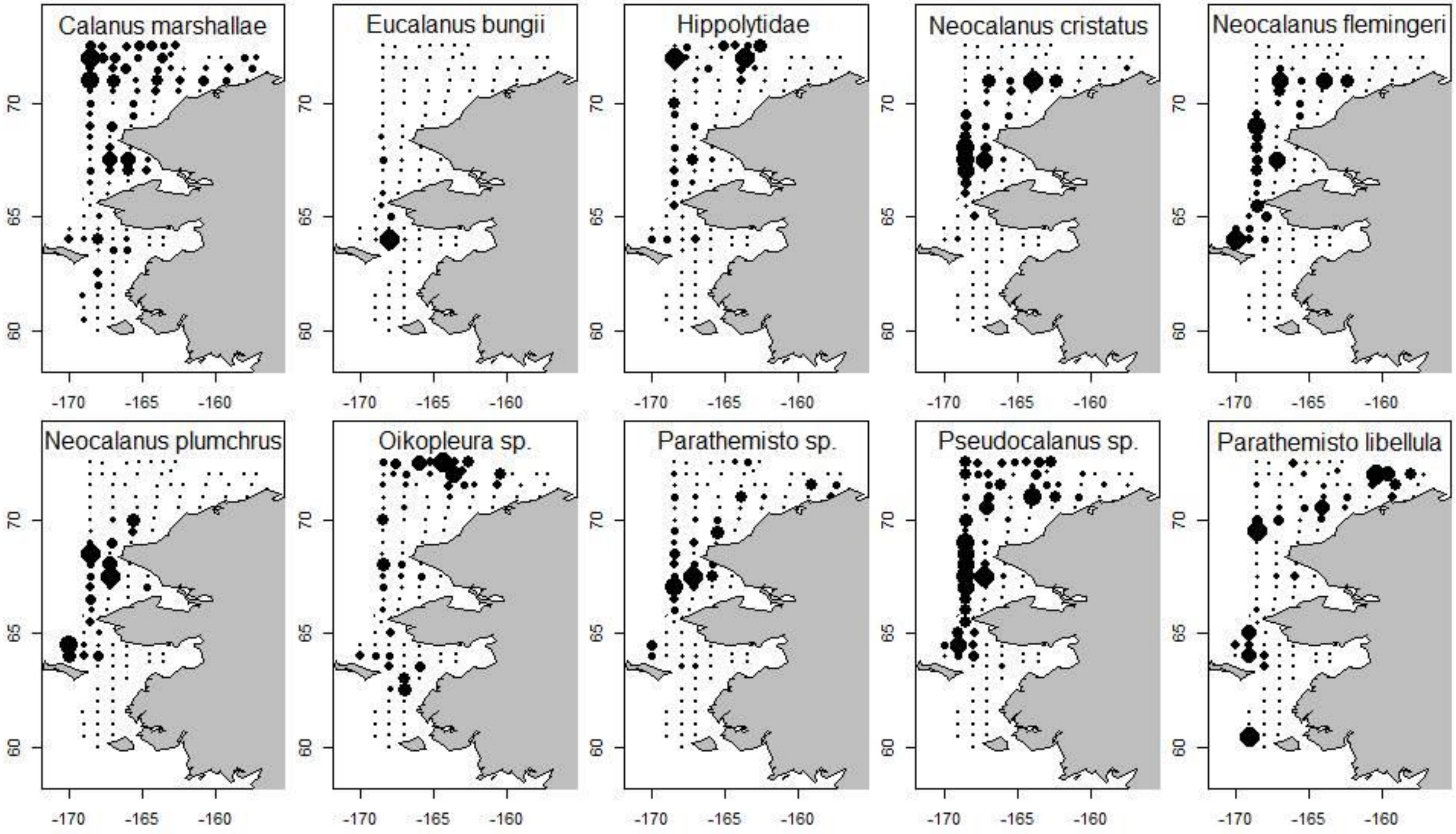
Table 5. Relationship among indices of species composition (NMDS scores) for four biological assemblages measured at 80 stations based on canonical correlation analysis. Each row summarizes the relationship between a “response” assemblage and an “explanatory” assemblage based on the canonical correlations for the first and second canonical axes, the adjusted canonical coefficient of determination (R^2) and a permutation-based significance level (*p*-value). Results in columns 1-5 are based on 2012 samples for all taxa and areas except 2010 samples for epibenthic taxa in the northern Bering Sea; results in column 6 are based on 2013 samples.

explanatory	response	Canonical correlations	adj. canonical R^2	*p*-value	2013 adj. canonical R^2
zooplankton	pelagic	0.850, 0.391	0.511	< 0.0001	0.275
zooplankton	benthic	0.855, 0.052	0.589	< 0.0001	
zooplankton	seabirds	0.738, 0.144	0.258	< 0.0001	0.344
pelagic	benthic	0.874, 0.166	0.609	< 0.0001	
pelagic	seabirds	0.587, 0.038	0.105	< 0.0001	0.258
benthic	pelagic	0.874, 0.166	0.465	< 0.0001	

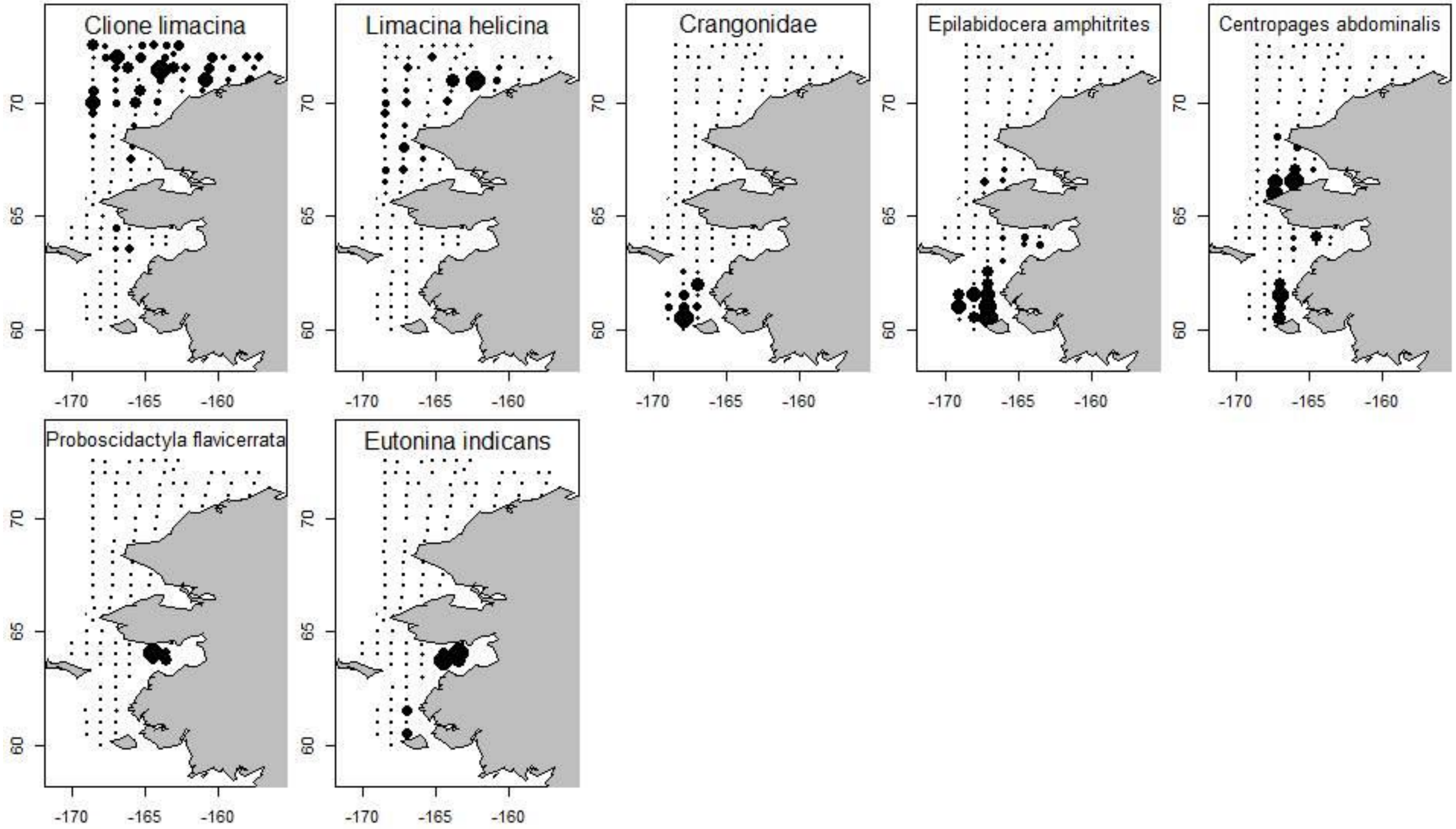
Appendix. Species distribution maps for indicator species: zooplankton axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



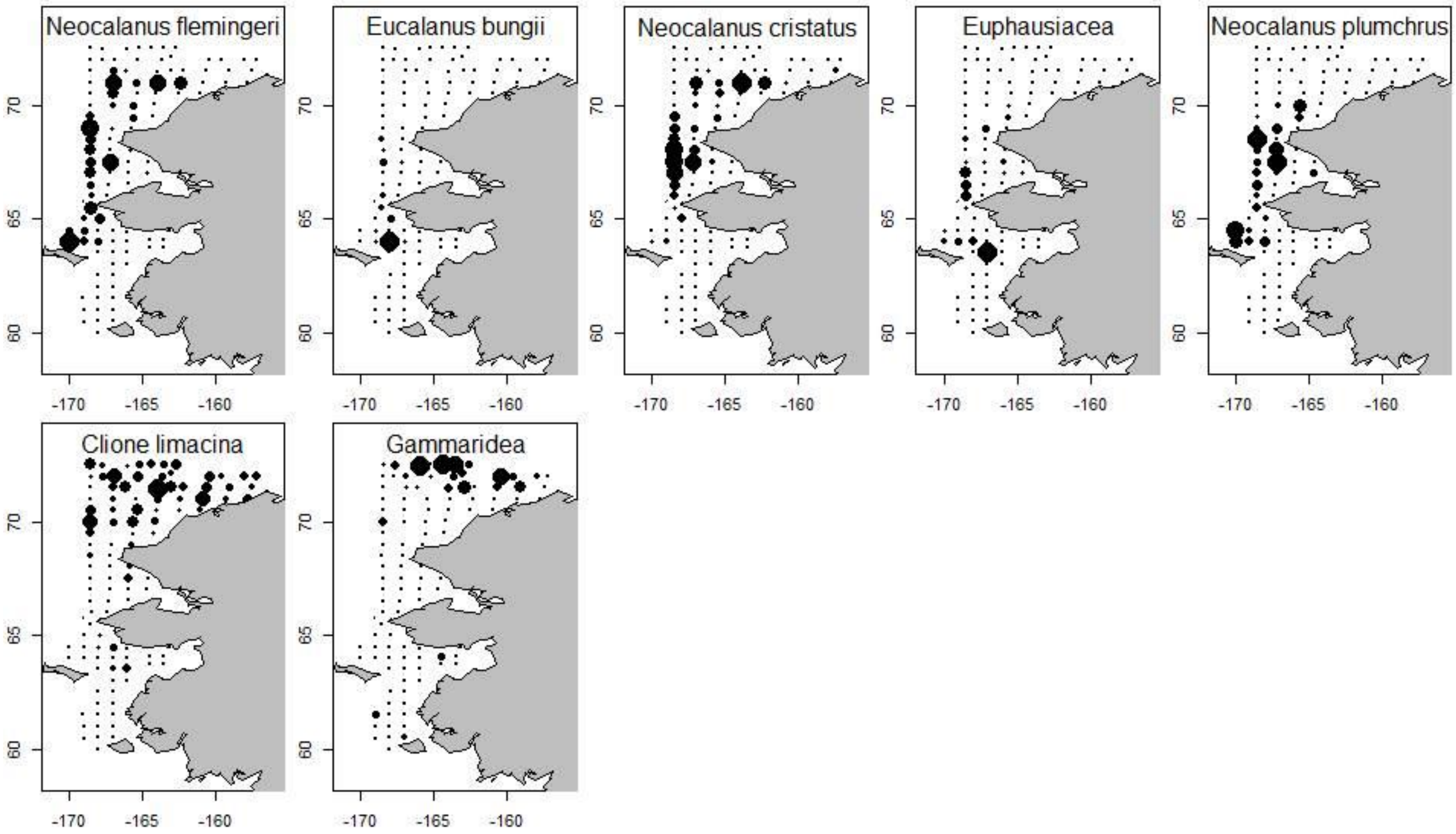
Appendix. Species distribution maps for indicator species: zooplankton axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea. PARATHEMISTO



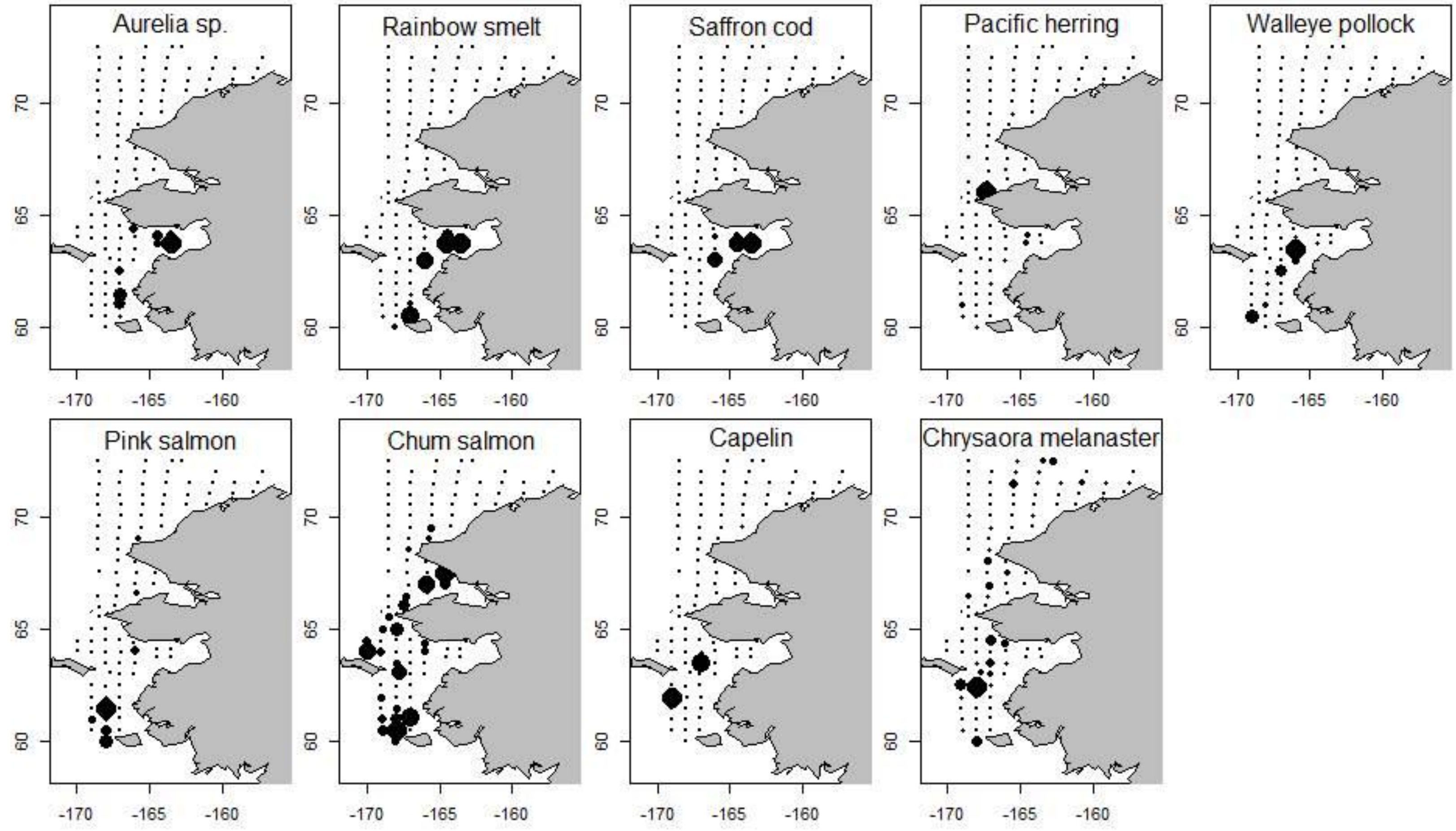
Appendix. Species distribution maps for indicator species: zooplankton axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



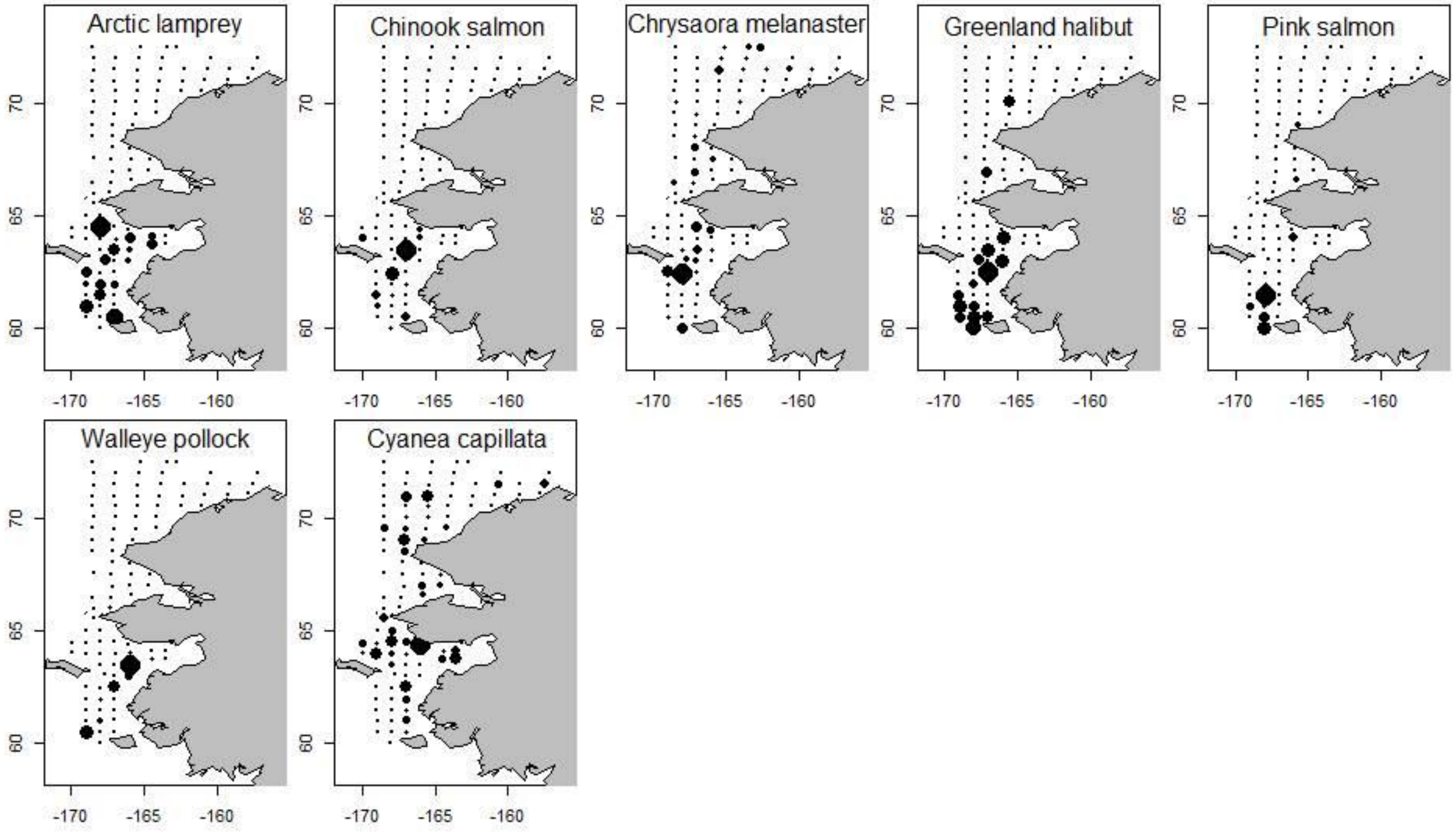
Appendix. Species distribution maps for indicator species: zooplankton axis 2. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



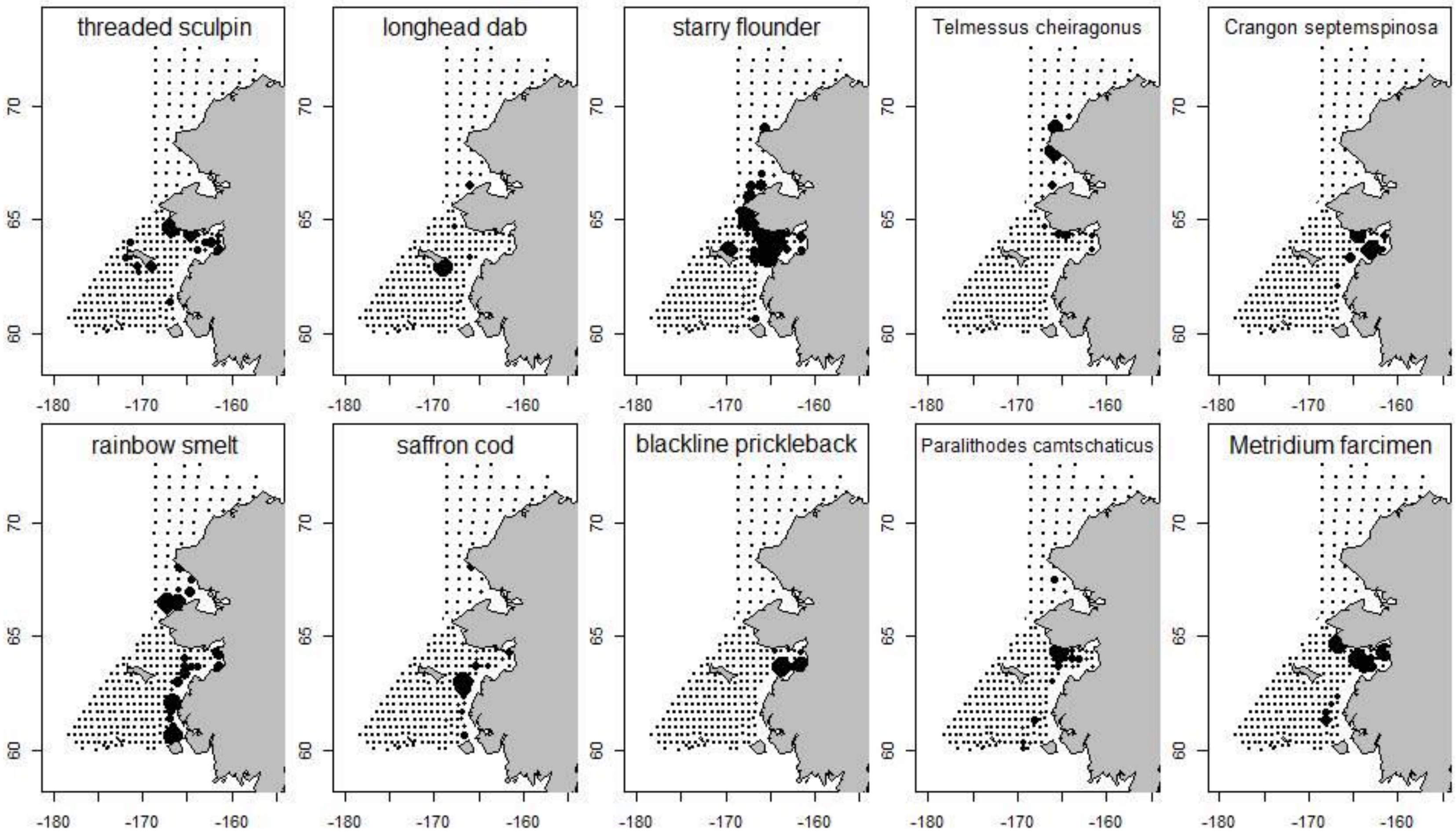
Appendix. Species distribution maps for indicator species: pelagic axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



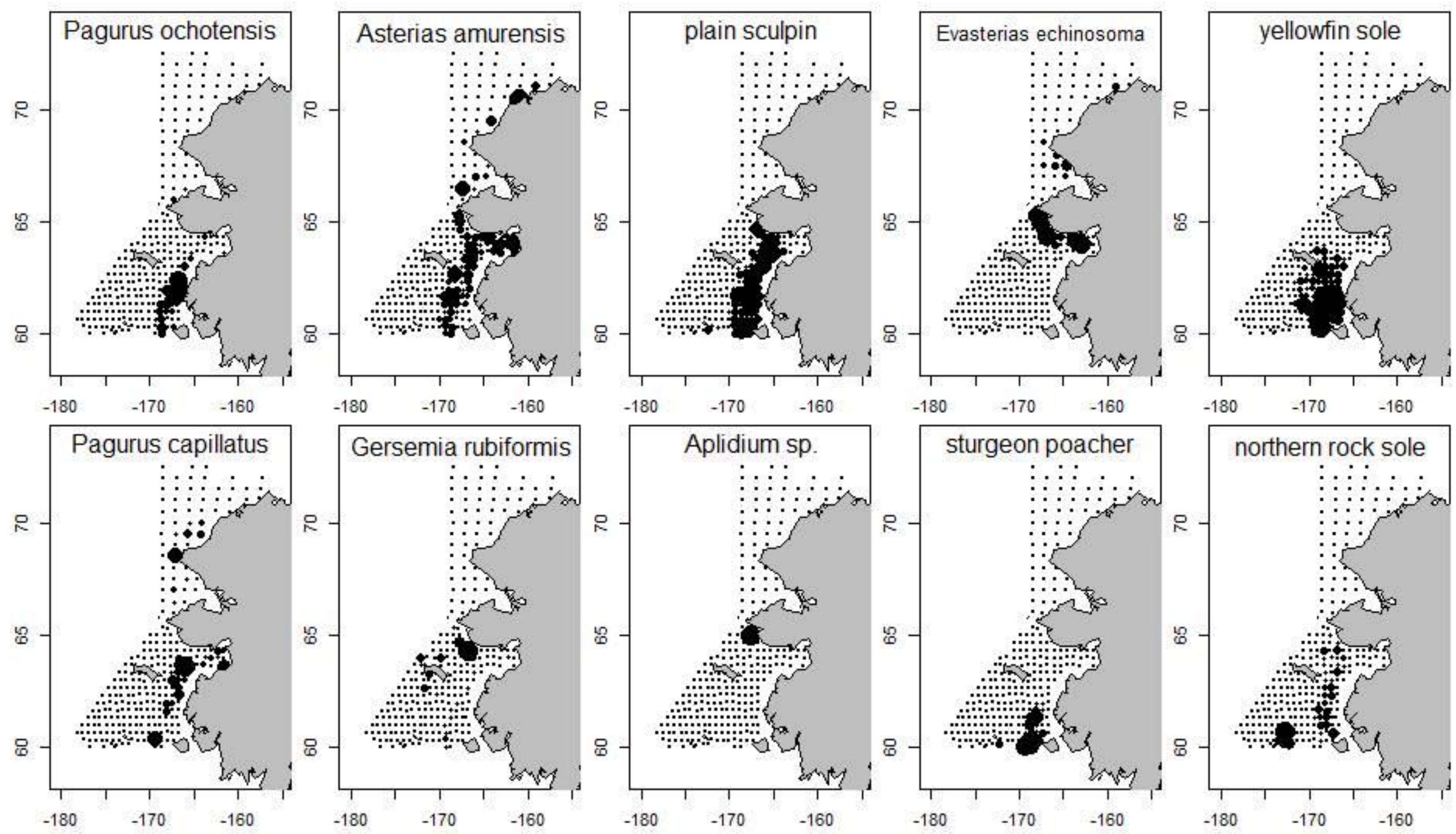
Appendix. Species distribution maps for indicator species: pelagic axis 2. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



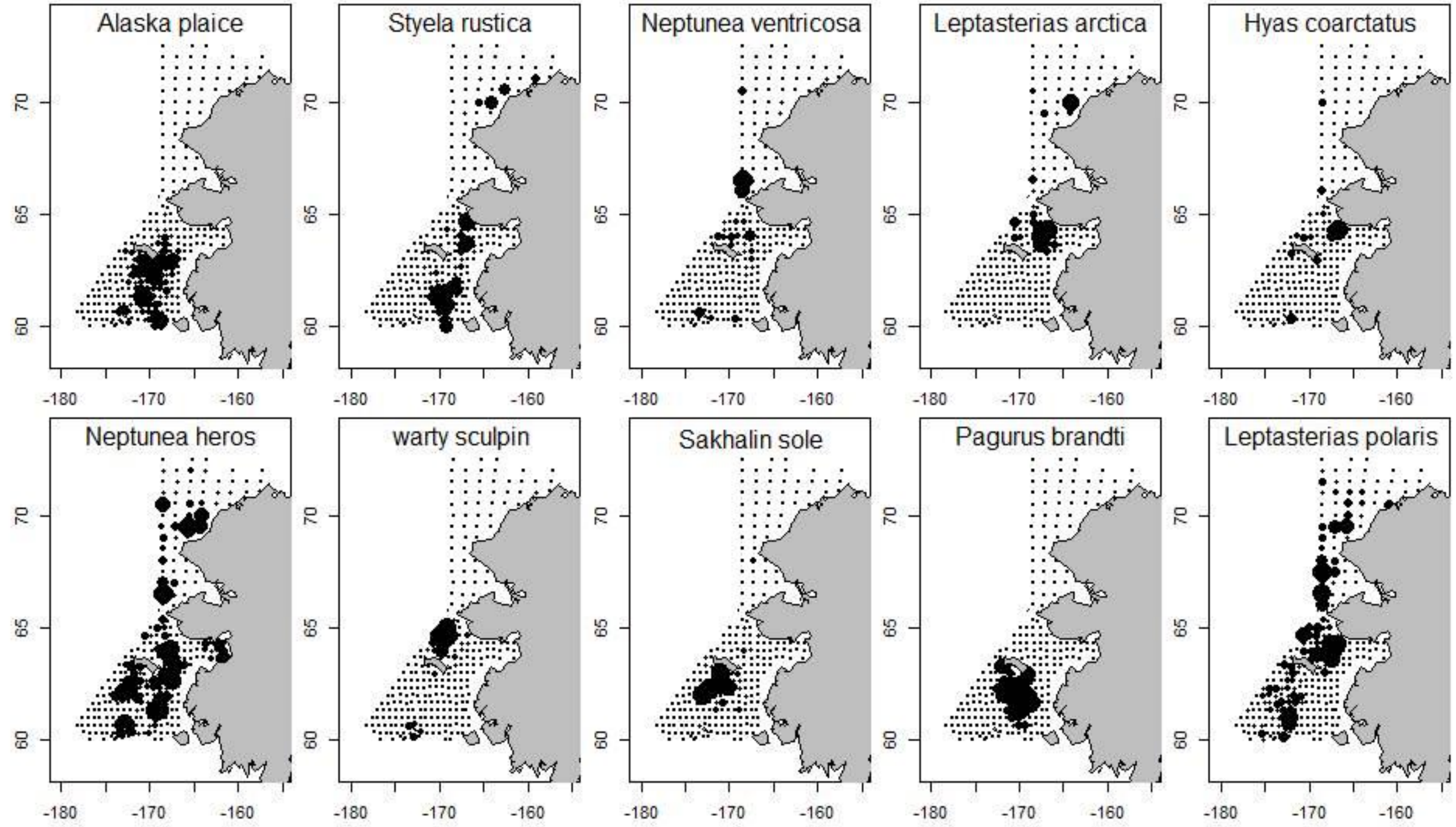
Appendix. Species distribution maps for indicator species: benthic axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



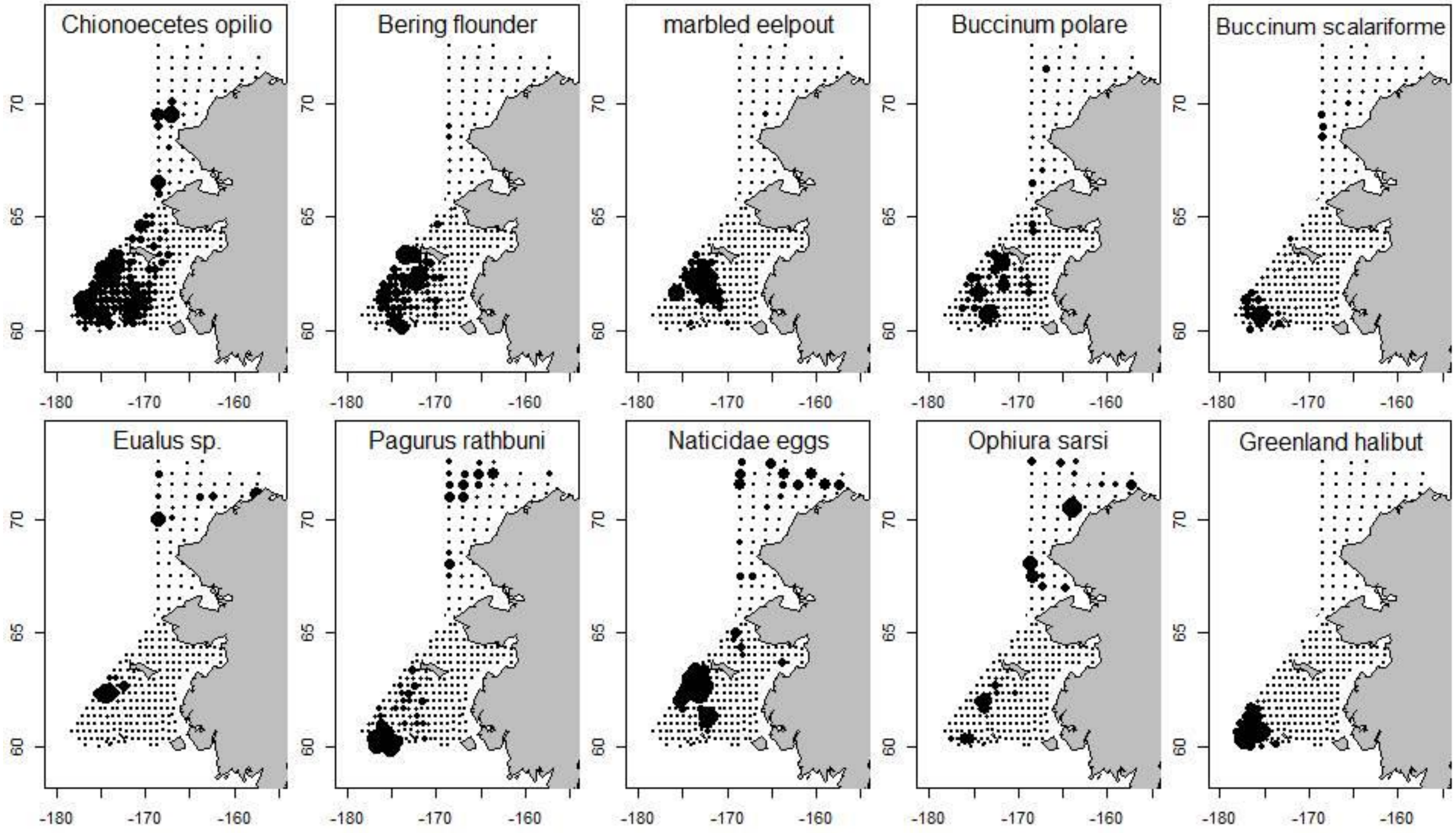
Appendix. Species distribution maps for indicator species: benthic axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



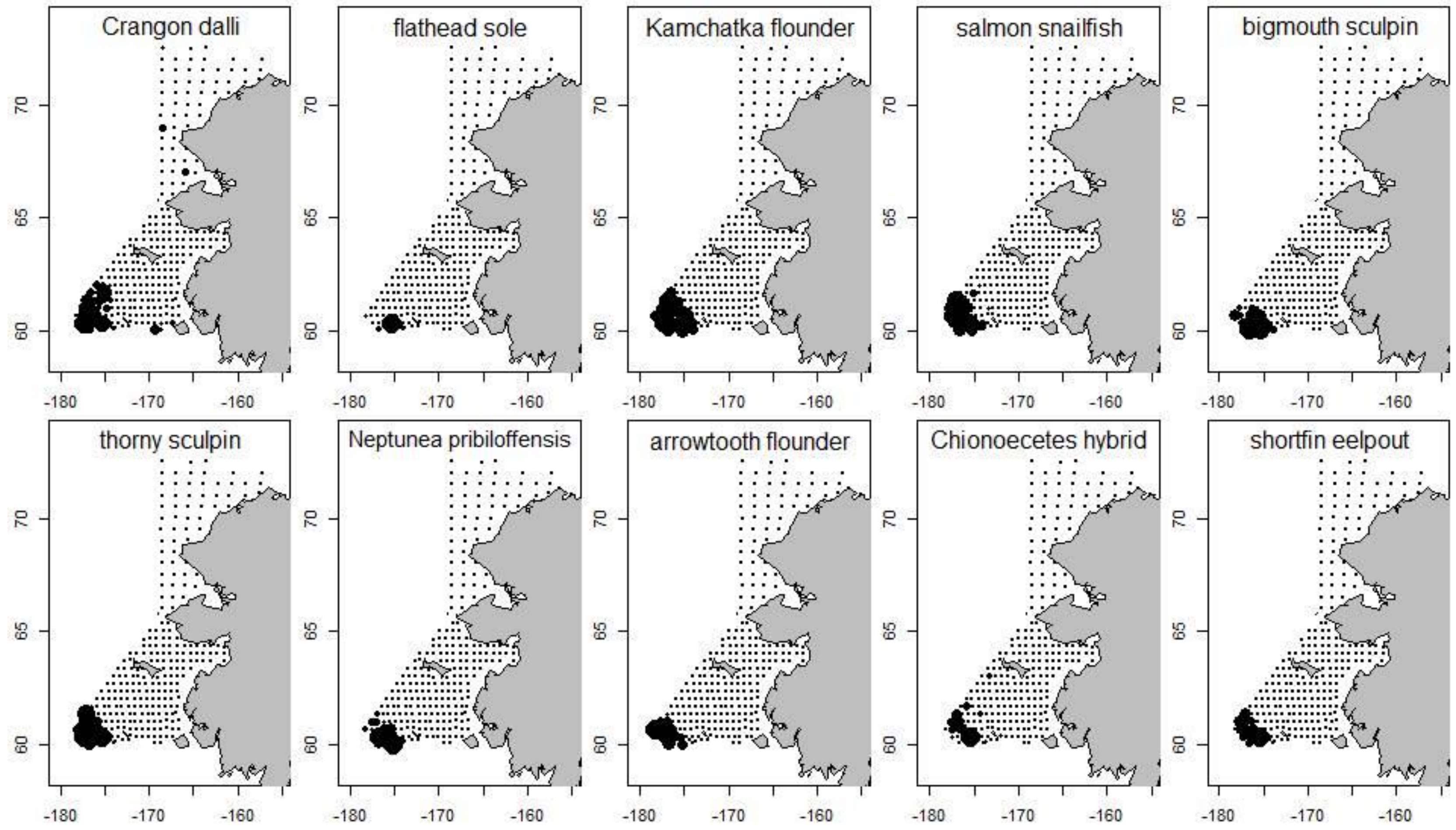
Appendix. Species distribution maps for indicator species: benthic axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



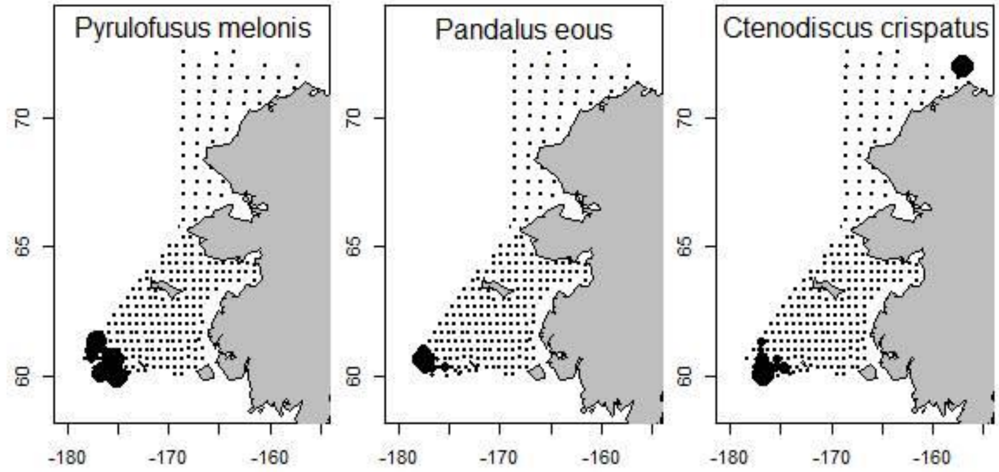
Appendix. Species distribution maps for indicator species: benthic axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



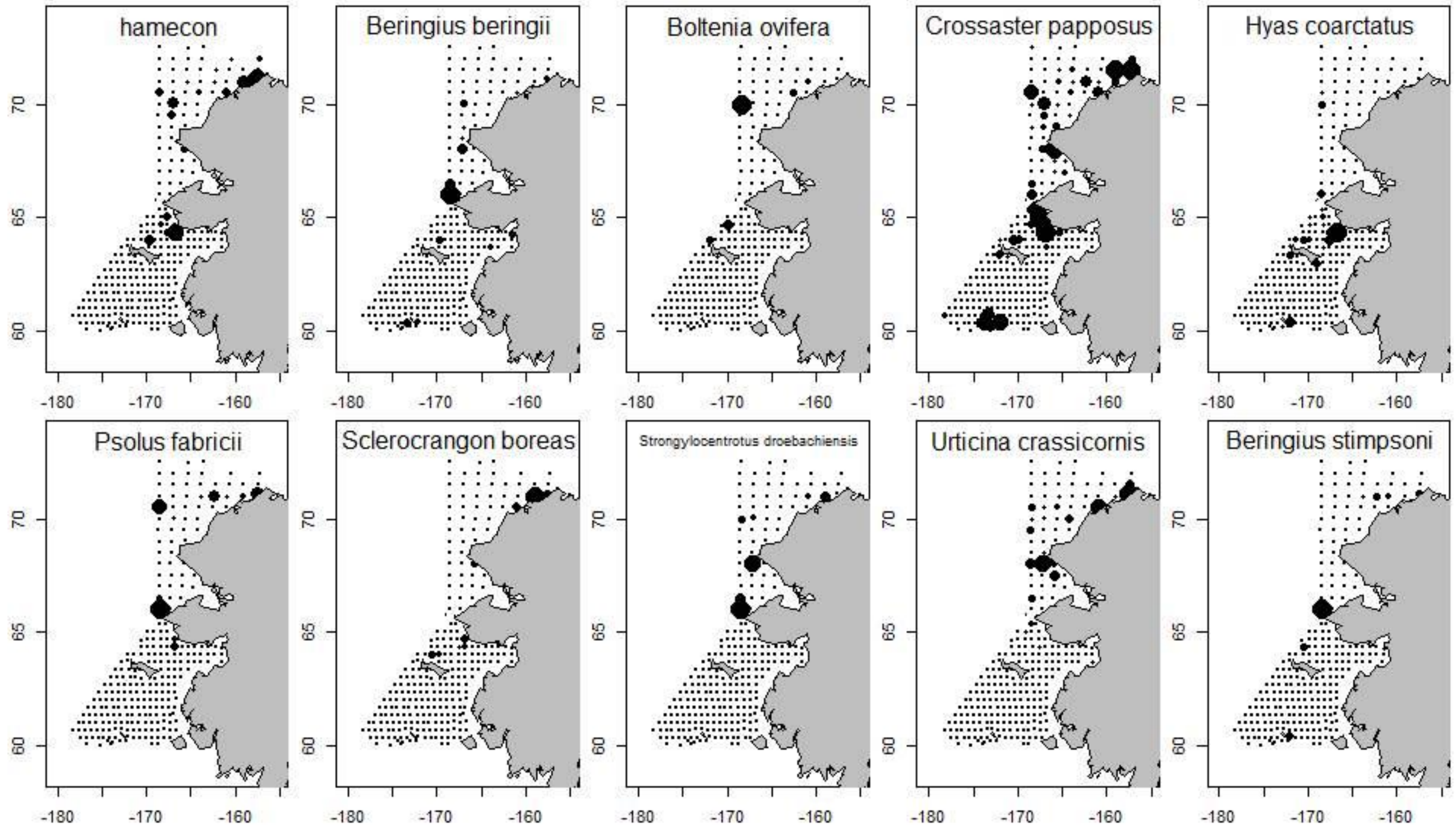
Appendix. Species distribution maps for indicator species: benthic axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



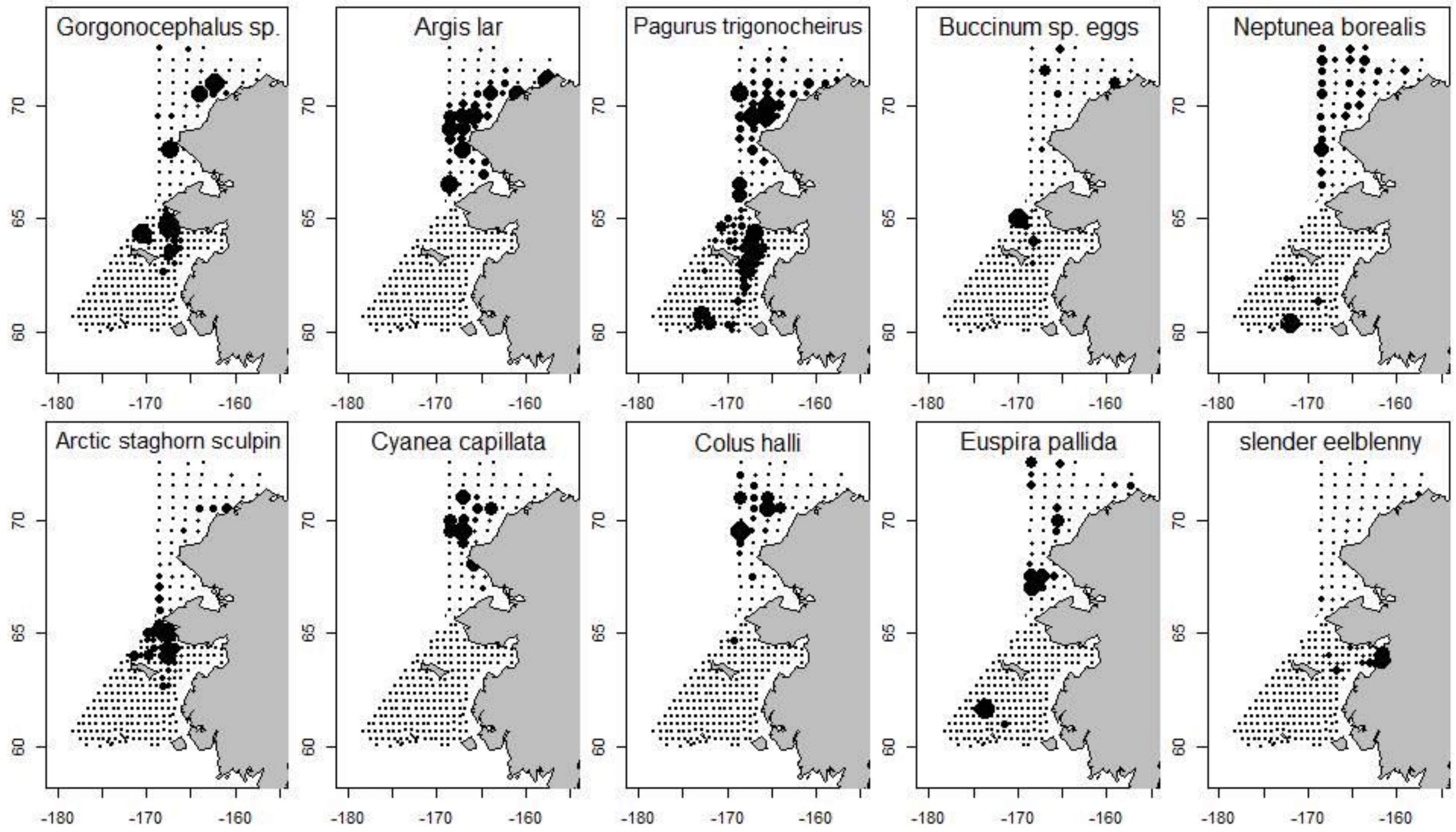
Appendix. Species distribution maps for indicator species: benthic axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



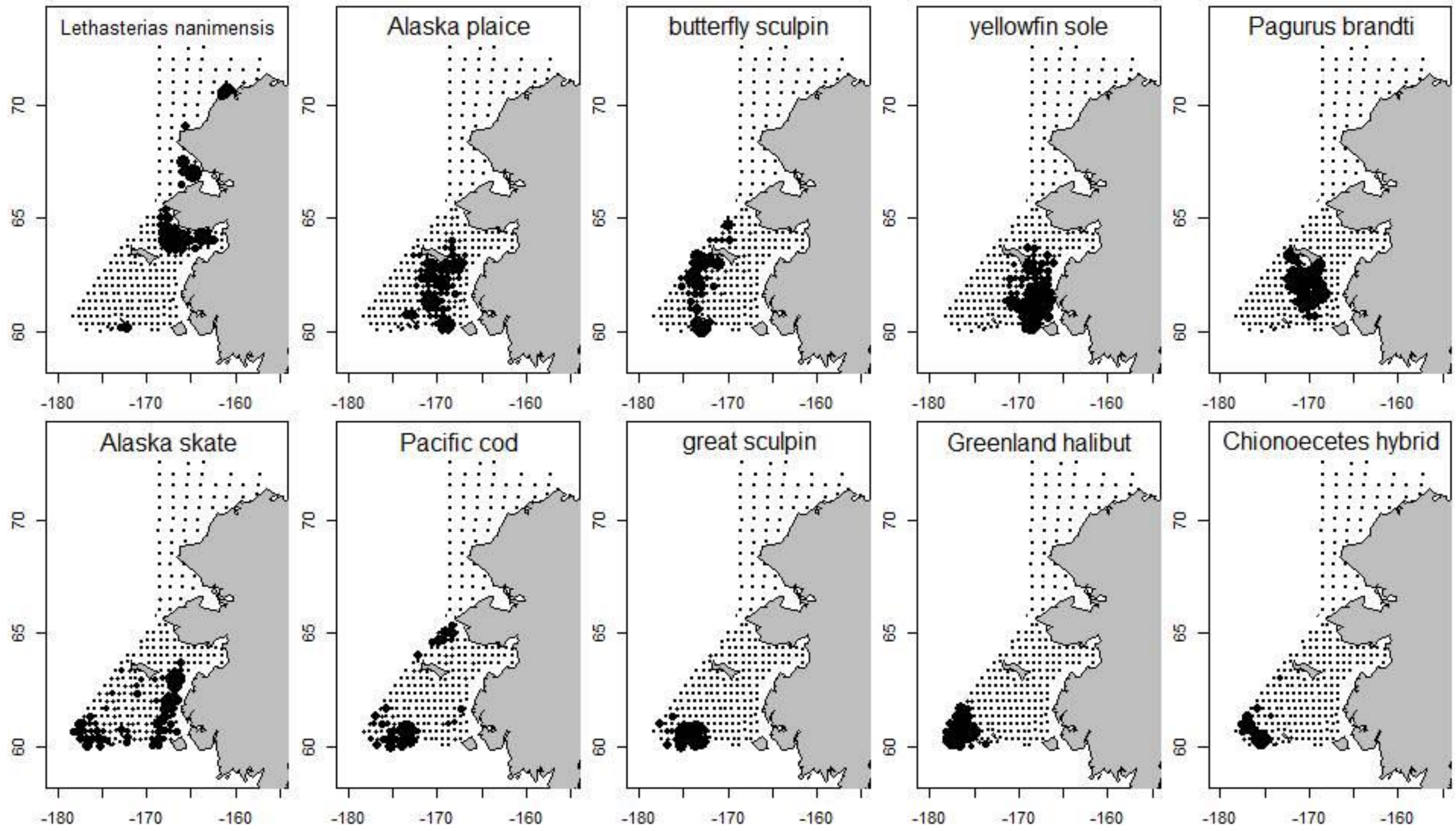
Appendix. Species distribution maps for indicator species: benthic axis 2. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



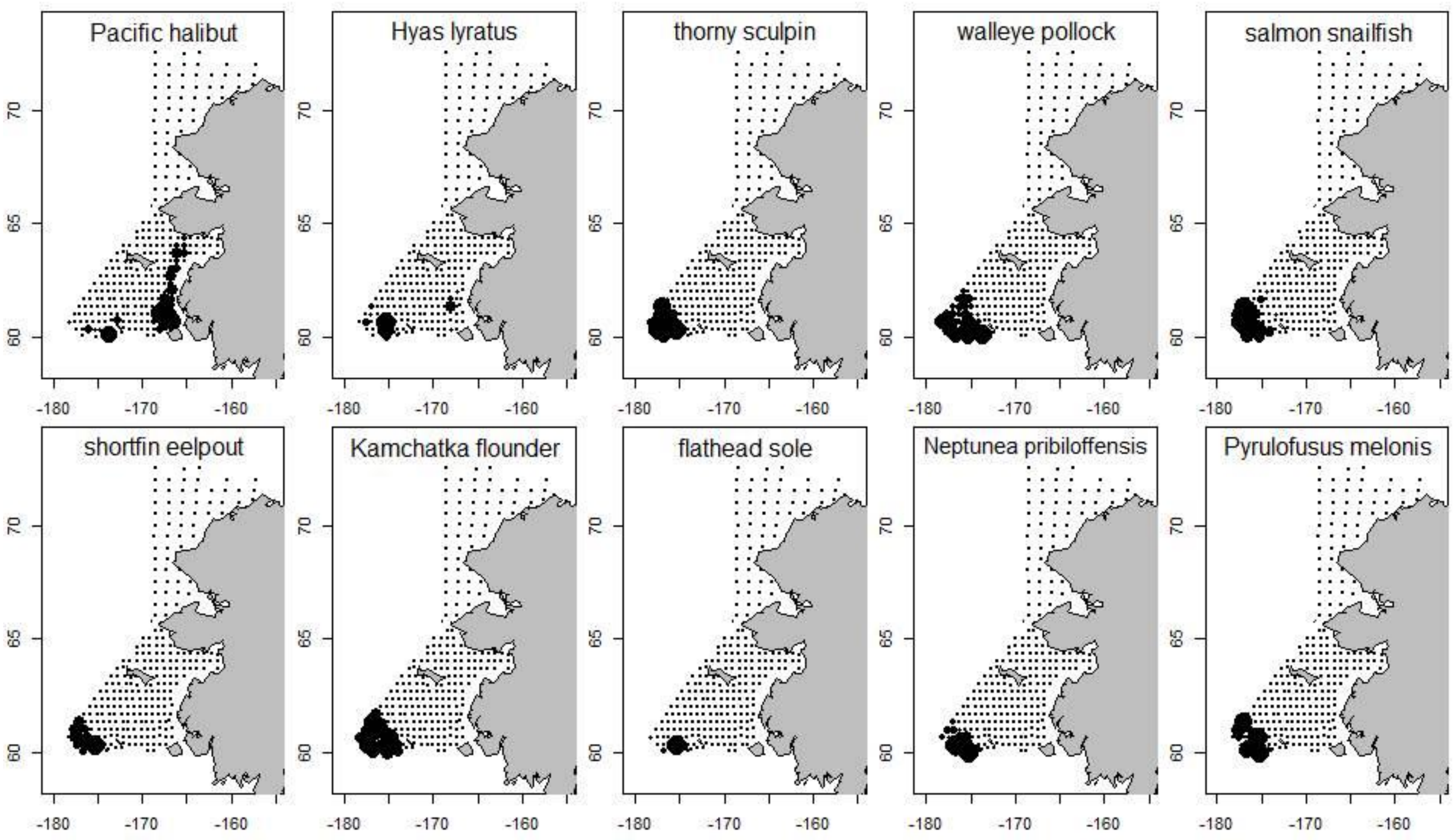
Appendix. Species distribution maps for indicator species: benthic axis 2. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



Appendix. Species distribution maps for indicator species: benthic axis 2. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



Appendix. Species distribution maps for indicator species: benthic axis 2. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



Pacific halibut

Hyas lyratus

thorny sculpin

walleye pollock

salmon snailfish

shortfin eelpout

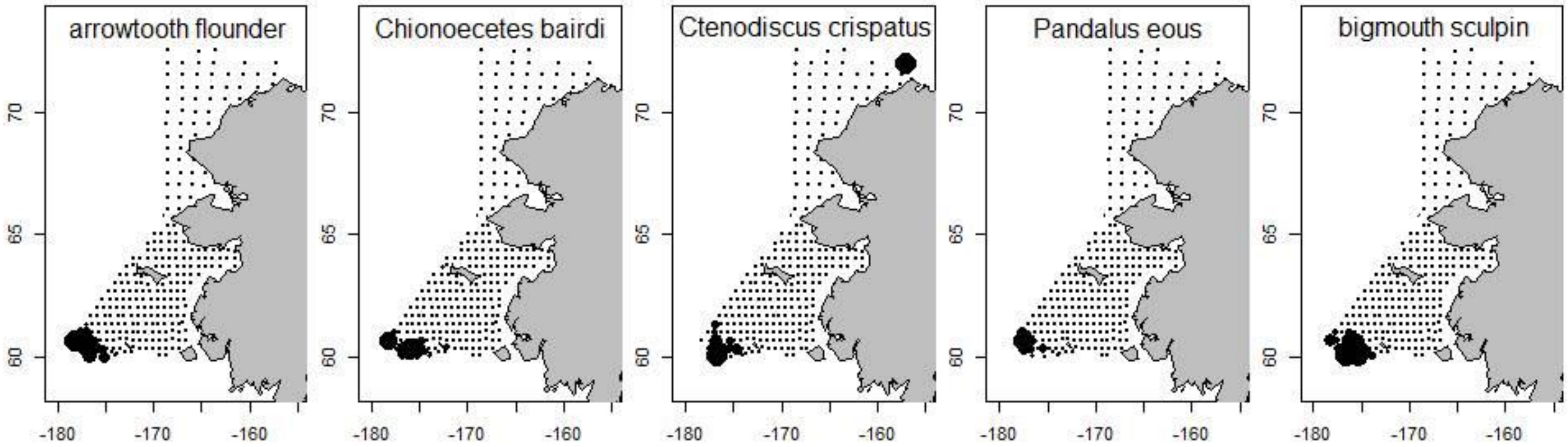
Kamchatka flounder

flathead sole

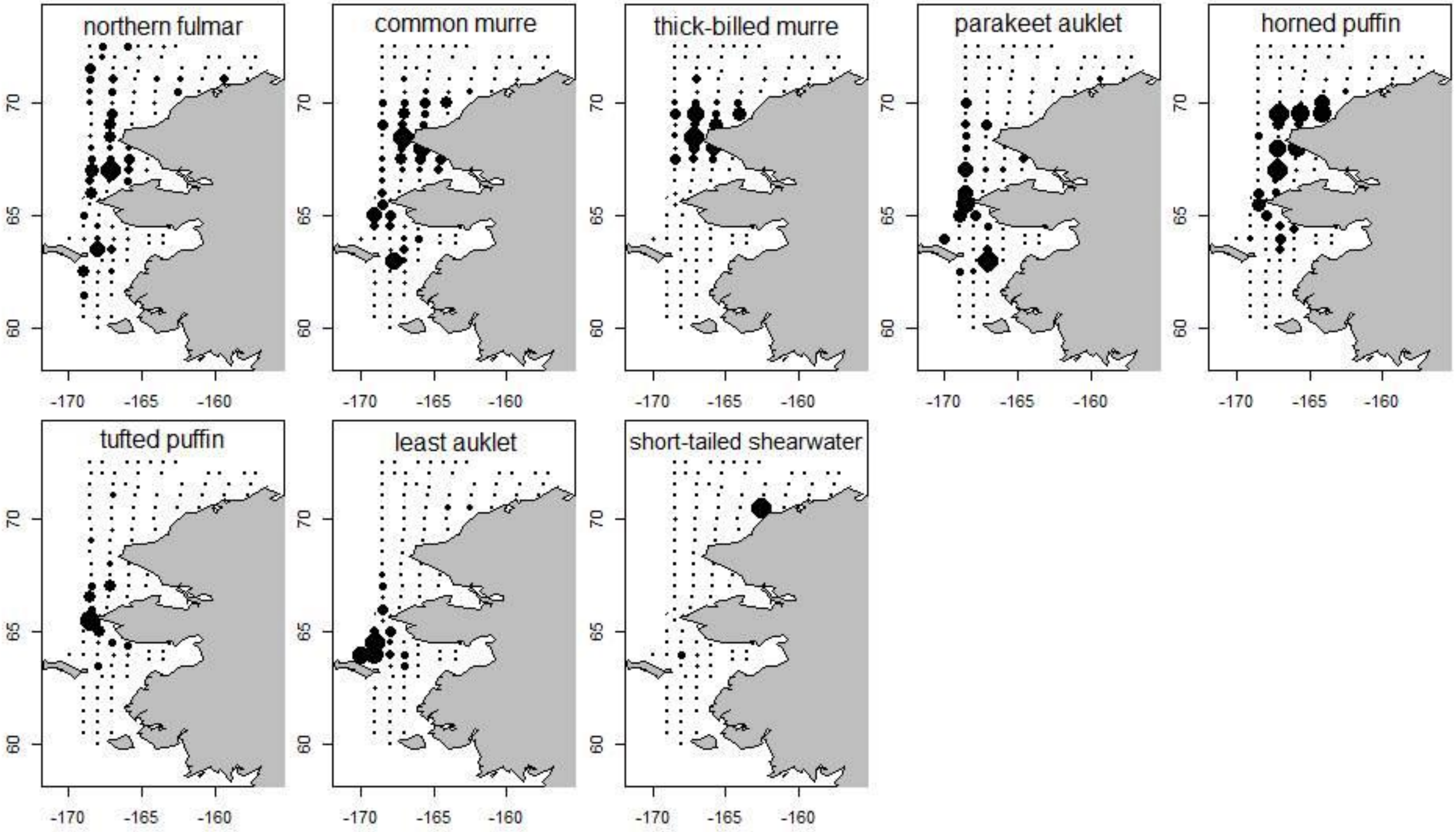
Neptunea pribiloffensis

Pyrulofusus melonis

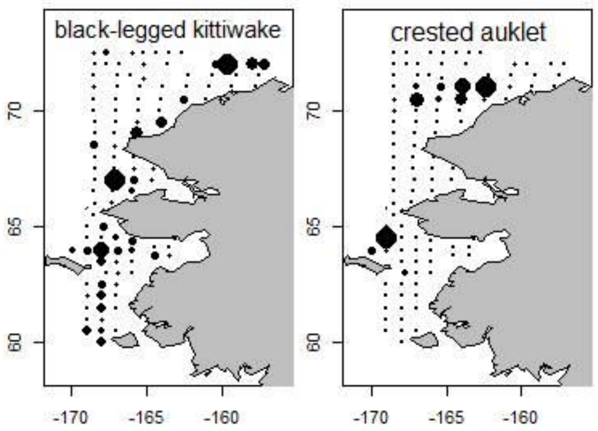
Appendix. Species distribution maps for indicator species: benthic axis 2. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



Appendix. Species distribution maps for indicator species: seabird axis 1. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



Appendix. Species distribution maps for indicator species: seabird axis 2. The species are ordered the same as in Figure 8 (i.e., from low to high NMDS axis values). Based on 2012 samples for all taxa and areas except 2010 samples for benthic taxa in the northern Bering Sea.



Appendix S.

Regional Discrimination of Chum Salmon in Alaskan Waters of the Bering and Chukchi Seas Using Otolith Elemental Analysis

Authors
Trent M. Sutton and Kevin L. Pangle

December 3, 2015

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
AYK	Arctic-Yukon-Kuskokwim
LDFA	Linear Discriminant Function Analysis
LOD	Limit of Detection
NIST	National Institute of Standards and Technology
BASIS	Bering-Aleutian Salmon International Survey
CV	Coefficient of Variation
LA-ICPMS	Laser Ablation–Inductively Coupled Plasma Mass Spectrometry

List of Oral and Poster Presentations

Pangle, K. L., and T. M. Sutton. 2014. Early marine ecology and regional discrimination of chum salmon. 145th Annual Meeting of the American Fisheries Society, August 2014, Quebec City, Quebec, Canada.

Sutton, T. M., and K. L. Pangle. 2013. Early marine ecology and regional discrimination of chum salmon in Alaskan waters using otolith elemental analysis. Alaska Chapter of the American Fisheries Society Meeting, October 2013, Fairbanks, Alaska.

Proposed Objectives and Study Chronology

Recent advances in fish otolith microchemistry analytical techniques provide a novel and powerful tool for distinguishing among fish stocks. For this study, we examined the utility of otolith elemental analyses to distinguish among stocks of juvenile Chum Salmon captured from Alaskan waters of the Bering and Chukchi seas. Specifically, we determined the feasibility and reliability of otolith elemental analysis for differentiating among and within-region variability for juvenile chum salmon stocks. This project represents a collaboration between the University of Alaska Fairbanks (Trent Sutton) and Central Michigan University (Kevin Pangle).

Spatial patterns in juvenile Chum Salmon otolith microchemistry were evaluated using fish collected from trawl surveys in the south Chukchi Sea in 2007 (n = 32) and from the north Bering Sea in 2007 and 2012 (n = 10), south Bering Sea in 2007 and 2012 (n = 49), and Bristol Bay in 2007 and 2012 (n = 6). Otoliths were mounted on a piece of transparency film, polished until the core was visible at 25X magnification, and then mounted to a petrographic slide. The microchemistry of juvenile Chum Salmon otoliths was measured using laser ablation–inductively coupled plasma mass spectrometry (LA-ICPMS) at Central Michigan University (Mount Pleasant, Michigan) by co-Principal Investigator Kevin Pangle in spring 2013 and 2014. For this analysis, we used a Photon Machines, Inc., Analyte 193 excimer laser system coupled to a Thermo Element 2 ICPMS (Thermo Fisher Scientific Inc., Waltham, Massachusetts). Otoliths were ablated with the laser across a transect that extended from the edge to the core. Trace element isotopes collected during these analyses included 25Mg, 48Ca, 55Mn, 65Cu, 66Zn, 88Sr, 137Ba, and 208Pb. The resulting dataset for each Chum Salmon otolith examined in this study consisted of the aforementioned trace element isotope concentrations (in ppm) at each sample (i.e., ablation) location along the otolith transect. These data were then georeferenced to the latitude and longitude for their respective collection locations.

Spatial patterns in juvenile Chum Salmon otolith microchemistry were examined at different spatial scales. Linear discriminant function analysis (LDFA) was used to test our ability to discriminate among our study regions (i.e., south Chukchi Sea, north Bering Sea, south Bering Sea, and Bristol Bay). Classification accuracy of the LDFA was evaluated using a jackknifed cross-validation procedure. To evaluate patterns at a finer spatial resolution, we used LDFA to test our ability to discriminate among our collection sites within each region. In addition, we also used Ward hierarchical cluster analysis to elucidate groupings of Chum Salmon otoliths of similar chemistry within each region that were independent of spatial proximity. All data are stored as CSV files, which were generated and converted from excel spreadsheets (Microsoft Excel 2010) and are available on Ocean Workspace. These data are not sensitive or classified, nor are there any legal restrictions on who may obtain or use the data. The project report below has been submitted for publication in Deep-Sea Research Part II: Topical Studies in Oceanography.

Regional Discrimination of Chum Salmon in Alaskan Waters of the Bering and Chukchi Seas Using Otolith Elemental Analysis

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Keywords: Chum Salmon; *Oncorhynchus keta*; Bering Sea; Chukchi Sea; Bristol Bay; Otolith Elemental Analysis

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1. Abstract

Chum Salmon *Oncorhynchus keta* exhibit lower genetic divergence than other Pacific salmon, thereby reducing reliable stock delineation using standard genetic methods. The objectives of this study were to examine the utility of using otolith elemental analysis to examine the early marine ecology of juvenile Chum Calmon and determine the feasibility for differentiating among and within-region variability of fish collected from the Chukchi Sea, North and South Bering Sea, and Bristol Bay. Elemental concentrations (particularly Strontium and Barium) along otolith transects provided a clear indication of the timing of ocean entry. Consistent peaks in Strontium concentration at the otolith core were indicative of maternal effects. Based on the otolith element composition associated with early life history in freshwater, accuracy of discrimination from neighboring regions was relatively high (mean = 85.8%). In contrast, the ability to discriminate fish among sites within a region was relatively poor (mean = 28.7%). These results suggest regional separation among Chum Salmon stocks, but a mixed-stock assemblage within regions. Hierarchical cluster analysis of otolith elemental composition revealed distinct Chum Salmon groups that were independent of location, further supporting the mixing of stocks within regions.

2. Introduction

Pacific salmon *Oncorhynchus* spp. support large, economically important commercial, subsistence, recreational, and personal use fisheries in Alaska. Alaskan waters, including the Bering and Chukchi seas, serve as important nursery areas for Pacific salmon, such as Chum Salmon *O. keta*. Most chum salmon migrate to sea from their natal river immediately following redd emergence from late winter to early spring (Behnke 2002; Quinn 2005). As a result, age-0 Chum Salmon have a limited opportunity to sequester freshwater elemental and isotopic markers or to deposit characteristic scale patterns relative to other Pacific salmon such as Chinook Salmon *O. tshawytscha*, Coho Salmon *O. kisutch*, and Sockeye Salmon *O. nerka* that have longer freshwater residence periods (1 to 2 years) during early life stages (Healey 1991; Urawa et al. 1998; Quinn 2005). Although genetic methods have been the primary means for resolving stock mixtures for salmonids (Shaklee et al. 1999; Behnke 2002; Seeb et al. 2004; Templin et al. 2006; Beacham et al. 2008),Chum Salmon in lower Yukon and Kuskokwim River tributaries exhibit lower genetic divergence than in other systems which reduces our ability to clearly delineate among stocks (A. Gharrett, UAF, unpublished data). Consequently, there is a need for the development of an approach that allows for more reliable differentiation of Chum Salmon stocks in Alaskan waters.

Recent advances in fish otolith microchemistry analytical techniques provide a novel and powerful tool for distinguishing among fish stocks. Otoliths are calcium-carbonate structures found in the inner ear of fish. Like fish scales, otoliths grow concentrically and, among other things, provide a means for aging fish. Because otoliths are chemically conservative and metabolically inert, elements or compounds incorporated in the calcium-carbonate matrix of the otolith are permanently retained, thus acting as an environmental monitor and archive (Campana 1999; Thresher 1999). Ambient water chemistry in the habitats where fish occur dictates the chemical composition of otoliths (Campana 1999; Kennedy et al. 2000; Milton and Chenery 2001; Kennedy et al. 2002; Dorval et al. 2007), and multi-elemental and stable isotope analyses of otoliths have been used to identify stream of origin, habitat associations, and fish stocks in a variety of fish species (e.g., Thresher 1999; Rooker et al. 2003; Wells et al. 2003; Brothers and Thresher 2004; Whitledge et al. 2006; Dorval et al. 2007; Whitledge et al. 2007; Walther et al. 2008). Because the trace element, rare earth element, and stable isotope composition of otoliths is a function of the chemical composition of local waters, which in turn reflects the geology and hydrology within the watershed, the use of these structures can serve as a useful fisheries management tool.

The microchemistry of fish otoliths has been used as a natural tag to discriminate stream of origin in salmonids. This technique has been validated independently through a combination of field collections and experimentation for a variety of fishes (Kalish 1991; Campana et al. 1994; Thorrold et al. 1998; Kennedy et al. 2000; Wells et al. 2000a, 2000b; Kennedy et al. 2002; Zimmerman and Reeves 2002; Wells et al. 2003; Bickford and Hannigan 2005; Warner et al. 2005; Zimmerman 2005; Whitledge et al. 2006; Dorval et al. 2007; Whitledge et al. 2007; Bradbury et al. 2008; Walther et al. 2008). In the case of salmonids, Kennedy et al. (2000) used stream-specific strontium isotope ratios to describe residence or movements in stocked Atlantic Salmon *Salmo salar* in tributaries of the Connecticut River. Otolith strontium ratios were successfully used as a natural tag and could be used to differentiate among streams based on 11 unique isotopic signatures. These authors were able to identify that 7% of the stocked age-0 fish had moved among streams. Wells et al. (2003) quantified molar ratios of magnesium, manganese, strontium, and barium to calcium in the first summer growth region of Westslope Cutthroat Trout *O. clarkii* from the Coeur d’Alene River, Idaho. Using three elements (Mn, Sr, and Ba), fish could be classified to particular streams with an accuracy of 82%. The authors attributed the different otolith signatures among streams to the geological heterogeneity of the surrounding drainage. These examples demonstrate that otolith microchemistry can be used to differentiate salmon stocks, even among streams, as long as there is sufficient geological heterogeneity to result in different elemental profiles of water.

For this study, we will examine the utility of otolith elemental analyses to distinguish among stocks of juvenile Chum Salmon captured from Alaskan waters of the Bering and Chukchi seas. Specifically, we will determine the feasibility and reliability of otolith elemental analysis for differentiating among and within-region variability for juvenile chum salmon stocks. These results will serve as the basis for future, more fine-scale analyses to identify stock level differences for chum salmon collected in mixed-stock fisheries in Alaska waters of the Bering and Chukchi seas.

3. Materials and Methods

3.1 Fish collection

In 2007, juvenile Chum Salmon were collected during the U.S. Bering-Aleutian Salmon International Survey (BASIS) mid-water rope trawl survey that was conducted from August through September onboard the National Oceanic and Atmospheric Administration (NOAA) fisheries *R/V Oscar Dyson*. Trawls were conducted using a Cantrawl model 300 hexagonal mesh trawl (198 m long, 55 m horizontal and 15 m vertical mouth opening, 1.2-cm mesh liner in the cod-end; Cantrawl Pacific Limited, Richmond, British Columbia) to sample the upper 13 m of the water column. Trawl tows were 30 minutes in duration and were completed at an average speed of 9.26 km per hour during daylight hours (0730-2100, Alaska Daylight Savings Time) every 55.6 km (along longitudinal meridians at stations spaced every 30 degrees of latitude) in the Chukchi (65.5°N-70°N) and northern Bering seas, including Bristol Bay (60°N-65°N; see Figure 2 in Moss et al. 2009).

During summers 2012 and 2013, juvenile Chum Salmon were collected during the Arctic Ecosystem Integrated Survey (Arctic Eis) mid-water rope trawl survey that was conducted from August through September onboard the *F/V Bristol Explorer*. Trawls were conducted using a Cantrawl model 400 hexagonal mesh trawl (198 m long, 55 m horizontal and 15 m vertical mouth opening, 1.2-cm mesh liner in the cod-end; Cantrawl Pacific Limited, Richmond, British Columbia) to sample the upper 20 m of the water column. Trawl tows were 30 minutes in duration and were completed at an average speed of 9.26 km per hour during daylight hours (0730-2100, Alaska Daylight Savings Time) every 55.6 km (along longitudinal meridians at stations spaced every 30 degrees of latitude) in the Chukchi (65.5°N-70°N) and northern Bering seas, including Bristol Bay (60°N-65°N; 2012: Figure 1; 2013: Figure 2).

Following completion of each tow haul during each trawl survey, trawl contents were sorted on the ship deck and fish samples were moved to an onboard laboratory, sorted by species, measured for fork length (FL; to the nearest 1 mm) and wet body weight (WW; to the nearest 0.01 g), and frozen pending subsequent laboratory analyses. All juvenile Chum Salmon were retained for otolith analyses in the laboratory if sample sizes were less than 50 individuals at each station. If catches were greater than 50 juvenile Chum Salmon at a given station, a random subsample of 50 individuals per station of all observed sizes were retained for subsequent laboratory analyses of otoliths.

3.2.Otolith processing

To remove otoliths from juvenile Chum Salmon, a dorso-ventral cut from the top of the head through the preopercle was made just anterior to the fleshy margin atop the head to expose the brain and semicircular canals (Secor et al. 1991). Both sagittal otoliths were removed and gently wiped of blood, fluids, and the otolithic membrane. Otoliths were rinsed in deionized water, placed in sterile 1.5-ml centrifuge tubes (otolith pairs from each fish were placed in separate vials), marked with collection information for that individual (e.g., station number, sampling date, sample number, etc.), and allowed to air dry for at least one week before laboratory processing.

Spatial patterns in juvenile Chum Salmon otolith microchemistry were evaluated using fish collected from the south Chukchi Sea in 2007 (n = 32) and from the north Bering Sea in 2007 and 2012 (n = 10), south Bering Sea in 2007 and 2012 (n = 49), and Bristol Bay in 2007 and 2012 (n = 6). After the otoliths were dry, they were mounted sulcus side up on a piece of transparency film using Superglue, and polished until the core was visible at 25X magnification. Polished otoliths were then mounted using Superglue to a petrographic slide, sonicated for five minutes, and rinsed three times with ultrapure water.

The microchemistry of juvenile Chum Salmon otoliths was measured using laser ablation–inductively coupled plasma mass spectrometry (LA-ICPMS). For this analysis, we used a Photon Machines, Inc., Analyte 193 excimer laser system coupled to a Thermo Element 2 ICPMS (Thermo Fisher Scientific Inc., Waltham, Massachusetts). Otoliths were ablated with the laser across a transect that extended from the edge to the core. Trace element isotopes collected during these analyses included ^{25}Mg, ^{48}Ca, ^{55}Mn, ^{65}Cu, ^{66}Zn, ^{88}Sr, ^{137}Ba, and ^{208}Pb. To correct for possible ablation yield differences among otoliths, we used ^{48}Ca as the internal standard because this element comprises a large, constant proportion of the otolith (approximately 99% $CaCO_3$). To account for instrumental precision and drift, a glass reference standard (National Institute of Standards and Technology (NIST) 610 or 612) was analyzed before and after every 16 otolith samples (n = 2 replicates before and after). All elements had concentrations above the limit of detection (LOD; defined by three standard deviations above background levels after correcting for ablation yield and drift), and all element concentrations were above the LOD for 90% of otoliths and a CV < 10.5%.

Because our study focused on spatial patterns in the natal origin of juvenile Chum Salmon, we included only the section of the ablation transect across the otoliths that reflected the time spent in their natal stream prior to outmigration to the marine environment. We delineated transects based on Sr and Ba concentrations, which have been shown in previous studies to be positively and negatively correlated with salinity, respectively (Elsdon and Gillanders 2005; Gillanders 2005). In our study, elemental concentrations of Sr^{88} and Ba^{137} along juvenile Chum Salmon otolith transects provided a clear indication of migration from freshwater to saltwater environments (see Figure 3 for fish sample #1711 which is representative of juvenile Chum Salmon otoliths examined in this study). The natal section of the transect was defined by the relatively stable Sr that existed between elevated Sr (reduced Ba) concentrations at the core of the otolith due to maternal effects, with the magnitudes serving as a proxy for the duration the mother spends in the stream prior to spawning. In contrast, elevated Sr (reduced Ba) are caused by migration to the ocean (Kraus and Secor 2004; Gillanders 2005). We used mean elemental concentrations from the natal section for subsequent spatial analyses.

3.3. Data analyses

We analyzed spatial patterns in juvenile Chum Salmon otolith microchemistry at different spatial scales. Linear discriminant function analysis (LDFA) was used to test our ability to discriminate among our study regions (i.e., south Chukchi Sea, north Bering Sea, south Bering Sea, and Bristol Bay). Classification accuracy of the LDFA was evaluated using a jackknifed cross-validation procedure. To evaluate patterns at a finer spatial resolution, we used LDFA to test our ability to discriminate among our collection sites within each region. In addition, we also used Ward hierarchical cluster analysis to elucidate groupings of Chum Salmon otoliths of similar chemistry within each region that were independent of spatial proximity.

4. Results

Juvenile Chum Salmon could be grouped into four regional pools to assess large-scale differences in otolith chemistry (Table 1). Based on otolith chemisty associated with the freshwater period of life history, accuracy of discrimination from neighboring regions was relatively high (mean = 85.8%; range 50-100%). In contrast, the ability of discriminate fish among sites within a region was relatively poor (mean = 28.7%; 23-34%). These results suggest distinct regional separation among juvenile Chum Salmon stocks, but a mixed-stock assemblage within regions. Hierarchical cluster analysis of otolith elemental composition revealed distinct groups of individuals that were independent of location, further supporting the mixing of Chum Salmon stocks within regions (Figure 4).

5. Discussion

Our analysis of Chum Salmon otolith microchemistry revealed strong patterns associated with large-scale movement. The out-migration exhibited by this species during their early life history was clearly reflected in the ablation transects, where regions of the otolith corresponding to maternal effects, the signature of the natal stream, and the signature of the marine environment could be readily demarcated based on distinct changes in Sr and Ba. This finding supports the utility of otolith chemistry to discriminate natal origin of Chum Salmon, despite their relatively short residency in natal streams (Behnke 2002; Quinn 2005), and builds on previous research (e.g., Kraus and Secor 2004, Gillanders 2005) by providing further evidence of the general use of Sr and Ba to capture the migratory history of anadromous fishes.

In addition to these temporal patterns, the natal chemical signature observed in the otoliths differed according to the collection location of juveniles; however, these differences were strongly dependent on spatial scale. At a large scale (i.e., 1,000s of km), we found that Chum Salmon otolith microchemistry was relative unique to each region. These regional differences may be a product of broad geological patterns, which can influence trace elemental concertation of the water in tributaries (Rondeau et al. 2005) and, in turn, the otoliths of fish inhabiting the tributaries (Bath et al. 2000; Wells et al. 2003) . For example, total strontium-calcium (Sr:Ca) ratios for adult Chinook Salmon from the Anvik (0.005896 ± 0.00036) and Salcha (0.003025 ± 0.00048) rivers were significantly different between these two rivers which are widely separated along the Yukon River drainage (M. Wooller, UAF, unpublished data). Because Chinook Salmon in these two rivers have the same life history, differences in the elemental composition of their otoliths is likely a function of the chemical composition of local waters, which in turn reflects watershed geology and hydrology.

These regional differences also suggest that Chum Salmon in our study are not migrating between regions; otherwise, the distinction between regions would have been muddle. Our results changed greatly at smaller, within-region spatial scales, where differences between collection locations in otolith microchemistry became less apparent. Importantly, this result suggests that fish of different natal origin are mixing at a regional level (i.e., a mixed-stock population). This inference is further supported by cluster analysis, which identified significant groupings of fish based on the natal chemical signature that was independent of collection location.

These spatial patterns in otolith microchemistry indicate that, following out-migration, Chum Salmon are acting as a mixed-stock population, which can have significant implications to the management these populations Managing such populations as a single unit may hamper predictions of population structure and dynamics and can lead to overexploitation of some stocks and an overall loss of genetic diversity (Begg et al. 1999; Hilborn et al. 2003). Rather, effective management of mixed-stock populations can require a finer-scale approach that considers how stocks (i.e., natal streams) differentially contribute individuals according to local processes. For example, for a stock that is found not to be contributing recruits to the fishery, agencies could (1) implement research programs designed to understand factors limiting that stock's contribution, or (2) implement conservation efforts designed to protect that stock (and perhaps its genetic distinctiveness). Likewise, agencies could simultaneously implement stock-specific harvest quotas designed to protect stocks that consistently contribute a large number of recruits to the fishery. In the Arctic-Yukon-Kuskokwim (AYK) area which drains into the Bering, Chukchi, and Beaufort seas, commercial harvests of Chum Salmon totaled over one million fish in 2012 (Eggers et al. 2013). Subsistence harvest of Chum Salmon is commonly the primary salmon resource available in these western and northwestern Alaska drainages (Wolfe and Spaeder 2009). Catches of Chum Salmon for subsistence use often exceed commercial harvests, with average catches in the Yukon and Kuskokwim River drainages over 100,000 fish per year since the 1990s and 60,000 fish per year since, respectively (Brown and Jallen 2012; Ikuta 2012). Given the magnitude of Chum Salmon fisheries in Alaskan waters, there is a definite need to better understand the composition of mixed-stock populations of this species.

6. Conclusion

These results of this study suggest regional separation among Chum Salmon stocks in the Bering and Chukchi seas, but a mixed-stock assemblage within regions in those systems. Hierarchical cluster analysis of otolith elemental composition revealed distinct Chum Salmon groups that were independent of location, further supporting the mixing of stocks within regions. The aforementioned approach to management requires the ability to identify the specific origin of individual fish. Our current study was not designed to test this requirement given that we did collect Chum Salmon directly from different natal tributaries. However, our study results demonstrate the potential for characterizing natal signatures that would allow for the identification of river of origin for Chum Salmon. Thus, future research that uses otolith microchemistry to discriminate Chum Salmon of known origin will likely be of significant value towards better understanding variability in stock structure and population dynamics of Chum Salmon.

7. Acknowledgements

We would like to thank all crewmembers aboard the NOAA ship *Oscar Dyson* and the F/V *Bristol Explorer*, as well as technicians from NOAA/Auke Bay Labs who helped collect and extract otolith samples for analysis. We would particularly like to thank J. Murphy, NOAA, National Marine Fisheries Service, for otolith samples and his expertise on juvenile salmon ecology. Additional thanks go out to S. Vega for sample preparation and H. Preston, F. Baker, and J. Student for sample processing. This study was primarily funded with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior. Additional funding was provided by the Central Michigan University Institute of Great Lakes Research and the University of Alaska Fairbanks School of Fisheries and Ocean Sciences. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Table 1. Accuracy of discrimination for juvenile chum salmon during the freshwater period of life history between the four geographic regions and between sites within each region based on otolith elemental analyses.

Region	Accuracy – Between Regions	Accuracy – Sites Within Regions
South Chukchi Sea	97%	23%
North Bering Sea	50%	29%
South Bering Sea	96%	34%
Bristol Bay	100%	Not Applicable

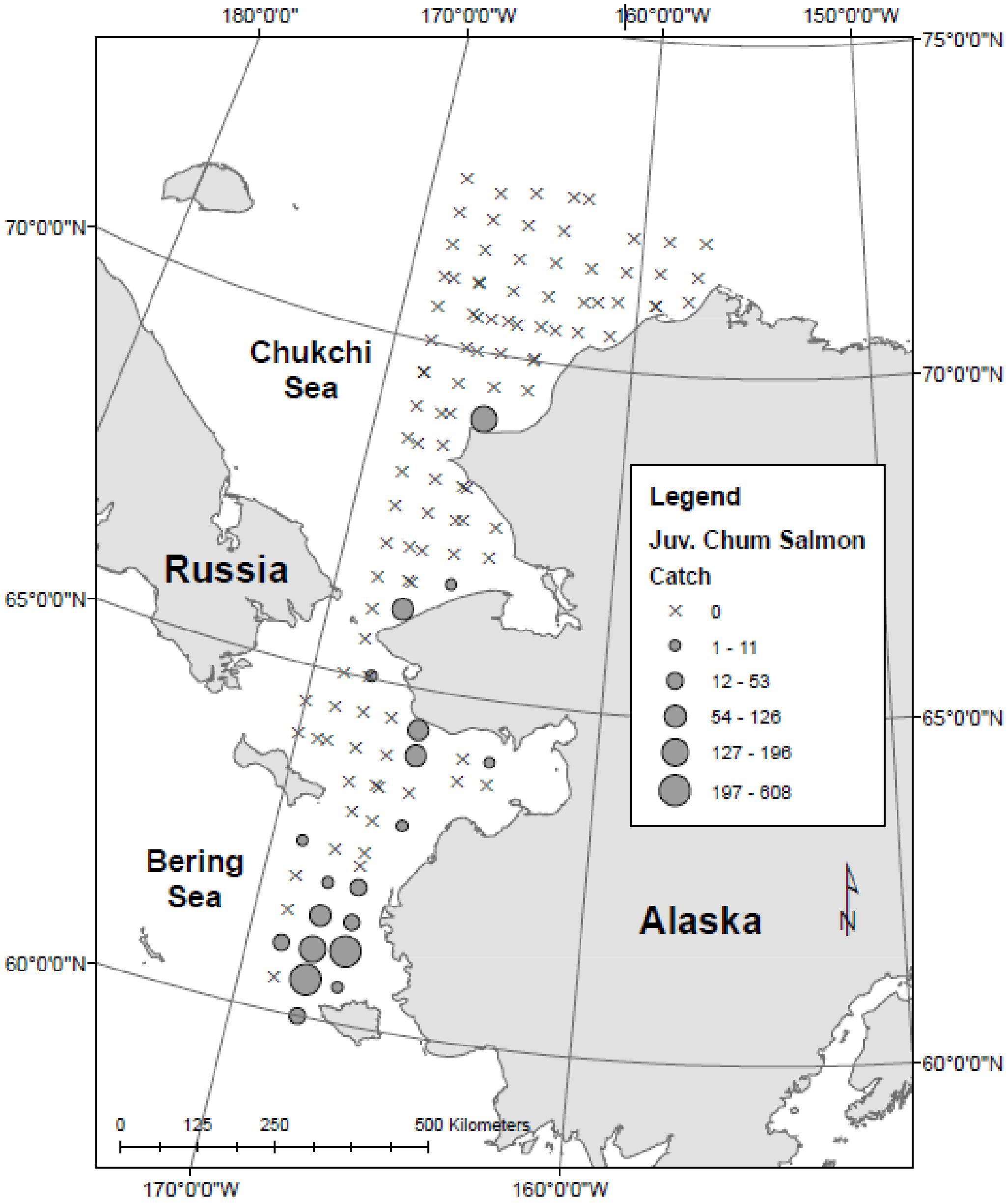


Figure 1. Distribution of sampling locations in the Chukchi and Bering seas in 2012 as part of the Arctic Eis trawl surveys.

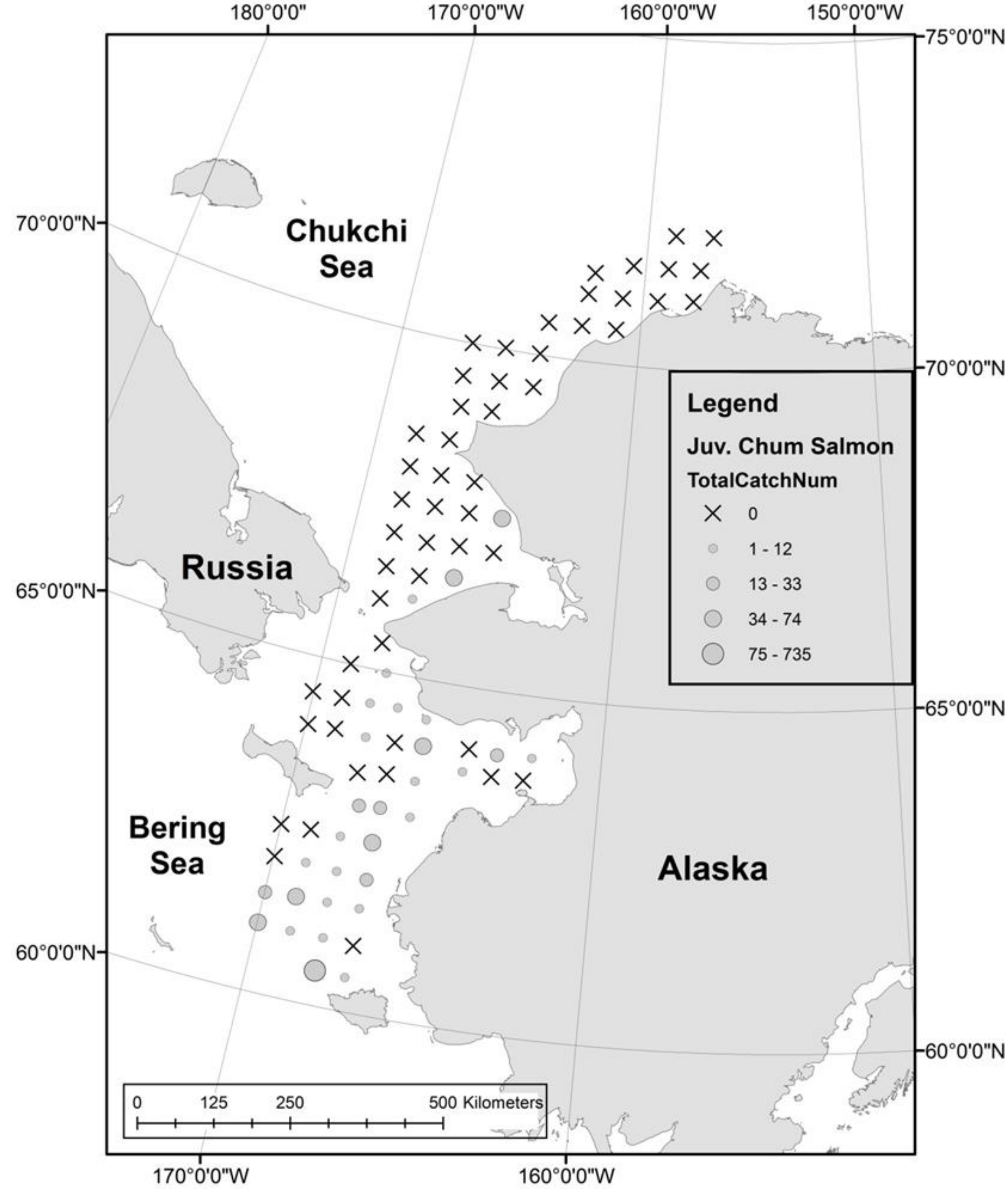


Figure 2. Distribution of sampling locations in the Chukchi and Bering seas in 2013 as part of the Arctic Eis trawl surveys.

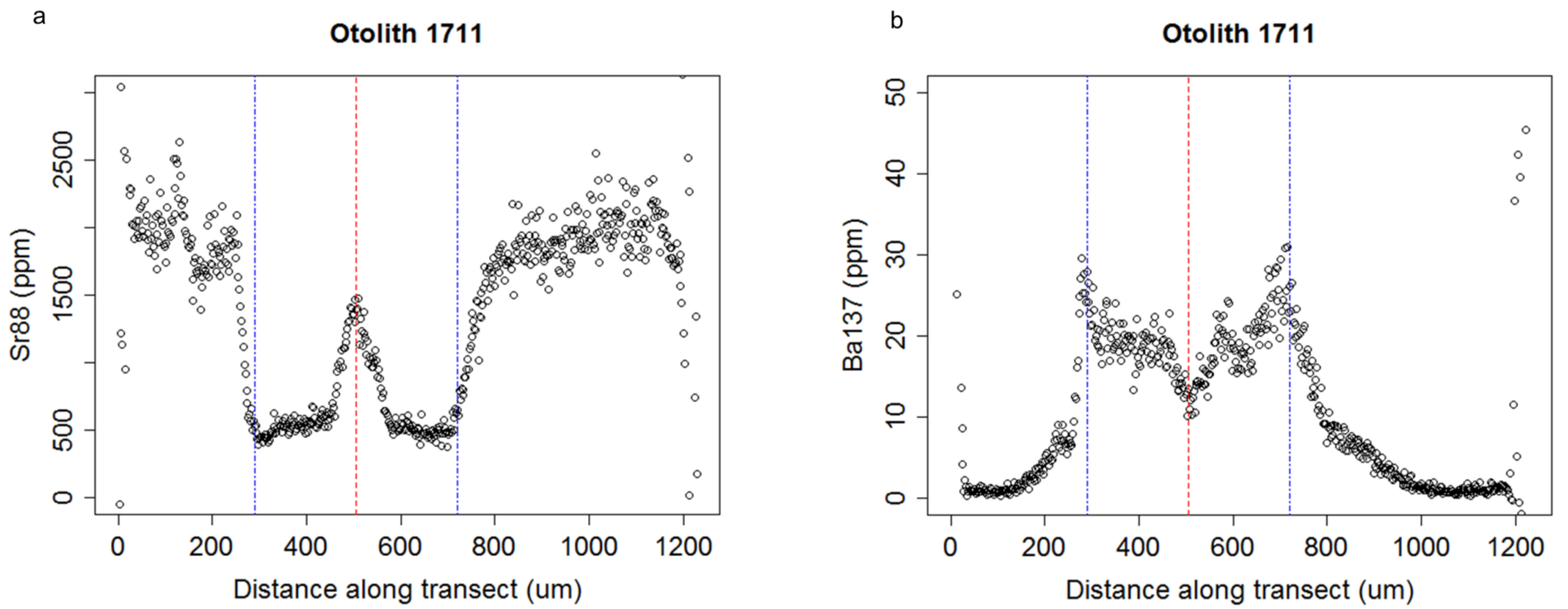
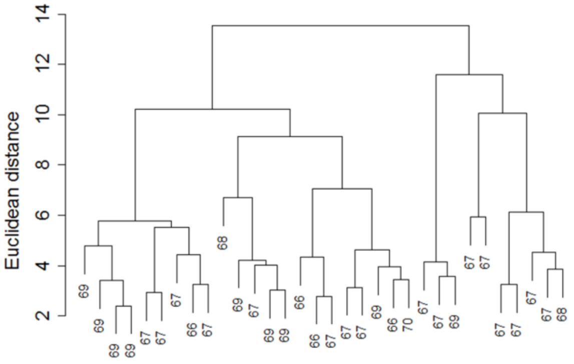
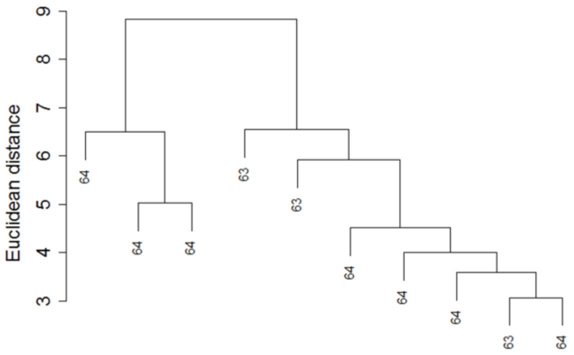


Figure 3. Elemental concentrations for (a) strontium (Sr^{88}; ppm) and (b) barium (Ba^{137}; ppm) by linear distance (measured in µm) along otolith transverse plane transects for a representative juvenile chum salmon (sample #1711). The dashed line and dot-dashed lines indicate the location of the core and fresh-to-saltwater transition, respectively.

a) South Chukchi



b) North Bering



c) South Bering

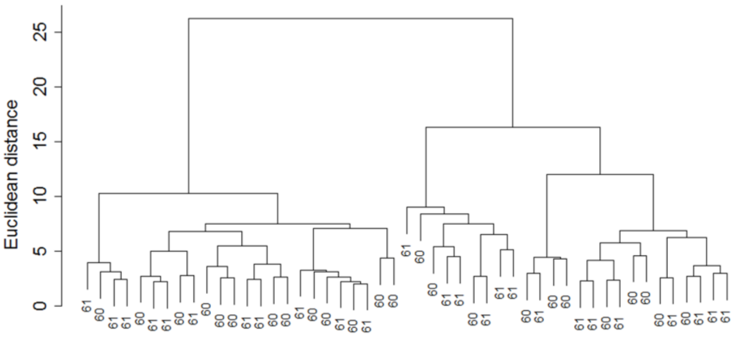


Figure 4. Ward hierarchical cluster analysis of otolith chemistry for juvenile chum salmon for three of the four study regions. Site labels represent the latitudes of the collection sites. Bristol Bay fish were not considered for this analysis because fish were collected from only one latitude.

Appendix T.

Marine-entry timing and growth rates of juvenile Chum Salmon in Alaskan waters of the Chukchi and northern Bering seas

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Date
January 11, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
BASIS	U.S. Bering-Aleutian Salmon International Survey
ICP-MS	Inductively Coupled Plasma-Mass Spectrometry
SST	Sea Surface Temperature

List of Oral and Poster Presentations

Vega, S. L. and T. M. Sutton. Marine-Entry Timing and Growth Rates of Juvenile Chum Salmon in Alaskan Waters of the Chukchi and Northern Bering Seas. Alaska Chapter of the American Fisheries Society Meeting, October 2014, Juneau, Alaska.

Vega, S. L., T. M. Sutton, M. D. Adkison and J. M. Murphy. Reconstruction of Ocean-Entry Timing and Growth Rates of Juvenile Chum Salmon in Alaskan Waters of the Chukchi and Northern Bering Seas. Annual Meeting of the American Fisheries Society, August 2014, Quebec City, Canada.

Vega, S. L., T. M. Sutton, M. D. Adkison and J. M. Murphy. Reconstruction of Ocean-Entry Timing and Growth Rates of Juvenile Chum Salmon in Alaskan Waters of the Chukchi and Northern Bering Seas. Alaska Chapter of the American Fisheries Society Meeting, October 2013, Fairbanks, Alaska.

Vega, S. L., T. M. Sutton, M. D. Adkison and J. M. Murphy. Reconstruction of Ocean-Entry Timing and Growth Rates of Juvenile Chum Salmon in Alaskan Waters of the Chukchi and Northern Bering Seas. 2013. Alaska Chapter of the American Fisheries Society Student Subunit Symposium, April 2013, Fairbanks, Alaska.

Proposed Objectives and Study Chronology

The objectives of this study were to determine the timing of marine entry and early marine growth rates of juvenile Chum Salmon *Oncorhynchus keta* in the Chukchi and northern Bering seas. Otolith samples were collected from juvenile Chum Salmon during the 2012 and 2013 Arctic Eis surveys, as well as from a previous BASIS survey in 2007. Laboratory preparation of otoliths occurred between September 2012 and March 2014. Daily age reads and data analyses were conducted from March 2014 to November 2014. The successful completion of Ms. Vega's master's degree occurred in July 2015, only one semester later than anticipated.

The data analyzed and described here can be found on AOOS Arctic Eis Ocean Workspace in the "Salmon Ecology" folder under "Pelagic Species". Data will be made publically available through the AOOS website before completion of the Arctic Eis project. This report has been submitted in manuscript form to the Arctic Eis special edition of Deep-Sea Research Part II and at the time of this report submission has been resubmitted after one round of revisions.

1. Abstract

Climate change in the Arctic has implications for influences on juvenile Chum Salmon Oncorhynchus keta early life-history patterns, such as altered timing of marine entry and/or early marine growth. Sagittal otoliths were used to estimate marine entry dates and daily growth rates of juvenile Chum Salmon collected during surface trawl surveys in summers 2007, 2012, and 2013 in the Chukchi and northern Bering seas. Inductively coupled plasma-mass spectrometry (ICP-MS) was used to discriminate between freshwater and marine sagittal growth on the otoliths, and daily growth increments were counted to determine marine-entry dates and growth rates to make temporal and regional comparisons of juvenile Chum Salmon characteristics. Marine-entry dates ranged from mid-June to mid-July, with all region and year combinations exhibiting similar characteristics in entry timing (i.e. larger individuals at the time of capture entered the marine environment earlier in the growing season than smaller individuals in the same region/year), as well as similar mean marine-entry dates. Juvenile Chum Salmon growth rates were on average 4.9% body weight per day in both regions in summers 2007 and 2012, and significantly higher (6.8% body weight per day) in the Chukchi Sea in 2013. These results suggest that juvenile Chum Salmon in the northern Bering and Chukchi seas currently exhibit consistent marine-entry timing and early marine growth rates, despite some differences in environmental conditions between regions and among years. This study also provides a baseline of early marine life-history characteristics of Chum Salmon for comparisons with future climate change studies.

2. Introduction

Pacific salmon *Oncorhynchus* spp. in the northern Bering and Chukchi seas may be affected by changing oceanographic conditions due to warming trends in the Arctic and sub-Arctic (Sigler et al. 2011; Nielsen et al. 2013). Climate-change predictions include warmer temperatures at higher latitudes, hydrographic changes for salmon-bearing streams, and rising sea surface temperatures (SSTs; Crozier et al. 2008). Future changes in climate may cause fish populations to exhibit shifts in response to ecological changes (Walther et al. 2002), which includes range extensions, altered timing of spawning runs, and modifications to ecology and of life-history stage dynamics (Nielsen et al. 2013). These changes have implications on the distribution and abundance of Chum Salmon in the northern Bering and Chukchi seas, which are an important commercial, subsistence, and recreational resource throughout Alaska. In the Arctic-Yukon-Kuskokwim (AYK) area which drains into the Bering, Chukchi, and Beaufort seas, commercial harvests of Chum Salmon totaled over one million fish in 2012 (Eggers et al. 2013). Subsistence harvest of Chum Salmon is commonly the primary salmon resource available in these western and northwestern Alaska drainages, with average catches in the Yukon and Kuskokwim River drainages between 60,000 and 100,000 fish per year since the 1990s (Wolfe and Spaeder 2009; Brown and Jallen 2012; Ikuta 2012).

The first summer spent in the ocean is a critical period for growth and survival of Pacific salmon. The timing of outmigration is important for juvenile salmon so that they reach the marine environment when food resources are available for optimal growth and survival (Mueter et al. 2005; Quinn 2005). Juvenile salmon that do not reach a critical size during their first summer at sea will likely not survive high size-dependent mortality (Beamish and Mahnken 2001) or the harsh metabolic demands of winter (Farley et al. 2009). Larger individuals are more likely to survive periods of starvation due to higher energy reserves than smaller fish, typically have greater tolerance to environmental variability, and are less vulnerable to predation (Sogard 1997; Beamish et al. 2004). As a result, year-class strength has been shown to be directly related to growth during the first marine year (Sogard 1997; Beamish et al. 2004).

Environmental diversity and behaviors exhibited by Pacific salmon allows for the alteration of life-history in response to climate change, including juvenile migration timing and early marine growth rates (Crozier et al. 2008). As a result, there is a clear need to understand the early marine period of Pacific salmon life history in the northern Bering and Chukchi Seas. Both regions are important for the feeding, growth, and survival of juvenile Chum Salmon from western Alaska watersheds (Farley and Moss 2009; Moss et al. 2009; Sigler et al. 2011). However, the Chukchi Sea is a data-poor region which has been minimally studied with respect to juvenile salmon ecology. By understanding the full range of juvenile Chum Salmon early life-history characteristics and growth information at a regional scale, managers will be better equipped for making predictions on climate change effects. The objectives of this study were to compare the timing of marine entry and early marine growth of juvenile Chum Salmon in the northern Bering and Chukchi seas. This research provides a baseline on the status of juvenile Chum Salmon in the northern Bering and Chukchi seas, and a benchmark for future comparisons that result from a changing Arctic climate.

3. Materials and Methods

3.1 Fish collection

Juvenile Chum Salmon were collected during the U.S. Bering-Aleutian Salmon International Survey (BASIS) in August-September 2007 onboard the NOAA ship *Oscar Dyson*. In August-September 2012 and 2013, trawls were conducted by the F/V *Bristol Explorer* during the Arctic Ecosystem Integrated Survey (Arctic Eis). A Cantrawl model 400/601 (Cantrawl Pacific Limited, Richmond, British Columbia) midwater hexagonal mesh trawl (198 m long, with a 50-m horizontal opening and a 120-m headrope; 12-mm mesh cod-end liner) was used to sample to a depth of 20 m. Sampling stations were spaced at 55-km intervals along latitudinal and longitudinal lines in the Chukchi Sea (CS; 66° N-70° N) and northern Bering Sea (NBS; 60° N-65.5° N) east of -170° W longitude (Figure 1; see Figure 2 in Moss et al. 2009).

During trawl surveys, collected juvenile salmon were sorted by species and subsamples of each species were measured for fork length (FL) to the nearest 1 mm and wet weight to the nearest 1 g. If more than 50 juvenile Chum Salmon were caught in a trawl haul, a random subsample of 50 fish across all measured sizes was selected for biological sampling. Samples from the NBS in 2013 were not included in these analyses due to a flooding event onboard the F/V *Bristol Explorer* which resulted in the loss of all samples collected from this region. To evaluate marine-entry timing and growth rates of juvenile Chum Salmon, a subsampling approach was used to select otolith samples from the CS and NBS. Fish were organized into 20-mm FL-frequency bins and all samples were used from FL-frequency bins with fewer than 10 samples. For all other FL-frequency bins and stations, samples were chosen at random, alternating among bins and chosen from all stations, until total sample sizes reached between 100 and 110 fish for consistency in sample sizes across regions and years. In the CS in 2012 and 2013, all samples were used for analyses due to low catches.

3.2 Otolith preparation

Left sagittal otoliths of juvenile Chum Salmon were mounted on microscope slides with Crystalbond™ thermoplastic resin mounting adhesive (Structure Probe, Inc., West Chester, Pennsylvania). Otoliths were thin sectioned along the sagittal plane using a Histolic Precision

Grinding Fixture (Buehler Ltd., Lake Bluff, Illinois) and hand-ground on wet 5-µm lapping film (Precision Surfaces International, Houston, Texas) until daily growth increments were visible. Just prior to reaching the core, the microscope slide was reheated and the otolith was turned over to polish the second side until the core and daily growth increments could be observed using a Leica compound microscope (Leica Microsystems, Wetzlar, Germany) with transmitted light.

Preparation of otoliths from the NBS in 2007 differed slightly from the other four sampling region/year combinations. These samples were prepared at the NOAA facilities in Juneau, Alaska, and polished by hand on a LaboPol-21 polishing machine (Struers, Inc., Cleveland Ohio) using 1200 and 4000 grit wet-dry sandpaper under flowing water (Murphy et al. 2009). Batch slides of otoliths were created, leveled using a digital micrometer to a uniform thickness, and briefly polished with 8000 grit micro-mesh polishing cloth (Murphy et al. 2009). All other facets of preparation were identical to procedures followed for 2012 and 2013 samples.

3.3 ICP-MS

Otolith chemical analyses were completed using an Agilent 7500ce inductively-coupled plasma mass spectrometer (ICP-MS; Agilent Technologies, Inc. Santa Clara, California) fitted with a cs lens stack and coupled with a New Wave UP213 laser ablation system (New Wave Research, Fremont, California) at the University of Alaska Fairbanks (UAF) Advanced Instrumentation Laboratory. A cs lens stack has a larger set of apertures for ions to enter and increases sensitivity and allows for lower limits of detection compared to the default ce lens stack. All ablations occurred in a helium atmosphere and a NIST 610 (Ca^{43}) standard reference material was used as a calibration standard. Raw data were processed and calibrated with the Iolite software package (Melbourne Iolite Group, Melbourne, Australia; Paton et al. 2011) using the method described in Longerich et al. (1996).

Ablations took place on a transverse cross-section from the ventral to the dorsal side of the otolith passing through the core. The chemical cores of otoliths were identified by a peak in the molar ratio of manganese to calcium (Mn:Ca). A sharp increase in otolith strontium concentration along the molar ratio transect gave a chemical reference point for marine entry. Although there is variation in the magnitude of strontium to calcium molar ratios (Sr:Ca) among different aquatic systems (Zimmerman 2005; Arai and Hirata 2006), the use of these ratios gives sufficient discrimination to distinguish between freshwater, brackish water, and seawater for the different life-history stages of diadromous fishes (Walther and Limberg 2012). To identify a marine-entry point on the otolith, the chemical reference points from Sr:Ca and Mn:Ca molar ratio plots were overlain onto the sectioned otolith images and inspected to identify the visual patterns that corresponded to increases in Sr:Ca molar ratios (i.e. the smolt check). Otolith chemistry using ICP-MS was used as a validation for the marine-entry point on the otolith, and a subsample of 20-22 otoliths (82 total) from the entire FL range for each region and year combination were used to establish the accuracy of estimating ocean entry using growth checks (Table 1). Samples from 2007 NBS were the exception to this subsampling approach, where Murphy et al. (2009) used all 112 prepared otoliths for chemical analysis using the ICP-MS (Table 1).

Growth increments were assumed to be deposited daily based on the validation of daily increment formation for juvenile Chum Salmon by Saito et al. (2007). Daily increments were counted back from the otolith edge to the beginning of the sharp transition from low to high Sr:Ca molar ratios (the smolt check) by two readers until agreement using Image Pro Plus software (Version 7.0, Media Cybernetics Inc., Rockville, Maryland). The date of marine entry for each fish was calculated by subtracting the total number of daily increments, which included the smolt check (beginning of the increase in strontium) from the date of fish capture. Between 51- 63% of prepared otoliths had an identifiable smolt check but did not yield clear daily growth increments that were countable. For those fish, the average number of increments found in the transition zone for readable otoliths for juvenile Chum Salmon captured in that region/year was added to the fully-marine age of non-readable otoliths (generally 12 or 13 increments) which gave a total marine age of fish in days (Murphy et al. (2009). This time period concurs with previous studies of Chum Salmon otolith analyses and smolt residency in river deltas and estuaries in the NBS region (Martin et al. 1987; Murphy et al. 2009). All analyses were conducted by including otoliths with this added average number, but were also conducted without its inclusion to be sure results did not differ.

4. Results

During 2007, juvenile Chum Salmon were caught at 20 stations in the CS and 36 stations in the NBS (see Figure 2 in Moss et al. 2009). Only three stations yielded juvenile Chum Salmon in the CS in 2012 and 2013, whereas 16 stations yielded juvenile Chum Salmon in the NBS in 2012 (Figure 1). The 2007 survey collected larger numbers of juvenile Chum Salmon from stations in the CS, totaling 292 fish from both near and offshore stations.

Juvenile Chum Salmon collected from the CS in 2007 ranged from 135 to 220 mm FL and 20 to 126 g in weight (Table 2). Northern Bering Sea juvenile Chum Salmon collected that year had similar lengths (141 to 252 mm FL) and weights (30 to 187 g), but had higher maximum FL and weights (Table 2). In 2012 and 2013, juvenile Chum Salmon collected from the CS ranged from 90 to 160 mm FL and 6 to 40 g in weight, whereas juveniles from the NBS ranged from 120 to 217 mm FL and 16 to 104 g in weight in 2012 (Table 2). It should be noted that all results remained the same when otoliths with unreadable smolt checks were left out of all of the analyses.

4.1 Juvenile Chum Salmon marine-entry timing

The timing of entry to the marine environment for juvenile Chum Salmon ranged from mid-June to mid-July among regions and years (Table 2). Fish captured earlier in the year (2012/2013 CS) were smaller in FL and had fewer marine increments than fish captured later in the year (CS 2007, NBS 2007, and NBS 2012; Table 2). Smaller fish at the time of capture entered the marine environment later in the growing season than larger individuals (i.e. mean marine otolith increments were fewer for smaller fish (Table 2)). Larger fish had more daily marine increments, with differences between the largest and smallest (FL) individuals in each region/year combination ranging from 12 to 23 increments, or 12 to 23 days (Table 2). The standard deviations of mean entry dates increased with both fish size and sample size in each length bin (Table 2). Mean marine entry dates between each region/year were significantly different (ANOVA, F = 17.65, $P < 0.001$). A Tukey's HSD (honest significant difference) multiple comparisons test determined that juvenile Chum Salmon from the CS in 2007 had the earliest mean entry date (Table 2), which was significantly earlier than the other region/year combinations (June 26, d 177; $P < 0.05$), with the exception of juvenile Chum Salmon from the CS in 2013. The mean entry date of juvenile Chum Salmon from the NBS in 2012 was the latest (Table 2) and was significantly later than of all region/year combinations (July 1, d 183; $P < 0.05$).

4.2 Juvenile Chum Salmon growth rates

Length-at-age linear regression slope coefficients and weight-at-age exponential slope coefficients determined growth rates of juvenile Chum Salmon among regions (i.e., CS and NBS) and years (i.e., 2007, 2012, and 2013). Exponential growth was modeled as:

$$y_i = \alpha e^{\beta_i},$$

where y_i was the wet fish weight in g, x_i was the age in days of the *i*th fish, parameter α was the intercept, e was a mathematical constant (natural log base), and parameter β was the slope, or relative growth rate, and can be used as an estimate of growth in weight per day (wt/d), which was converted to percent body weight per day (%/d) when multiplied by 100 (Murphy et al. 2009).

Growth rates of juvenile Chum Salmon in length-at-age and weight-at-age showed similar characteristics across regions and years. Length-at-age did not differ significantly among sampled regions and years (ANCOVA, F = 1.29, P = 0.272; Figure 2). Slope coefficients of linear models of length-at-age showed growth rates of 2.31mm/d, 2.47 mm/d, 2.60 mm/d, 2.82 mm/d, and 2.41 mm/d for CS 2007, CS 2012, CS 2013, NBS 2007, and NBS 2012, respectively, with an overall average of 2.52mm/d (Figure 2). Differences in weight-at-age were detected among regions and years (ANCOVA, F = 345.2, P < 0.001; Figure 3). Exponential growth models of weight-at-age showed that growth rates of juvenile Chum Salmon were 4.18%/d, 5.34%/d, 6.77%/d, 4.96%/d, and 4.88%/d for CS 2007, CS 2012, CS 2013, NBS 2007, and NBS 2012, respectively, with an overall average of 5.23%/d (Figure 3). Only juvenile Chum Salmon weight-at-age growth rates from the CS in 2013 were significantly different from the other region/year combinations (F = 8.2, P = 0.005; Figure 3). Growth rates from all others region/year combinations were not significantly different from each other (P > 0.05).

5. Discussion

Early marine life-history patterns of Chum Salmon are important features in their overall strategy for survival (Beamish et al. 2004; Farley et al. 2009; Tomaro et al. 2012). Marine-entry timing of juvenile Chum Salmon were similar among the three years and between the two regions sampled in this study, and early marine growth rates had significant differences. Timing of marine entry occurred consistently between mid-June and mid-July, and fish exhibited similar characteristics in marine-entry timing in both regions. The larger Chum Salmon that were captured in the northern Bering Sea (NBS) and Chukchi Sea (CS) most likely entered the marine environment earlier in the growing period (i.e. had an earlier timing of marine entry) than smaller individuals. This outcome (i.e. larger body size) was likely due to earlier outmigrants having a longer time to feed and grow in the marine environment relative to smaller fish which entered marine waters later in the growing season. Growth rate estimates were consistently 4-5% of body weight per day (%/d), with the exception of the CS in summer 2013 which had a higher growth rate (6.8%/d) than the other region/year combinations. These early marine life-history stage attributes of Chum Salmon have the potential to be affected by climate change in these regions of the Alaskan Arctic and sub-Arctic, as has been suggested by other studies (Crozier et al. 2008; Irvine and Fukuwaka 2011; Sigler et al. 2011).

5.1 Juvenile Chum Salmon marine-entry timing

Marine-entry timing of juvenile Chum Salmon in this study was consistent between the NBS and CS and among sampling years, which corroborates previous evaluations of marine-entry timing for early life stages of this species. Dates of marine entry in the CS ranged from June 16 in summer 2013 to July 16 in summer 2007, while marine-entry timing in the NBS ranged from June 8 in summer 2007 to July 17 in summer 2012. Merritt and Raymond (1983) observed peak outmigration of juvenile Chum Salmon from the Noatak River, a tributary of Kotzebue Sound and the CS, to occur from mid to late June in 1981. In summer 1986, Martin et al. (1987) observed that catch per unit effort (CPUE) of outmigrating juvenile Chum Salmon in the Yukon River delta peaked from mid to late June. Nemeth et al. (2006) observed similar outmigration timing for juvenile Chum Salmon in northern Norton Sound, with peaks in CPUE occurring in mid-June and mid-July in 2003 and 2004. In summer 2014, CPUE for juvenile Chum Salmon outmigrating from the Yukon River delta peaked the final week of May and again the third week of June (K. Howard, ADF&G, unpublished data). These findings are consistent with known Chum Salmon life-history strategies, where downstream movement of fry occurs after ice break-up in spring and continues through the summer months (Salo 1991; Quinn 2005).

There are several environmental determinants of marine-entry timing for juvenile Pacific salmon in Arctic and sub-Arctic regions. Outmigration timing is influenced by the synergistic interaction of increasing photoperiod, water temperature, and river discharge during spring months, which corresponds to spring ice retreat and river ice break-up in high latitude rivers (McCormick et al. 1998; Jensen et al. 2012). These environmental changes are cues for initiating outmigration and downstream movement to marine environments for juvenile salmonids (McCormick et al. 1998; Quinn 2005). Chum Salmon are known to migrate quickly downstream after redd emergence at a rate similar to ambient water velocity (Salo 1991; Quinn 2005). As a result, marine entry of juvenile Chum Salmon is coupled with the timing of these environmental cues during spring as day length increases, discharge increases with ice and snow melt, and water warms into summer. It has been suggested that the timing of smolt outmigration may be an adaptation to environmental conditions at varying latitudes and systems (Holtby et al. 1989; Jensen et al. 2012). Consequently, the consistency in marine-entry timing for juvenile Chum Salmon in this study suggests that the timing of marine entry in the NBS and CS systems may be an adaptation to allow for the greatest utilization of abiotic and biotic resources during the short growing season that occurs at high latitudes (Tomaro et al. 2012; Miller et al. 2014).

Although marine-entry timing was consistent between regions and among years in this study, the longer distance that juvenile Chum Salmon travel downstream in NBS tributaries (up to 3,000 km to the headwaters of the Yukon River) compared to Kotzebue Sound tributaries (up to 160 km to the headwaters of the Noatak River; Bigler and Burwen 1984) is likely a contributing factor for more variable marine-entry timing of Chum Salmon in the NBS than the

CS. Previous studies have suggested that Chum Salmon stocks with different life-history types (i.e., summer and fall Chum Salmon in the Yukon River) could cause more variability in marine-entry timing in the NBS (Martin et al. 1987; Murphy et al. 2009). Nemeth et al. (2006) showed that juvenile Chum Salmon entered the marine environment as three distinct groups in northern Norton Sound, which could also be a factor in variability of marine-entry timing of juvenile Chum Salmon in the NBS. The mixed-stock sampling of these Chum Salmon populations in the marine environment (Kondzela et al. 2014) causes potential restrictions in outmigration timing estimation of juvenile Chum Salmon in these regions. Stock-specific comparisons of size and timing of outmigration at the mouth of the Yukon River and in Kotzebue Sound are needed to provide information on the linkage between survival and life-history dynamics of the different stocks collected in this study. More information on life-history type and river of origin is needed to differentiate marine-entry timing of mixed stocks of Chum Salmon in the NBS and CS.

Climate change in the Arctic could influence the timing of marine entry for juvenile Chum Salmon through warming water temperatures and changes in ice break-up timing in spawning tributaries. Marine-entry timing dates for juvenile Chum Salmon in this study corresponded with the timing of ice break-up in the spawning tributaries for Chum Salmon (NBS: the Yukon and Kuskokwim rivers, Norton Sound area, and northeastern Russia; CS: the Seward Peninsula, and the Kobuk and Noatak rivers of Kotzebue Sound; Kondzela et al. 2009, 2014). Previous research has shown that ice break-up during spring months is the primary determinant of juvenile salmonid outmigration from freshwater to marine environments (Jutila et al. 2005; Jensen et al. 2012). River ice break-up occurred in early May 2007, mid-May 2012, and late May 2013 in tributaries of the NBS, whereas break-up in tributaries of the CS took place during the final week of May for all three sampling years (NWS 2015). More variable river ice break-up dates in NBS tributaries (NWS 2015), are likely to be contributing factors for the more variable marine-entry timing of Chum Salmon in the NBS.

Previous studies have shown that in years when the timing of marine entry for juvenile salmon co-occurs with the availability of lipid-rich copepods and other favorable abiotic conditions (i.e. temperature), fish survival is higher (Cross et al. 2008; Tomaro et al. 2012; Miller et al. 2014). Therefore, earlier river ice break-up in spring that is to be expected to result from warming temperatures in the Arctic could lead to earlier outmigration timing of juvenile Chum Salmon into nearshore marine environments. This potential shift towards earlier outmigration timing could lead to a mismatch in the arrival of juvenile fish to the marine environment relative to prey availability (Satterthwaite et al. 2014), which could have negative impacts on growth and survival during the first marine summer. Altered timing of ice retreat in the Bering and/or Chukchi seas could also cause plankton blooms to occur at different times in the spring, which has implications for the assemblage, quality, and quantity of available zooplankton prey available (Hunt et al. 2011). As a result, alterations to temperature, ice break-up, and river discharge that will likely accompany a warming climate will not only affect the timing of key life-history stages, but also likely the productivity of Chum Salmon in Arctic waters (Crozier et al. 2008; Sigler et al. 2011).

5.2 Juvenile Chum Salmon growth rates

Juvenile Chum Salmon growth rates in this study were consistent between regions and among years, and are in agreement with previous growth rate estimates for juveniles of this species. For the NBS, growth rates were roughly 5%/d. Similarly, Murphy et al. (2009) estimated growth rates of juvenile Chum Salmon collected from the southern and northern Bering seas in summer 2007 to be 5.1%/d. Relatively high growth rates have also been observed for juvenile

Chum Salmon in Puget Sound, Washington (5.7 to 8.6%/d; Duffy et al. 2005), nearshore areas of British Columbia (4 to 6%/d, with an upper limit of 6.7%/d; Salo 1991), and thermal-marked Chum Salmon in southeast Alaska (3 to 6%/d; J. Murphy, NOAA, personal communication). These growth rate estimates suggest that differences in environmental conditions throughout Alaska might differentially affect growth rates of juvenile Chum Salmon in different regions.

Observed differences in the daily age at which juvenile Chum Salmon attained the same weight between the NBS and the CS (i.e., fish of the same weight differed by 20 or more marine increments between these regions) suggests that there may be differences in the timing of smolt check formation. There appears to be a time lag between check formation on an otolith and when Sr:Ca ratios are observed to increase following marine entry on that same otolith. The lower observed weight at a given daily age for juvenile Chum Salmon in the NBS could be due to differences in environmental conditions between regions and, in turn, how these differences may affect the timing of the smolt check deposition (Campana 1999), specifically differences in estuarine environments. Kotzebue Sound, the major embayment into which several northwestern Alaskan tributaries flow, is a more typical estuary that grades from freshwater to saltwater toward the outlet at the CS (Merritt and Raymond 1983). Conversely, the Yukon River delta is a large, freshwater-dominated estuary near the river mouth and is highly variable in salinity between the many different locations in the delta where juvenile Chum Salmon inhabit (Martin et al. 1987; Murphy et al. 2009). These conditions make for somewhat harsh rearing environments for juvenile Chum Salmon; Martin et al. (1987) suggested that Yukon River delta habitats serve as staging areas for juveniles before they quickly move offshore, generally at a smaller size than in typical estuarine environments. These contrasting conditions may be a contributing factor for the later smolt check deposition on juvenile NBS Chum Salmon otoliths and their lower weight at a given age than juveniles in the CS. When estimated smolt checks were removed from daily age estimates and the subsequent growth models, no differences in growth rate estimates were found, suggesting that the observed differences were likely due to variances in the period of smoltification and/or timing of smolt check formation that occurs between regions and not due to error in the estimated location of smolt checks or daily age.

Although the range of juvenile Chum Salmon growth rates estimated in this study are comparable to other studies on early marine growth for this species, variable environmental conditions among sampling years, such as temperature, food availability, and photoperiod may have contributed to the observed differences in growth rates. Warmer water temperatures increase fish metabolic rate and, if thermal maxima have not been reached and food availability is sufficient, fish will grow at faster rates (Brett 1979). During the current study, mean SST was 1°C warmer during summers 2007 and 2013 than in summer 2012 (L. Eisner, NOAA, unpublished data). The relatively high growth rate of juvenile Chum Salmon in the CS in 2013 suggests that conditions were more energetically favorable for growth and that prey quality may be higher in the CS than the NBS, perhaps due to the shallower shelf habitat (i.e., warmer SSTs; Grebmeier et al. 2006), coupled with increased feeding opportunities and greater primary and secondary productivity from longer day lengths/photoperiod (Moss et al. 2009). Although SSTs were relatively warm in summers 2007 and 2013 for both regions, the relatively low growth rate exhibited by juvenile Chum Salmon in the CS in summer 2007 (4.2%/d) is most likely a result of sampling dates that occurred one month later than in 2012/2013. Because growth rates typically decline as fish grow larger and older (Brett 1979), the later sampling dates in the CS in 2007 may have contributed to the lower observed weight-at-age growth for that region/year combination.

Growth rates for juvenile salmon in the NBS and CS may respond to climate change due to altered metabolic rates and timing of important life-history periods relative to changes in prey abundance, composition, and distribution (Crozier et al. 2008; Nielsen et al. 2013). Higher growth rates of juvenile Chum Salmon in the NBS and CS would be expected to yield higher survival through the first winter period, with positive implications for adult fish returns (Moss et al. 2005). Although warmer SSTs might benefit growth when prey quality is high, bottom-up regulation of nutrients and prey availability will likely be affected by changes in sea ice extent, the timing of sea ice retreat and, therefore, plankton production and growth (Hunt et al. 2011). Continued monitoring of Chum Salmon in the NBS and CS will lead to a greater understanding of how climate change will affect early marine growth and subsequent survival to the adult life stage. The complexities of juvenile salmon growth cannot be understated and while this study provides insight into differences between regions, the myriad of causal mechanisms of growth of juvenile Chum Salmon in the NBS and CS must be further investigated, including diet and energetic studies to untangle the current energetic status and dynamics for these populations and how they might be affected by climate change.

6. Conclusions

The results of this study suggest that juvenile Chum Salmon in the NBS and CS currently exhibit consistent early marine life-history characteristics in the NBS and CS, such as marine-entry timing and growth rates during their first marine summer, despite some differences in environmental conditions between regions and among years. However, changes in climate variability in the Arctic have the potential to alter key life-history stages of Pacific salmon stocks in Alaska, including entry to the marine environment and early marine growth. Warming oceans with higher SSTs during summer months have been shown to support higher marine survival rates and productivity for some Pacific salmon populations in the northeast Pacific, Gulf of Alaska, and the Bering Sea (Mueter et al. 2002; Mantua 2009). While the relatively warmer SSTs might have positively influenced juvenile Chum Salmon growth in this study, the effects that warming temperatures may have on other factors such as marine-entry timing, prey availability, and survival during their first marine year are also important to understand within the context of climate change. Warming temperatures in freshwater environments might have significant effects on the outmigration timing of salmon smolts, leading to potential mismatches with optimal prey availability in nearshore marine environments (Tomaro et al. 2012; Satterthwaite et al. 2014). This complex suite of biotic and abiotic variables that influence juvenile Chum Salmon early life history in the NBS and CS and the complexity associated with early growth dynamics of this species cannot be understated. As a result, it is critical to understand how these environmental conditions interact to impact early life stages and subsequent adult returns of Chum Salmon due to climate change in these regions. We recommended that monitoring and similar analyses of juvenile Chum Salmon be conducted as often as possible to be able to determine variability in life-history characteristics of each brood year of fish. However, sampling continually over years with large variation in climate indices (changes in PDO, ENSO, etc.) or over large anomalies in SST, is highly recommended.

7. Acknowledgements

We would like to thank all crewmembers aboard the NOAA ship *Oscar Dyson* and the F/V *Bristol Explorer*, as well as technicians from NOAA/Auke Bay Labs who helped collect and extract otolith samples for analysis. A special thanks to K. Spaleta at the UAF Advanced Instrumentation Lab for assistance with the ICP-MS. Thanks to M. Adkison for assistance in the early stages of this study and N.

Smith for assisting with laboratory analyses for this project. This study was funded with qualified outer continental shelf oil and gas revenues by the Coastal Impact Assistance Program, Fish and Wildlife Service, U.S. Department of the Interior. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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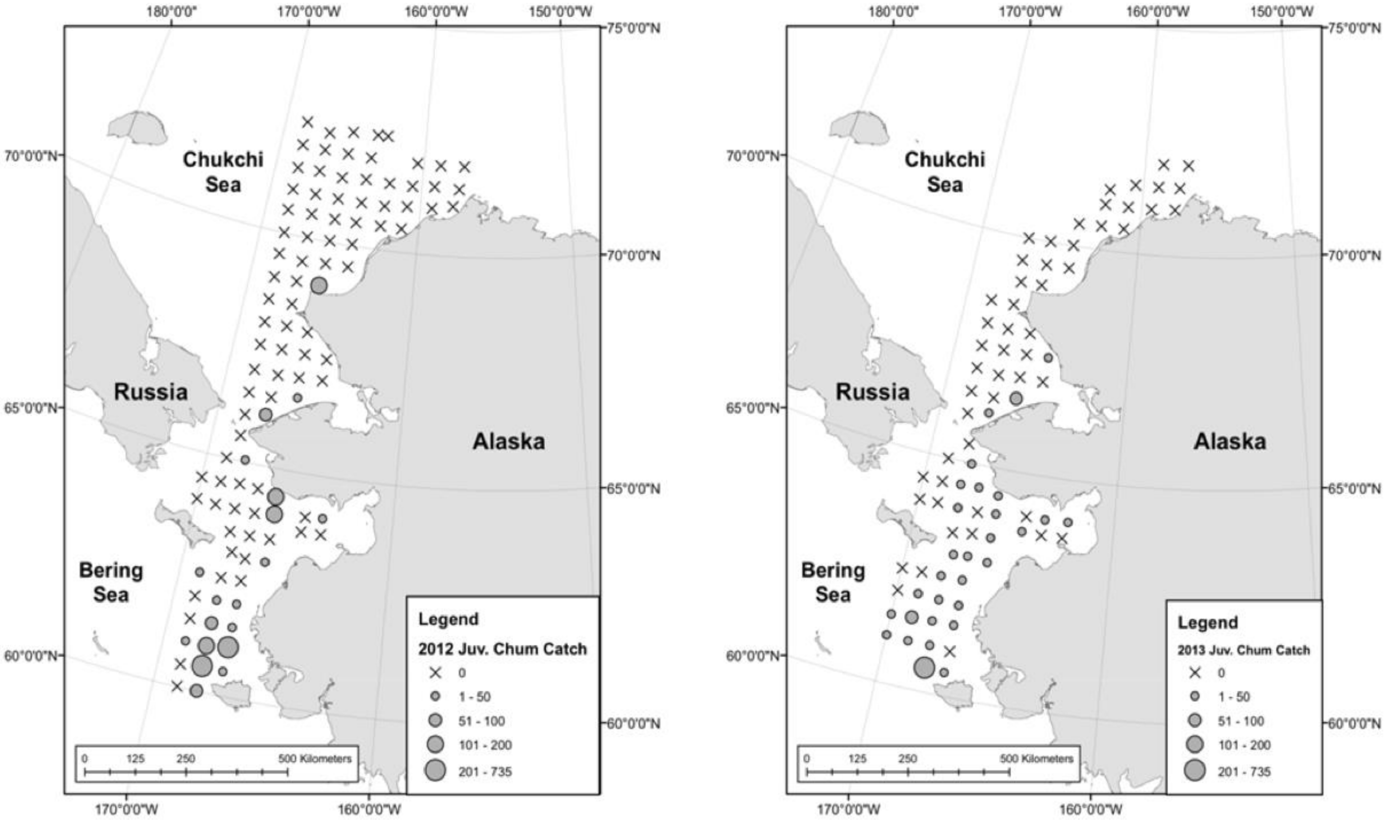

Figure 1. Station array and catches of juvenile Chum Salmon during the 2012 (left) and 2013 (right) Arctic Eis surveys. Circle sizes represent catches for one 30-minute surface trawl at each station. Stations with an "X" denote locations where no juvenile Chum Salmon were caught. Reproduced with permission from NOAA.

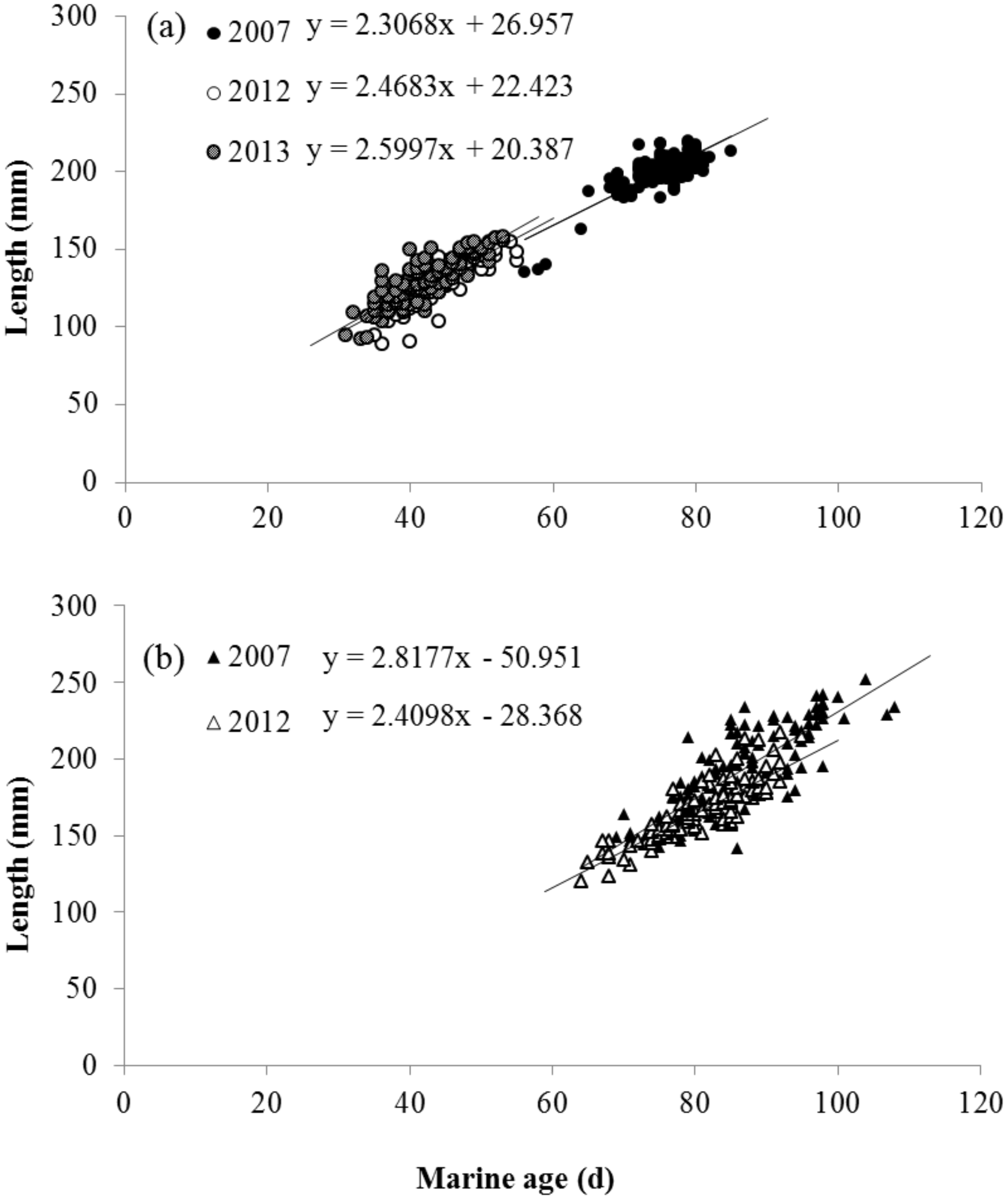

Figure 2. Linear regression models of fork length-at-age for (a) Chukchi Sea and (b) northern Bering Sea juvenile Chum Salmon. The slope coefficient in each equation indicates the growth rate of that particular region and year.

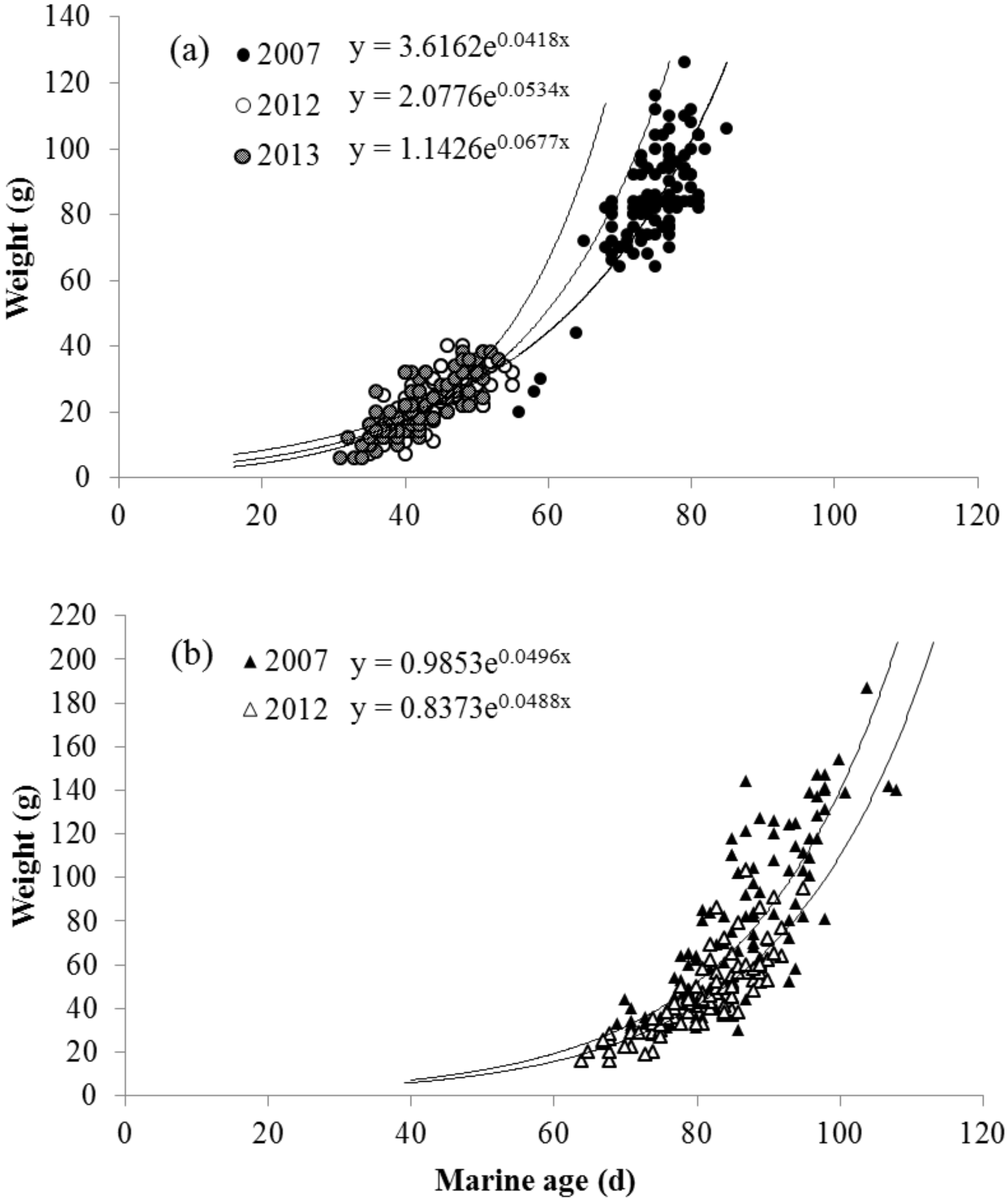

Figure 3. Exponential growth models of wet weight-at-age for (a) Chukchi Sea and (b) northern Bering Sea juvenile Chum Salmon. The exponential term in each equation indicates the growth rate of that particular region and year when multiplied by 100.

Table 1. Number of surface trawl stations that yielded juvenile Chum Salmon, number of juvenile Chum Salmon collected from trawl hauls, number of otoliths used for aging, and number of otoliths used for chemical analysis from each region and year. Numbers with asterisks (*) denote samples prepared, read, and analyzed by J. Murphy, NOAA, Juneau, Alaska. Note: NBS 2013 samples are not included due to a flooding event that occurred onboard in which all samples were either lost at sea or recovered and rendered unusable.

Region	Year	Stations	Total Fish Subsampled from all Stations	Otoliths Read	Otoliths Used for Chemical Analysis
Chukchi Sea	2007	20	292	108	22
	2012	3	104	98	20
	2013	3	95	93	20
	Total	26	491	299	62
Northern Bering Sea	2007	36	559	112*	112*
	2012	16	480	109	20
	Total	52	1039	221	132

Table 2. Aging analysis of marine otolith increments for juvenile Chum Salmon. Fork length bin, weight range, number of otoliths analyzed, mean number of marine increments, standard deviation, mean entry date, and range of entry dates per length bin are listed by region and year. Dashes (-) indicate that no fish were collected in that length bin. Both calendar and Julian dates (in parentheses) are provided. Numbers with asterisks (*) denote samples prepared, read, and analyzed by J. Murphy, NOAA, Juneau, Alaska.

Region	Year	Fork Length Bin (mm)	Weight Range (g)	Number of Otoliths	Mean Marine Increments	StDev Marine Increments	Mean Capture Date (Julian)	Mean Entry Date (Julian)	Minimum Entry Date (Julian)	Maximum Entry Date (Julian)
Chukchi Sea	2007	120-140	20-30	3	57.67	1.53	9/8 (251)	7/12 (193)	7/11 (192)	7/16 (197)
		141-160	-	-	-	-	-	-	-	-
		161-180	44	1	64.00	0.00	9/11 (254)	7/9 (190)	7/9 (190)	7/9 (190)
		181-200	64-86	45	73.16	3.57	9/9 (252)	6/28 (179)	6/22 (173)	7/7 (188)
		201-220	76-126	59	76.86	3.00	9/9 (252)	6/24 (175)	6/16 167)	7/1 (182)
		Mean			74.67			6/26 (177)		
	2012	80-100	7-12	3	37.00	2.65	8/12 (225)	7/6 (188)	7/3 (185)	7/10 (192)
		101-120	10-20	18	39.17	2.36	8/11 (224)	7/3 (185)	6/28 (180)	7/8 (190)
		121-140	14-34	54	43.26	2.93	8/11 (224)	6/29 (181)	6/22 (174)	7/7 (189)
		141-160	22-40	23	49.35	3.19	8/11 (224)	6/23 (175)	6/14 (166)	6/28 (180)
		Mean			43.75			6/29 (181)		
	2013	80-100	6	3	32.67	1.53	8/8 (220)	7/6 (187)	7/5 (186)	7/8 (189)
		101-120	8-16	25	37.32	2.48	8/8 (220)	7/1 (182)	6/27 (178)	7/7 (188)
		121-140	18-30	40	41.95	3.00	8/9 (221)	6/28 (179)	6/24 (175)	7/6 (187)
		141-160	22-38	25	47.92	3.48	8/10 (222)	6/23 (174)	6/16 (167)	7/2 (183)
		Mean			42.01			6/28 (179)		

Northern Bering Sea	2007	140-160	30-44	23	76.61	4.52	9/18 (261)	7/4 (185)	6/24 (175)	7/12 (193)
		161-180	36-65	21	80.67	5.49	9/23 (266)	7/2 (183)	6/22 (173)	7/12 (193)
		181-200	58-86	23	86.22	5.13	9/24 (267)	6/30 (181)	6/20 (171)	7/14 (195)
		201-220	82-114	20	89.40	4.88	9/23 (266)	6/26 (177)	6/12 (163)	7/11 (192)
		221-240	110-154	22	95.27	6.27	9/24 (267)	6/21 (172)	6/10 (161)	7/1 (182)
		241-260	147-187	3	99.75	3.79	9/29 (272)	6/18 (169)	6/14 (165)	7/1 (182)
		Mean			85.88			6/28 (179)		
	2012	120-140	16-26	9	68.33	3.04	9/16 (260)	7/9 (191)	6/30 (182)	7/17 (199)
		141-160	19-43	31	76.74	4.57	9/17 (261)	7/2 (184)	6/27 (179)	7/8 (190)
		161-180	38-62	46	83.22	3.87	9/22 (266)	6/30 (182)	6/25 (177)	7/7 (189)
		181-200	50-79	17	86.94	3.52	9/23 (267)	6/28 (180)	6/23 (175)	7/4 (186)
		201-220	86-104	6	89.38	4.18	9/24 (268)	6/26 (178)	6/21 (173)	7/4 (186)
		Mean			81.08			7/1 (183)		

OCS Study
BOEM AK-11-08a/b

Appendix U.

Arctic Fish Energetics

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December 14, 2016

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Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

List of Oral and Poster Presentations

Papers

Barton, M., J. Moran, J. Vollenweider, R. Heintz, K. Boswell. In Press. Latitudinal dependence of energetics and stable isotopes of juvenile capelin (*Mallotus villosus*) in the Bering and Chukchi Seas. Polar Biology.

Presentations

Copeman, L., B. Laurel, R. Heintz, J. Vollenweider. Contrasting strategies of lipid storage in juvenile Arctic cod *(Boreogadus saida*) and saffron cod (*Eleginus gracilis*) under variable thermal regimes. Alaska Marine Science Symposium, January 2015, Anchorage, AK.

Copeman, L., B. Laurel, R. Heintz, J. Vollenweider, K. Boswell. Ontogenetic variability in trophic biomarkers of saffron cod (*Eleginus gracilis*) from the western Arctic and northern Pacific. Association for the Sciences of Limnology and Oceanography, February 2015, Granada, Spain.

Moran, J. J. Vollenweider, R. Heintz, K. Boswell. Latitudinal variation in energy allocation of juvenile capelin in the Bering and Chukchi Seas. Lowell Wakefield Symposium, March 2013, Anchorage, AK.

Vollenweider, J., R. Heintz, K. Boswell, B. Norcross, J. Moran, C. Li, A. Robertson, M. Barton, A. Pinchuk, L. Sousa, S. Danielson, S. Johnson, J. Thedinga, D. Neff, J. Maselko. A small boat in a big sea: Assessing nearshore Arctic fish communities. UAF seminar, April 2015, Juneau, AK.

Vollenweider, J., R. Heintz, K. Boswell, M. Barton, A. Robertson, C. Li, B. Norcross, L. Sousa, A. Pinchuk, S. Danielson, M. Callahan. Factors structuring nearshore fish assemblages in the Alaskan Arctic. Ocean Science Meeting, February, 2016, New Orleans, LA.

Vollenweider, J., R. Heintz, J. Moran, K. Boswell, M. Barton, A. Robertson, S. Johnson, J. Thedinga, D. Neff, J. Maselko. Short term variation in Arctic juvenile fish nursery areas during the brief ice-free season. Alaska Fisheries Society, October 2014, Juneau, AK.

Posters:

Barton, M., K. Boswell, J. Vollenweider, R. Heintz. Spatial variation of trophic dynamics and energy allocation in capelin (*Mallotus villosus*) across a latitudinal gradient. FIU Biology Symposium, February 2014, North Miami, Fl.

Callahan, M., J. Vollenweider, A. Pinchuk, L. Sousa, R. Heintz. Energetics of Arctic zooplankton. Ocean Sciences Meeting, February, 2016, New Orleans, LA.

Callahan, M. J. Vollenweider, R. Heintz, L. Sousa, F. Mueter. Arctic fish energetics. Arctic Eis Meeting. June 2014, Juneau, AK.

Copeman, L., B. Laurel, R. Heintz, J. Vollenweider. Storage and utilization of lipid classes and fatty acids during the early ontogeny of cold-ocean gadids. Arctic Eis PI Meeting, June 2014, Juneau, AK.

Mosher, S., J. Vollenweider, R. Heintz, B. Laurel, M. Barton, A. Robertson, M. Callahan, S. George, L. Sousa, F. Mueter, K. Boswell. Climate-induced changes in Arctic cod and saffron cod distributions may alter Arctic trophic ecology. Alaska Marine Science Symposium, January 2016, Anchorage, AK.

Vollenweider, J., R. Heintz, L. DeSousa, K. Boswell, M. Callahan, A. Robertson, J. Moran. Energetics of Arctic fish. Alaska Marine Science Symposium, January 2015, Anchorage, AK.

Vollenweider, J., R. Heintz, M. Callahan, A. Robertson, L. DeSousa, J. Moran, K. Boswell, M. Barton. Arctic forage fish energetics. Arctic Eis PI Meeting, June 2014, Juneau, AK

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Proposed Objectives and Study Chronology

The objectives of the energetics component were to quantify the energetic condition of dominant forage fish in the Chukchi Sea and attempt to discern mechanisms contributing to variation in fish condition. Fish were collected from the ArcticEis project as well as several other concurrent projects described in further detail in the body of the report. Fish were frozen at sea and returned to Auke Bay Labs in Juneau for further biological processing and chemical analysis. The final report depicted here was written with collaboration from the oceanographic component that delineated water masses within the study area. The report will be developed into a manuscript for peer review and publication upon further development, drawing in prey availability, fish diet, and potentially bioenergetic modeling. All project-associated data is archived on the Ocean Workspace.

1. Introduction

Understanding the mechanisms contributing to variability in fish body condition and consequently their survival will be important in predicting how Arctic marine ecosystems will evolve in light of a changing climate. Knowing the mechanisms structuring fish survival and recruitment Food web modeling will be an integral tool in predicting how Arctic marine ecosystems will change in the light of climate change. The Arctic is warming faster than the rest of the globe as a result of polar amplification and feedback processes associated with melting sea ice, incurring immediate and pronounced climatological effects relative to the rest of the globe (Screen and Simmonds 2010). Warming conditions and cascading environmental effects (ice melting, increases in precipitation, increased storm activity) have already been linked to changes in marine Arctic community composition. Northward range extensions of fish species have been documented in the Chukchi and Beaufort Seas and will likely continue (Rand and Logerwell 2010; Mecklenburg et al. 2007). Arctic fish species are also expected adapt differentially to changing conditions, with some species such as saffron cod being more resilient to warming conditions, and others such as Arctic cod faring poorly with reductions in growth (Laurel et al. 2016). How changes in fish community composition affect piscivorous fish and their marine mammal and seabird predators is relatively unexplored. Changes in species composition of fishes may have complex cumulative and synergistic effects that cannot be assessed without the inclusion of bioenergetic considerations. For example, laboratory studies of Steller sea lions and northern fur seals found they were not able to compensate for a lack of high-lipid/high-energy prey by consuming more biomass or a diversity of low-quality prey species (Gomez et al. 2016, Rosen and Trites 2000). Therefore food web modeling will be an important predictive tool to understand predator-prey relationships and energy flow under different scenarios, providing a holistic means to evaluate how Arctic fish and their predators may fare with climate change.

Food web models rely on accurate quantification of fish condition parameters which are sparse to nonexistent. Modeling efforts, in particular for marine mammals, have been forced to rely on literature values from disparate locations (Bluhm and Gradinger 2008). We provide a library of the energetic condition measures of the most abundant Arctic fish species caught in the Chukchi Sea and western Beaufort Sea in an effort to provide accurate data for use in food web and other bioenergetic models. Additionaly, we examine variability in body condition and explore oceanographic mechanisms underpinning that variability.

2. Methods

Fish Collections

Fish were collected from the U.S. waters of the Chukchi Sea, the western Beaufort Sea and Elson Lagoon between 2005 and 2015 from multiple surveys, including 2 nearshore projects, Ecology of Forage Fishes in the Arctic Nearshore (AFF), and The Arctic Coastal Ecosystem Survey (ACES); an offshore project, ArcticEis; and a project spanning the nearshore and offshore, Shelf Habitat and EcoLogy of Fish and Zooplankton (SHELFZ) (Figure 1). Sampling timing and fishing methodology varied by project (Table 1). Greater detail on fishing techniques can be found in Marsh et al. 2016, Norcross et al. 2010, Stauffer 2004, and Thedinga et al. 2013. Generally, five to fifteen fish of each species representative of each catch were retained from each haul/station and frozen. Additional samples were obtained from subsistence collections in Barrow and Kotzebue, AK. In the laboratory, fish were measured, weighed whole, and stomach contents were removed.

Condition Analyses

Instantaneous growth rate was assessed from a subset of fish using RNA/DNA analysis. Individual fish to be analyzed had a 10 mg piece of dorsal muscle tissue dissected from below the dorsal fin and frozen at -80 °C until analysis. If fish were to undergo additional chemical analyses, RNA/DNA analysis was constrained to fish greater than 200 mg (< 5 % fish mass removed). RNA/DNA analysis followed a one dye-two enzyme fluorometric protocol modified from Caldarone et al. (2001) (Sreenivasan and Heintz 2016). Briefly, muscle was sonicated, vortexed and centrifuged with a buffer and the supernatant was treated with ethidium bromide. RNA and DNA fluorescence was measured using a spectrophotometer and compared to standard curves generated from standards.

Small fish (< 0.5 g) were dried whole to a constant weight then homogenized, while large fish (≥ 0.5 g) were homogenized wet and an aliquot was dried to a constant weight. Drying occurred in either drying ovens set to 60 °C or using a LECO Thermogravimetric Analyzer (TGA) 601[1] or 701 at 135 °C. A replicate sample was included in each batch of samples when sufficient mass was available, otherwise herring homogenate or purchased meat standards (NIST Meat1546) were replicated (not to exceed 15 % from target values). Dried samples were homogenized to a uniform consistency. When fish were too small to accommodate sample sizes needed for chemical analyses, several individuals of relatively similar size were composited by collection.

Energy density (ED; kJ/g dry mass) was measured using bomb calorimetry. Dried homogenates of 30-70 mg (small pellets) or 70-200 mg (large pellets) were pressed into pellets and combusted using a Parr 6725 semi-micro bomb calorimeter[1] using standard instrument operating procedures from the manufacturer's instrument manual. Quality assurance samples with each batch of samples included 1) duplicate benzoic acid standards (not to exceed 0.5% CV for large pellets or 1.5 % for small pellets, and 0.5 % error from target values for large pellets or 2.0 % for small pellets), 2) a sample replicate when sample mass permitted (not to exceed 1.5 standard deviation for both large and small pellets), and 3) a tissue reference sample of Pacific herring or walleye pollock homogenate (not to exceed 2.75 % error from the target value for large pellets or 3.0 % error for small pellets). Energy densities were converted to a wet-mass basis using moisture content. Total energy (kJ) was calculated as energy density x wet mass.

If fish were large enough, lipid (% wet mass) was measured using a modification of Folch's method as described in Vollenweider et al. (2011). Briefly, lipid was extracted from approximately 40 mg of dried homogenate using a 2:1 chloroform:methanol solution using an Accelerated Solvent Extractor 200[1]. Lipid extracts were washed with 0.88% KCl and 1:1 (v:v) methanol:deionized water. The excess solved was evaporated and percent lipid was calculated gravimetrically. Quality assurance samples with each batch of 17 samples included 1) a blank (not to exceed 0.3 mg), 2) a sample replicate when sample mass permitted (not to exceed 15 % CV), and 3) a reference material of walleye pollock homogenate (not to exceed 15 % error from the target value).

For larger fish with remaining dried homogenate, protein content was measured using a LECO[1] nitrogen determinator TruSpec CHN[8]. For this analysis, an aliquot of > 0.07 g dried

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[8] Mention of trade names or commercial companies does not imply endorsement by the National Marine Fisheries Service, NOAA.

homogenate was dropped into a hot furnace (950° C) and flushed with oxygen for very rapid and complete combustion the expelled nitrogen was quantified. Before samples were analyzed the instrument was calibrated with 1) EDTA for a known nitrogen value, 2) sucrose for a non-nitrogen value, then 3) a standard reference material Meat1546 obtained from the National Institute of Standards (NIS). Quality assurance samples included one EDTA and two atmospheric blanks for every 10 sample analysis. A replicate sample and Meat1546 was included with each batch of 17 samples. If quality assurance samples exceeded prescribed limits (15% variation for reference samples, 0.1% protein for blanks, and 1.5 standard deviation for replicates), samples were re-analyzed.

Oceanographic Mechanisms Affecting Fish Condition

Oceanographic parameters were measured at pre-determined gridded stations for the Arctic Eis and SHELFZ projects, and during each beach seine haul for the ACES, AFF and SHELFZ projects. Vessel-based conductivity-temperature-depth (CTD) measurements were collected with Sea-bird (SBE) instruments, including models 911 and 25. For the beach seine oceanography, measurements of ocean temperature and salinity were made using hand-held thermometers, refractometers and a YSI instrument.

As part of the ArcticEis project, CTD measurements were used to characterize water masses in the surface waters (0-10 m) and bottom waters (within 5 m of the CTD maximum depth) based on temperature and salinity values (Danielson et al. 2016). Watter masses include 1) Anadyr, Bering, Chukchi Shelf Water (ABCSW), 2) Alaska Coastal Water (ACW), 3) Bering, Chukchi Winter Water (BCWW), and 4) Chukchi Shelf Winter Water (CWW). Water mass characterizations were extended to CTD measurements from the SHELFZ project using the same process, while oceanographic measurements from the nearshore sampling using hand-held devices were characterized as Beach. Beach water masses were expected to be unique and therefore further delineated into three subcategories, including Beach-Chukchi Sea (Beach-C), Beach-Beufort Sea (Beach-B), and Beach Elson Lagoon (Beach-E). Oceanographic characteristics of those water masses tended to be similar to those of Melt Water and Alaska Coastal Water (Table 2). Fish condition measurements of Arctic cod and capelin, the two applicable species, were compared by water mass using General Linear Models when fish and oceanography were measured concurrently. For all ANOVA's fish length was not a significant covariate unless otherwise noted. In addition, linear regressions of fish condition versus temperature and salinity were examined.

3. Results

Prey Quality

Pacific herring were the most energy-rich (7.98±0.32 kJ/g wet mass; mean±SE) of the 24 species evaluated, having 2.4 times greater energy density than the most energy-deplete Alaska plaice (3.27 kJ/g) (Table 3, Figure 2). The three species of cisco were also relatively energy-rich, while all other species were similarly low, only varying by 1.7 kJ/g amongst them. Within families, there was little difference in energy density by species, with the exception that Arctic cod were significantly more energy-rich than the other gadids, being 11% more energy-rich than walleye pollock and 24% more energy-rich than saffron cod (ANOVA $p<0.000$) (Figure 3). The cottids also had some differentiation by species, with Artic staghorn, belligerent, and Arctic sculpins having approximately 17% higher energy density than shorthorn and fourhorn sculpin (ANOVA p<0.000).

Correlations between energy density and length could only be evaluated for 5 species which spanned relatively large size ranges. In general, there were moderate positive correlations between fish length and energy density (Table 4, Figure 4). In contrast, energy density of fourhorn sculpin decreased with length. When the effect of water content was removed, correlations between energy density and length increased slightly on a dry mass basis. For a given increase in length, Pacific herring and capelin increased their energy density at more than twice the rate of the 2 gadids. When compared to their counterparts in the Gulf of Alaska during summer months (July – September) Arctic fish accumulated energy at a slower rate than those in the Gulf of Alaska, evidenced by a significant interaction effect (P=0.006) (Figure 5). Similarly, Pacific herring in the Arctic accumulated energy at a slower rate than those in the Gulf of Alaska (P=0.002).

Total energy content (kJ) of individual fish integrates size-related changes in energy density and fish size. Arctic cisco had statistically the greatest energy content per individual fish of all the species (2,126.9±381.6 kJ, p<0.000), followed by the other 2 species of cisco (Bering cisco: 1,273.2±461.8 kJ and least cisco: 1,271.8±73.5 kJ) (Figure 6). Pacific herring and Alaska plaice were also among the top 5 species with the highest energy content. Within families, the ranking of species by total energy contne was different than when energy density was compared (Figure 7). For example, on a gram-for-gram comparison, Arctic cod have significantly more energy per gram than walleye pollock or saffron cod. But when the energy density is scaled up to the total energy content of a whole fish, saffron cod have the most energy due to their large size.

Of the 5 most energy-rich species, the ciscos and Pacific herring had the highest energy densities and were also the largest of the fish, culminating in the greatest total energy content (Figures 6-8). Alaska plaice, however, had the lowest energy density of all species (though only one animal was analyzed), but the relatively large size of the fish overwhelmed the low energy density, resulting in a high total energy content. The importance of fish size became more pronounced as fish size increased, which could be seen by the clear discrimination between Pacific herring and saffron cod larger than 200 mm (Figure 9).

Oceanographic Mechanisms Affecting Fish Condition

Arctic cod

In surface waters, collections of Arctic cod occurred in the same water masses in both years, with the exception of beach seine catches where cod were found only in 2013 in very small numbers. Within water masses, energy density was consistent between years in Alaska Coastal Water ($p = 0.526$) and Melt Water ($p = 0.064$), but 3% higher in shelf waters in 2013 than 2012 ($p = 0.017$) (Figure 10). Within years, energy content of Arctic cod was invariable between water masses ($p > 0.202$). Consequently, energy content of Arctic cod in all surface waters was 5% higher in 2013 than 2012 ($p = 0.002$).

In surface waters, RNA/DNA of Arctic cod showed similar patterns to energy content. Within water masses, RNA/DNA was also consistent between years in Alaska Coastal Water ($p = 0.109$, length covariate $p = 0.028$) and Melt Water ($p = 0.793$), but 25% higher in shelf waters in 2013 than 2012 ($p < 0.000$) (Figure 11). Fish length was not a factor in this large discrepancy between years ($p = 0.326$). As seen in the energy content, water mass did not affect RNA/DNA within years (2012: p = 0.704, length p = 0.001; 2013: p = 0.148). Consequently, RNA/DNA of Arctic cod in all surface waters was 21% higher in 2013 than 2012 (p < 0.000, length covariate = 0.004).

Pooled over all water masses in surface waters, Arctic cod had a 5% higher energy density in 2013 than 2012 (23.4 vs 22.3 kJ/g; p = 0.002) and 21% higher RNA/DNA in 2013 than 2012 (20.6 vs 16.3; p < 0.001, length covariate p = 0.004). These differences were associated with fish that were 22% smaller in 2013 (46 vs 59 mm; p = 0.012).

In bottom waters, collections of Arctic cod in shelf water masses occurred in both 2012 and 2013, while in all other water masses Arctic cod were collected in only one year. For the one possible comparison in Shelf Water, no interannual difference in energy content was detected between 2012 and 2013 (p = 0.575) (Figure 10). Comparison of energy content between all water masses over both years showed significant differences. Arctic cod were most energy-rich in Shelf Water, having 7% more energy per gram (23.69±0.19) than fish that were least energy-rich in Alaska Coastal Water (22.07±0.16) (Figure 11). Fish in winter waters were intermediate in energy density.

In bottom waters, RNA/DNA content of Arctic cod was higher in 2013 (18.9±0.7) than 2012 (17.3±0.3) in Shelf Water (p = 0.052), the only water mass in which fish were collected both years. Higher RNA/DNA in 2013 was associated with significantly smaller fish (82±8 vs. 112±2 mm; p < 0.000) (Figure 11). Similar to energy density, RNA/DNA content was significantly depleted in Alaska Coastal Water relative to all other water bodies (RNA/DNA p = 0.052, length covariate p = 0.003).

Pooled over all water masses in bottom waters, Arctic cod had similar energy densities in 2012 and 2013 (23.3 vs. 23.1 kJ/g; $p = 0.478$) and similar RNA/DNA in both years (17.1 vs 17.2; $p = 0.314$, length covariate $p = 0.001$). Body condition parameters were invariable despite Arctic cod being 8% larger in 2013 than 2012 (123 vs 113 mm; $p < 0.001$).

Capelin

In surface waters, collections of capelin occurred in the same water masses in both years with the exception of two of the Beach Seine Water masses. Within water masses, energy density of capelin was consistent between years in all water masses ($p > 0.0426$) except in Alaska Coastal Water which was 3% higher in 2013 than 2012 ($p = 0.005$, length covariate $p < 0.000$) (Figure 12) and having slightly larger fish in 2012 (88±1 mm) than 2013 (84±2 mm) ($p = 0.060$). Within years, energy content of capelin was highest in Shelf Water and Alaska Coastal Water, lowest in all Beach Waters, and intermediate in Melt Water.

In surface waters, interannual comparisons of RNA/DNA were possible for 3 water masses. RNA/DNA was 16% higher in 2013 than 2012 in Shelf Water ($p < 0.001$, length covariate $p = 0.001$) and similarly 13% higher in Alaska Coastal Water in 2013 than 2012 ($p = 0.027$), but similar across years in Melt Water ($p = 0.468$) (Figure 13). During 2012, RNA/DNA was 31% lower in both Beach Seine Water masses (average = 15.0) than the offshore water masses (average = 21.7) ($p = 0.016$, length covariate = 0.001). In 2013, no capelin RNA/DNA was analyzed in Beach Seine Water, but values were 24% higher in Melt Water than Shelf Water and Alaska Coastal Water ($p = 0.009$, length covariate $p = 0.004$).

Pooled over all water masses in surface waters, capelin had a 2% higher energy density in 2012 than 2013 (23.2 vs 22.7 kJ/g; $p = 0.003$, length covariate $p < 0.001$) but 22% higher RNA/DNA in 2013 than 2012 (24.9 vs 19.5; $p < 0.001$, length covariate $p = 0.001$). These differences were associated with fish that were 25% smaller in 2013 (67 vs 88 mm; $p < 0.001$).

In bottom waters, collections of capelin only occurred in one year in each water mass, preventing any interannual comparisons within water masses. Pooled across both years, there were no differences in energy content between water masses ($p = 0.248$, length covariate $p < 0.000$) (Figure 12) yet fish were significantly smaller in Alaska Coastal Water (101±5 mm) and Chukchi Winter Water (89±5 mm) than Shelf Water (119±3 mm) and Bering Chukchi Winter Water (115±4 mm) ($p < 0.000$). In contrast, pooled across both years RNA/DNA was 41% higher in Shelf Water than Bering-Chukchi Winter Water, despite their similar sizes ($p = 0.029$, length covariate <0.000) (Figure 13).

Pooled over all water masses in bottom waters, capelin had similar energy densities in 2012 and 2013 (24.7 vs. 23.8 kJ/g; $p = 0.104$, length covariate $p < 0.001$) but 43% higher RNA/DNA in 2012 than 2013 (26.1 vs 14.7; $p = 0.004$, length covariate $p < 0.001$). Capelin size did not vary between years (109 vs 115 mm; $p = 0.555$).

Linear regressions of Arctic cod and capelin condition indices (energy density and RNA/DNA) versus temperature and salinity were poorly correlated when examined by species or broken into surface and bottom waters (R2 < 12.8).

4. Discussion

Prey Quality

When considering the energy density of the Arctic species examined, the most energy-rich species are not highly abundant nor wide-spread (see Arctic Eis project results). For example, Pacific herring were not caught in great abundance north of Norton Sound, and cisco species are limited to brackish waters in lagoon habitats. Arctic sand lance, Arctic staghorn sculpin and rainbow smelt were also caught in low abundance. Therefore the most energy-rich species with a wide distribution and large abundance is Arctic cod. Another very abundant and wide-spread species, capelin, was only 5% lower in energy density than Arctic cod. In contrast, another species of great interest because of its' tolerance of warm waters and potential to thrive with ocean temperature increases is saffron cod (Laurel et al. 2016). If Arctic cod were to diminish in abundance coincident with increases in saffron cod, the concern is that saffron cod are a significantly suboptimal prey having 25% lower energy density than Arctic cod. A caveat to this scenario, however, is that saffron cod are distributed close to the coast and it is unknown if their distribution would expand under warming conditions and become available to offshore predators.

Accounting for fish size and scaling energy up to total energy of an individual fish, the fish species with the greatest total energy content are similarly low in abundance with limited distributions. Again, ciscos and herring have the greatest energy content of the species examined but with distribution limitations discussed above. Alaska plaice and eelpouts are low in abundance, leaving saffron cod as the abundant/widespread species with the greatest total energy content per fish, having 4 times the energy content as an Arctic cod or more than 7 times the energy content of a capelin. From these comparisons, it is plain that a combination of abundance, distribution and fish size must be accounted for when determining the value of a prey species for it's predators.

There are some similarities and stark differences between the summertime energetics of the 24 Arctic species examined here compared to more southerly species in Alaska. We conducted a similar study in the Gulf of Alaska (GOA) where we analyzed the energy content of the 23 most abundant marine fish species (Vollenweider et al. 2011). The average energy density of the Arctic species examined in this study were very similar to that of the GOA, ranging from 3.27-7.98 kJ/g wet mass, while those in the GOA ranged from 3.64-9.78 kJ/g. In contrast, the range of average total energy of fish in the GOA was 14 times as great as Arctic fish (Arctic fish: 0.3-2,127 kJ; SEAK: 30-30,624 kJ). This stark difference is due to the large size discrepancy of abundant fish between the two regions, with the Arctic comprised of many juveniles as well as adult fish of diminutive size.

Only 2 species of fish could be directly compared between the Artic study and the Gulf of Alaska study. Pacific herring and capelin spanning a large size range were caught in both regions. From the energy density-length relationships, we saw slower energy accumulation with size in the Arctic than in the GOA for both species of fish. This is somewhat of a counterintuitive phenomenon, as one might expect Arctic fish to put on energy at a faster rate during the brief summer months in preparation for the longer, colder Arctic winters. On the other hand, Arctic fish in colder water may have significantly reduced metabolic rates and may therefore require less energy to sustain themselves.

This is the most thorough library of Arctic fish condition and prey quality to date. However, a significant limitation of this dataset is the lack year-round sampling due to substantial logistic constraints imposed by Arctic winters. Pelagic fish species in particular, are known to undergo significant season cycles in energy content in relation to their ontogenetic development, food availability and maturation state (Vollenweider et al. 2011). Generally, there is an increase in energy content during productive summer conditions, followed by a decrease in energy over winter when food is scarce and gonad development may concurrently take place in preparation for spawning. Most extreme are Pacific herring for which energy density (on a wet mass basis) can nearly double from spring minima to fall maxima. Demersal species cycle less, likely due to a more steady-state conditions near the sea floor. To what degree the prey quality of Arctic fish species fluctuates seasonally requires further investigation.

Oceanographic Mechanisms Affecting Fish Condition

Arctic cod and capelin body condition responded differently to environmental parameters near the ocean surface. In surface waters, water masses characterized by distinct temperatures and salinities had no influence on Arctic cod body condition. In contrast, surface water masses influenced capelin body condition, with fish from Beach Water consistently having the lowest energy density, lowest RNA/DNA in combination with the smallest fish. This combination of factors suggests that fish are energy-limited and could not put energy into storage, have not yet reached optimal size and are growing quickly. Capelin are caught frequently in the very nearshore, which indicates they could be utilizing these habitats for reasons such as predator avoidance in turbid nearshore waters at the expense of their body condition. Energy density of capelin was consistently highest in Shelf Water whereas RNA/DNA was greatest in Melt Water. Differences between water masses in capelin body condition was most pronounced in their RNA/DNA as opposed to their energy densities.

The influence of water masses on fish body condition was more pronounced in Arctic cod near the ocean floor. For Arctic cod, Shelf Water appeared to confer better fish condition, fish having both high energy densities concurrent with high growth rates indicating enough energy availability to be directed towards both storage and growth. Arctic cod in Alaska Coastal Water were in the poorest condition, having the lowest energy densities concurrent with low growth rates. Shelf Water similarly conferred high growth rates to large capelin near the ocean floor. Shelf Water is characterized as intermediate temperature and salinity, having warmed up from previous years or advected from the Bering Sea and through the Gulf of Anadyr (Danielson et al. 2016).

Both Arctic cod and capelin incurred interannual differences in fish body condition in near-surface water. Pooled across all water masses near-surface, energy density of Arctic cod was slightly greater (5%) in 2013 while that of capelin was slightly greater (2%) in 2012. However, both species had significantly higher RNA/DNA (>20%) and were smaller (>22%) in 2013 than 2012. Consistent small size and high growth rates across species in 2013 indicates that fish may have incured limited growth during the year in which nutrient content was low attributed to decreased transportation from the Bering Strait (Danielson et al. 2016). Pooled across all water masses, fish near-bottom showed less influence of year. Near the bottom, Arctic cod energy density and RNA/DNA was similar between years, but fish were bigger in 2013. The only parameter variable between years for capelin near-bottom was that growth was significantly enhanced in 2012. The lack of annual differences in fish condition in near-bottom water could be a factor of the sampling that had disparate bottom trawling locations between years. In 2012 the ArcticEis project conducted bottom trawling over a broad area further offshore area while during 2013 bottom trawling was conducted in the SHELFZ project on a finer scale and relatively closer to shore.

A cautionary note must be made regarding RNA/DNA. RNA/DNA is confounded by temperature and therefore strict comparisons across fish collected in vastly different temperatures is not directly correlated to specific growth rates (Caldarone 2001). However, comparison amongst water bodies with differing temperatures can still be illustrative and provide indications of energetic trade-offs.

Summary

Arctic cod and capelin, two of the most abundant forage species in the Chukchi Sea, had different responses in body condition relative to oceanographic parameters. Capelin body condition was responsive to discrete water masses in surface waters whereas the body condition of Arctic cod was not. However, body condition of both species was influenced by water mass in near-bottom water, where both species experienced enhanced condition in Shelf Water stemming from water transported from the Bering Sea. Capelin also had consistently low body condition in very nearshore Beach Water, though they can be very abundant in that habitat whereas Arctic cod were not caught there. Another consistent pattern observed in both species was that both Arctic cod and capelin were smaller and had significantly higher growth rates in 2013, suggesting fish were compensating for a period of prior poor growth. As fish condition of both species never correlated directly with temperature or salinity, this suggests other characteristics of the different water masses are more important aspects influencing fish condition, such as prey availability, competition, or predation.

5. Acknowledgements

We would like to thank the multiple funding sources that payed for fish collections and energetics analysis, including the North Pacific Research Board (NPRB), the Bureau of Ocean Energy Management (BOEM), North Slope Borough (NSB), and the US Fish and Wildlife Service. The NSB also provided invaluable and generous logistical help that made many of these fish collections possible, in particular Todd Sformo, Craig George, Brian Person, Billy Adams, Robert Suydam and Taqulik Hepa. We also thank the scientists and vessel crew of the ACES, AFF2015, SHELFZ, and ArcticEis projects, in particular Kevin Boswell, Brenda Norcross, Alexei Pinchuk, Franz Mueter, Jared Weems, Ed Farley, Kris Cieciel, Libby Logerwell, Sandra Parker-Stetter, and Darcie Neff. Additional key field personnel include Mark Barton, Ann Robertson, and Sam George who spent several summers in Barrow, AK running the beach seining effort, as well as Eric Wood, Alyssa Frothingham, Stella Moser, and Wyatt Fournier. Many people in the lab were instrumental in sample analyses, including Stella Mosher, Corey Fugate, Tayler Jarvis, Sarah Ballard, Bryan Cormack, Aswhin Sreenivasan, Hannah Findlay, Kevin Heffern and Casey Debenham.

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Tables

Table 1. Survey details of the projects from which samples were obtained, including 1) Ecology of Forage Fishes in the Arctic Nearshore (AFF), 2) The Arctic Coastal Ecosystem Survey (ACES), 3) ArcticEis, and 4) Shelf Habitat and EcoLogy of Fish and Zooplankton (SHELFZ).

Project	Type	Year	Months	Fishing Methods
AFF	Nearshore	2015	July - September	1) 37 m variable mesh beach seine 2) 5 x 3.5 m Aluette mid-water trawl 3) 4.7 m Plumb staff beam trawl 4) 2.6 x 1.2 m Otter trawl
ACES	Nearshore	2005, 2007, 2012-2014	July - August	1) 37 m variable mesh beach seine 2) 2.6 x 1.2 m Otter trawl
ArcticEis	Offshore	2012-2013	August - September	1) 122 m CanTrawl 400/601 mid-water trawl 2) 6.1 x 6.1 m Marinovich mid-water trawl 3) 4.7 m Plumb staff beam trawl 4) 34.1 m 83-112 Eastern otter trawl
SHELFZ	Intermediate	2013	August - September	1) 5 x 3.5 m Aluette mid-water trawl 2) 6.1 x 6.1 m Marinovich mid-water trawl 3) 4.7 m Plumb staff beam trawl 4) 34.1 m 83-112 Eastern otter trawl

Table 2. Water mass characteristics of nearshore Beach water masses from the ACES, AFF, and SHELFZ projects.Values indicate mean + standard error, and range.

Beach Water Mass	Temperature (C)	Salinity (PSU)
Beaufort Sea	5.4+0.2 3.4-7.4	26.5+0.3 19.0-29.2
Chukchi Sea	6.2+0.3 2.5-11.6	28.5+0.4 22.0-35.0
Elson Lagoon	9.6+0.6 4.5-11.8	22.0+2.1 4.9-29.0

Table 3. Values indicate mean ± standard error, (sample size). Energy Density = ED

Common Name	**Family**	**Genus species**	**Length (mm)**	**Mass (g)**	**ED (kJ/g wet)**	**ED (kJ/g dry)**	**Total Energy (kJ)**	**RNA/ DNA**	**Lipid (% wet mass)**	**Protein (% wet mass)**	**%Moisture**
Alaska plaice	Pleuronectidae	*Pleuronectes quadrituberculatus*	232 (1)	151.65 (1)	3.3 (1)	17.5 (1)	495.7 (1)	11.4 (1)	1.2 (1)	n/a	81.3 (1)
Arctic cod	Gadidae	*Boreogadus saida*	80±1 (985)	6.82±0.27 (984)	4.7±0.0 (355)	21.2±0.1 (356)	29.3±2.0 (356)	20.1±0.4 (623)	4.0±0.1 (320)	14.7±0.1 (179)	78.2±0.1 (781)
Arctic flounder	Pleuronectidae	*Liopsetta glacialis*	61±5 (4)	2.55±0.60 (4)	4.5±0.1 (4)	21.0±0.3 (4)	11.5±2.7 (4)	n/a	2.5±0.1 (4)	n/a	78.6±0.1 (4)
Arctic sand lance	Ammodytidae	*Ammodytes hexapterus*	66±1 (150)	0.95±0.06 (150)	4.9±0.1 (89)	21.3±0.2 (89)	5.7±0.4 (89)	14.2±0.4 (96)	4.3±0.1 (145)	16.3±0.1 (81)	77.0±0.1 (150)
Capelin	Osmeridae	*Mallotus catervarius*	72±1 (744)	2.63±0.12 (739)	4.5±0.1 (265)	21.7±0.2 (265)	14.1±1.2 (265)	21.7+0.4 (394)	2.3+0.1 (458)	14.2+0.0 (371)	79.6+0.1 (742)
Cisco, Arctic	Salmonidae	*Coregonus autumnalis*	302±10 (3)	298.21±47.38 (3)	7.1±0.2 (3)	24.9±0.3 (3)	2126.9±381.6 (3)	n/a	n/a	18.9±0.6 (3)	71.5±0.7 (3)
Cisco, Bering	Salmonidae	*Coregonus laurettae*	267±35 (3)	195.91±70.57 (3)	6.4±0.3 (3)	23.5±0.4 (3)	1273.2±461.8 (3)	n/a	n/a	20.0±0.2 (3)	72.8±0.8 (3)
Cisco, least	Salmonidae	*Coregonus sardinella*	279±4 (12)	210.60±10.67 (12)	6.0±0.2 (12)	21.9±0.3 (12)	1271.8±73.5 (12)	n/a	n/a	20.6±0.3 (12)	72.4±0.6 (12)
Eelpout, estuarine	Zoarcidae	*Lycodes turneri*	142 (1)	17.52 (1)	4.1 (1)	20.8 (1)	71.8 (1)	16.2 (1)	n/a	n/a	80.4 (1)
Eelpout, marbled	Zoarcidae	*Lycodes raridens*	135±15 (3)	15.34±4.76 (3)	4.4±0.1 (3)	21.5±0.2 (3)	68.4±22.9 (3)	13.2±1.9 (3)	n/a	n/a	79.5±0.3 (3)
Eelpout, polar	Zoarcidae	*Lycodes polaris*	176±13 (14)	36.68±11.61 (14)	4.2±0.3 (13)	19.9±0.6 (14)	145.0±39.7 (13)	11.1±1.0 (14)	n/a	n/a	79.1±0.6 (14)
Eelpout, wattled	Zoarcidae	*Lycodes palearis*	186±9 (15)	34.25±4.60 (15)	4.4±0.1 (15)	20.9±0.3 (15)	157.2±23.6 (15)	18.8+1.0 (15)	n/a	n/a	78.8+0.4 (15)
Longhead dab	Pleuronectidae	*Limanda proboscidea*	57±4 (16)	2.34±0.74 (16)	4.6±0.2 (16)	20.0±0.4 (16)	11.6±3.9 (16)	13.7±1.5 (16)	3.0±0.3 (16)	14.2±0.0 (9)	76.9±0.5 (16)
Pacific herring	Clupeaidae	*Clupea pallasii*	188±5 (135)	85.08±3.89 (135)	8.0±0.3 (35)	26.2±0.4 (35)	739.2±72.2 (35)	8.3±0.3 (100)	13.3±1.0 (35)	15.6±0.3 (35)	70.0±0.8 (35)
Rainbow smelt	Osmeridae	*Osmerus mordax*	115±22 (12)	23.44±10.12 (12)	4.8±0.1 (12)	21.7±0.3 (12)	114.9±48.3 (12)	n/a	n/a	16.5±0.3 (8)	77.9±0.3 (12)

Saffron cod	Gadidae	*Eleginus gracilis*	39±2 (455)	3.74±1.01 (455)	3.6±0.1 (143)	17.7±0.2 (144)	52.8±14.8 (143)	15.9+0.4 (154)	1.8+0.1 (207)	15.9+0.1 (61)	80.0+0.1 (455)
Sculpin, Arctic	Cottidae	*Myoxocephalus scorpioides*	41±1 (18)	0.83±0.04 (18)	4.6±0.1 (17)	20.5±0.2 (18)	3.6±0.3 (18)	n/a	3.0+0.2 (17)	n/a	77.6+0.2 (18)
Sculpin, Arctic staghorn	Cottidae	*Gymnocanthus tricuspis*	44±2 (10)	0.97±0.18 (10)	4.8±0.1 (10)	20.8±0.2 (10)	4.7±0.9 (10)	n/a	2.0+0.2 (9)	n/a	76.7+0.3 (10)
Sculpin, belligerent	Cottidae	*Megalocottus platycephalus*	57±1 (18)	2.73±0.26 (18)	4.6±0.1 (17)	21.0±0.2 (18)	12.9±1.4 (17)	n/a	4.1±0.2 (17)	14.2±0.1 (18)	77.9±0.1 (18)
Sculpin, fourhorn	Cottidae	*Myoxocephalus quadricornis*	93±5 (93)	14.27±2.41 (92)	3.9±0.1 (91)	19.6±0.1 (92)	52.0±8.8 (92)	7.3±0.6 (20)	2.0±0.1 (50)	13.0±0.2 (62)	80.0±0.2 (93)
Sculpin, ribbed	Cottidae	*Triglops pingelii*	34±2 (5)	0.27±0.03 (5)	4.3±0.2 (4)	20.2±0.2 (5)	1.3±0.1 (4)	n/a	n/a	n/a	78.4±0.5 (5)
Sculpin, shorthorn	Cottidae	*Myoxocephalus scorpius*	34±2 (6)	0.46±0.08 (6)	4.1±0.1 (6)	18.2±0.3 (6)	1.9±0.3 (6)	n/a	1.9±1.1 (2)	n/a	77.7±0.6 (6)
Slender eelblenny	Stichaeidae	*Lumpenus fabricii*	46±2 (113)	0.36±0.05 (113)	4.5±0.1 (44)	20.1±0.2 (44)	3.4±0.6 (44)	13.6±0.6 (23)	3.0±0.1 (42)	16.5±0.1 (40)	78.0±0.1 (113)
Walleye pollock	Gadidae	*Gadus chalcogrammus*	93±3 (26)	5.89±0.58 (26)	4.2±0.1 (26)	21.5±0.2 (26)	24.8±2.5 (26)	8.5±0.2 (26)	n/a	n/a	80.5±0.2 (26)

Table 4. Correlation of energy density (ED; kJ/g) to fish length from linear regression for 5 species of Arctic fish. Energy density (kJ/g) is expressed on both a wet mass and dry mass basis.

Common Name	**Regression Equation Wet Mass**	**Regression Equation Dry Mass**
Arctic cod	ED=4.215+0.005706*Length ($R^2 = 0.09$)	ED=19.11+0.02704*Length ($R^2 = 0.20$)
Saffron cod	ED=3.224+0.006485*Length ($R^2 = 0.47$)	ED=16.41+0.01909*Length ($R^2 = 0.36$)
Pacific herring	ED=3.090+0.02599*Length (R^2=0.57)	ED=19.36+0.03660*Length (R^2=0.61)
Capelin	ED=2.952+0.01911* Length (R^2=0.26)	ED=17.15+0.05866* Length (R^2=0.37)
Fourhorn sculpin	ED=4.392–0.004842*Length (R^2=0.19)	ED=21.02–0.01514*Length (R^2=0.35)

Figures

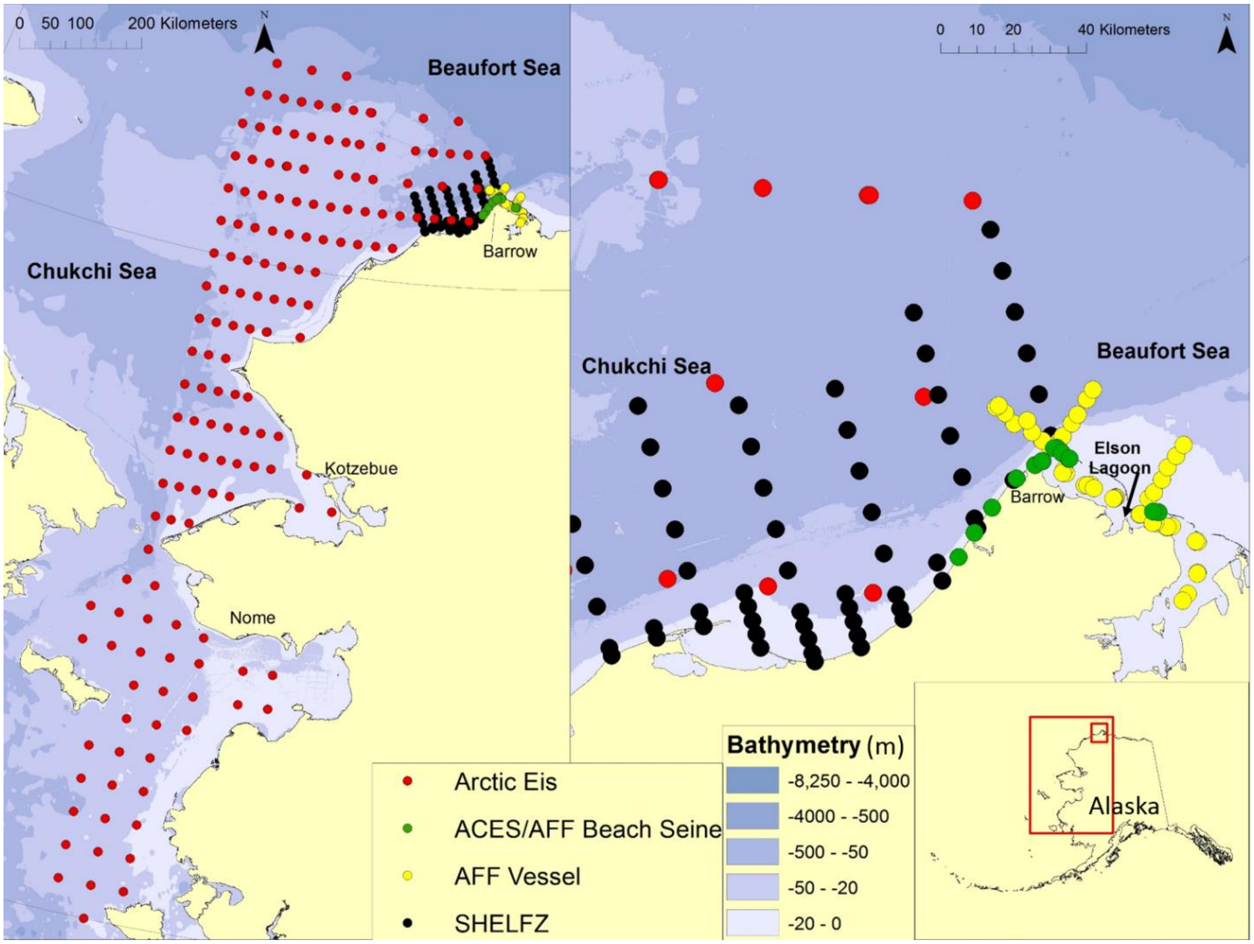

Figure 1. Station design of the projects from which samples were obtained, including 1) Ecology of Forage Fishes in the Arctic Nearshore (AFF), 2) The Arctic Coastal Ecosystem Survey (ACES), 3) ArcticEis, and 4) Shelf Habitat and EcoLogy of Fish and Zooplankton (SHELFZ). Additional samples were obtained from subsistence collections in Barrow and Kotzebue.

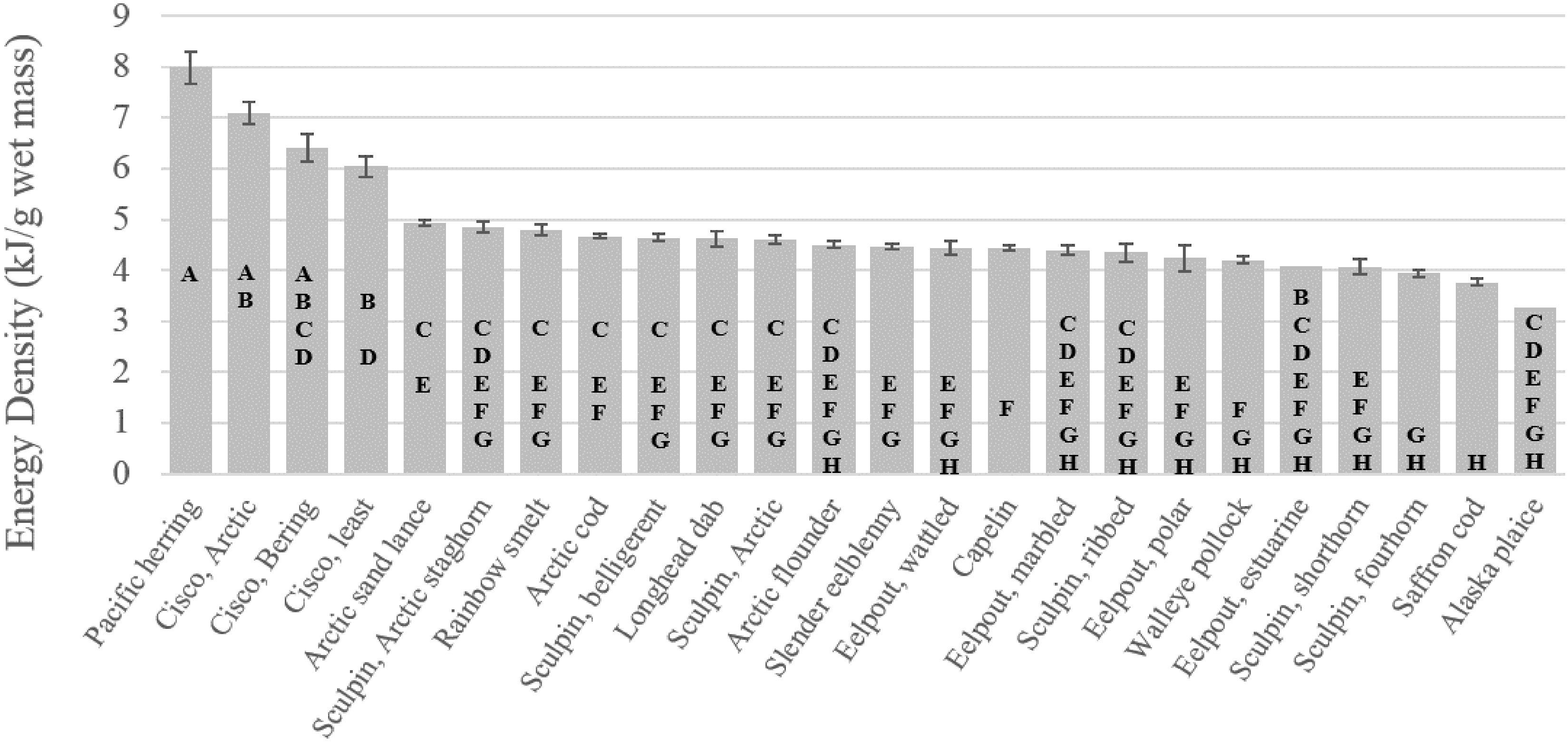

Figure 2. Average energy density (kJ/g wet mass) of all sampled Arctic fish species. Like letters indicate statistical similarity determined by ANOVA.

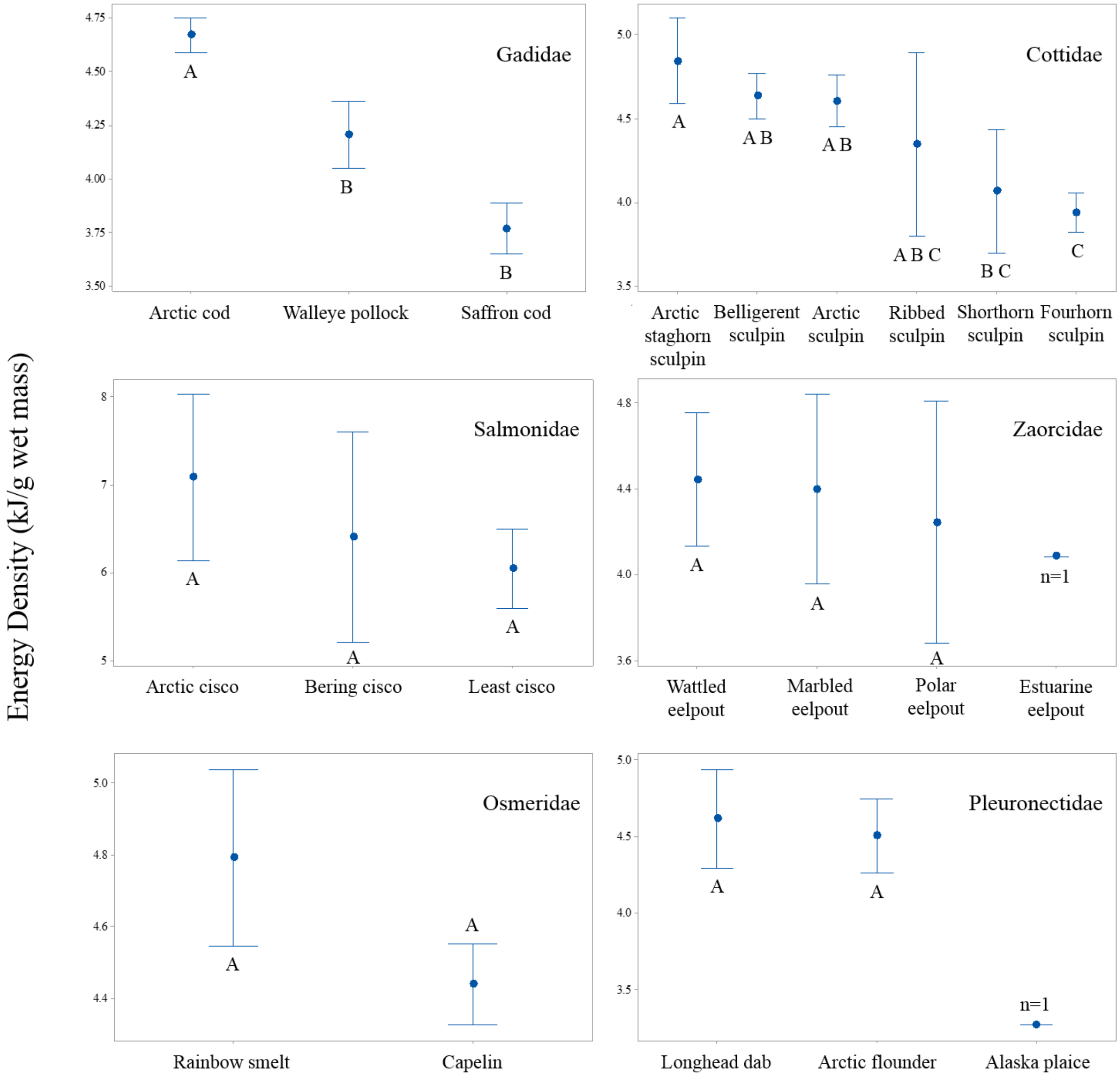

Figure 3. Average energy density (kJ/g wet mass) by family of Arctic fish species. Like letters indicate statistical similarity determined by ANOVA.

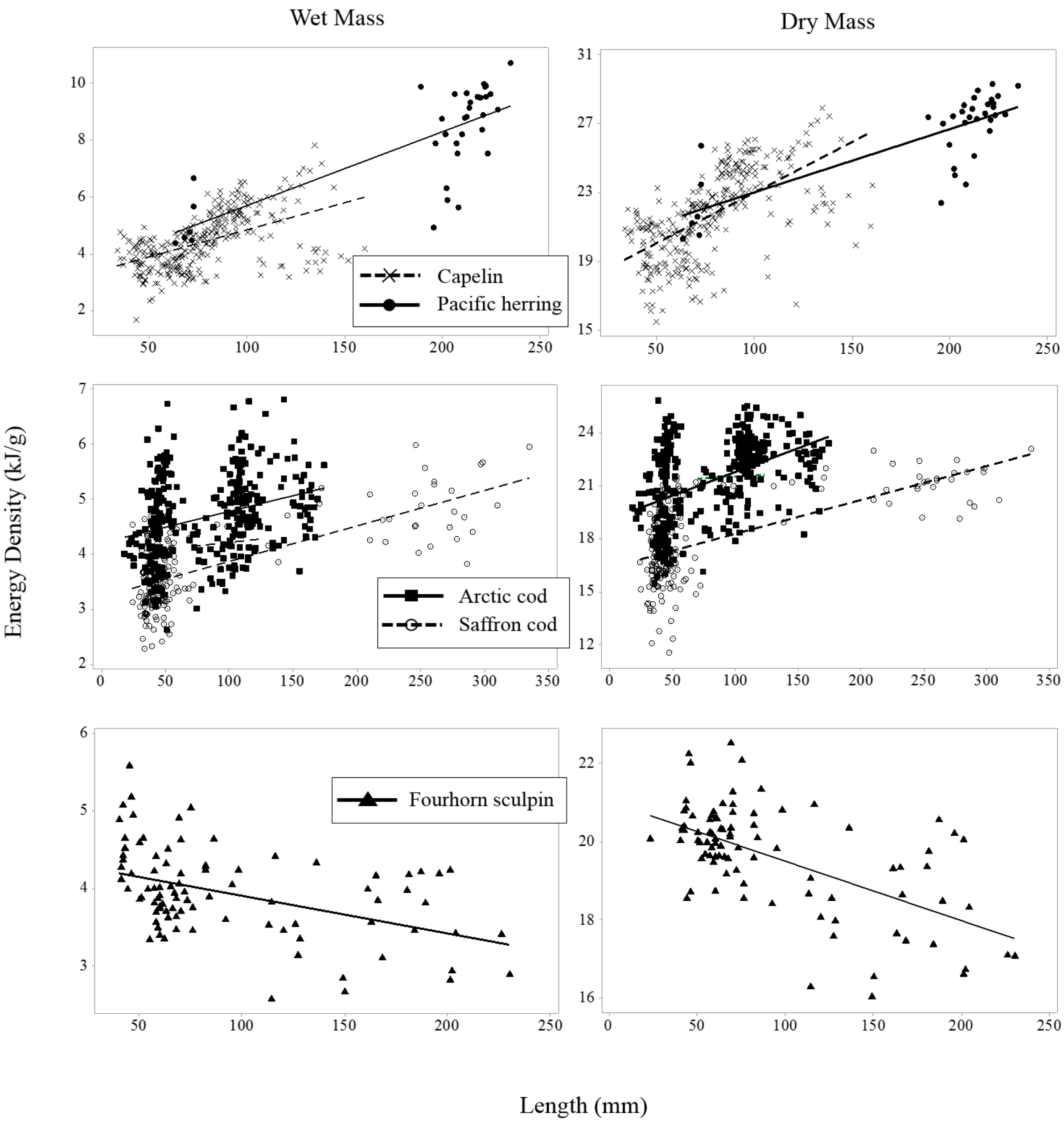

Figure 4. Energy density (ED; kJ/g) as a function of length for Arctic fish species. Panels on the left show ED on a wet mass basis (kJ/g wet mass) and panels on the right show ED on a dry mass basis (kJ/g dry mass). The top panels depict linear regressions for capelin (R^2=0.26 wet mass, 0.37 dry mass) and Pacific herring (R^2=0.57 wet mass, 0.61 dry mass), the central panels depict Arctic cod (R^2=0.09 wet mass, 0.20 dry mass) and saffron cod (R^2=0.47 wet mass, 0.36 dry mass) and the bottom panels depict fourhorn sculpin (R^2=0.19 wet mass, 0.35 dry mass).

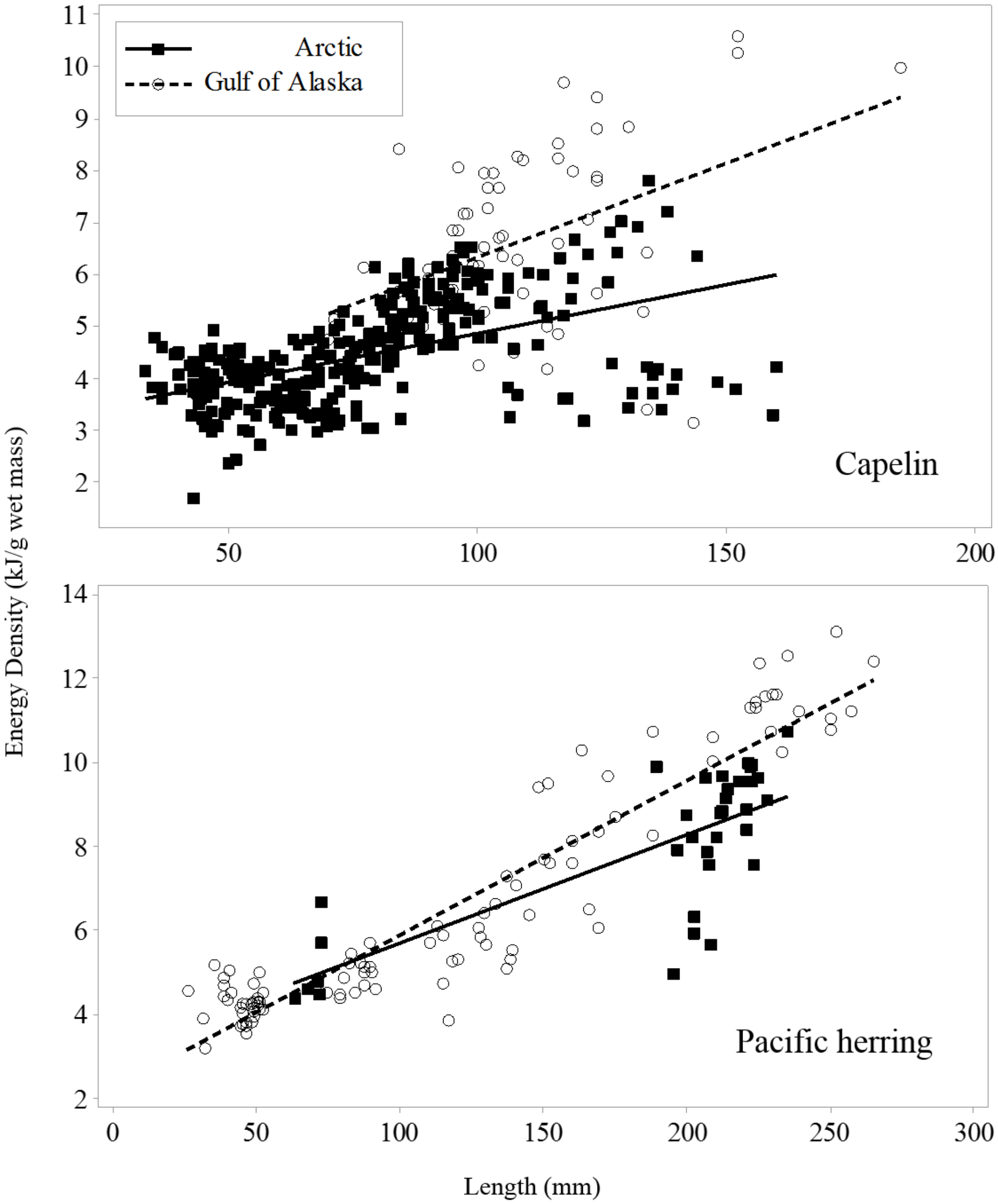

Figure 5. Length-energy density relationship of Pacific herring and capelin collected in the summer (July – September) from two Large Marine Ecosystems, the Arctic and the Gulf of Alaska.

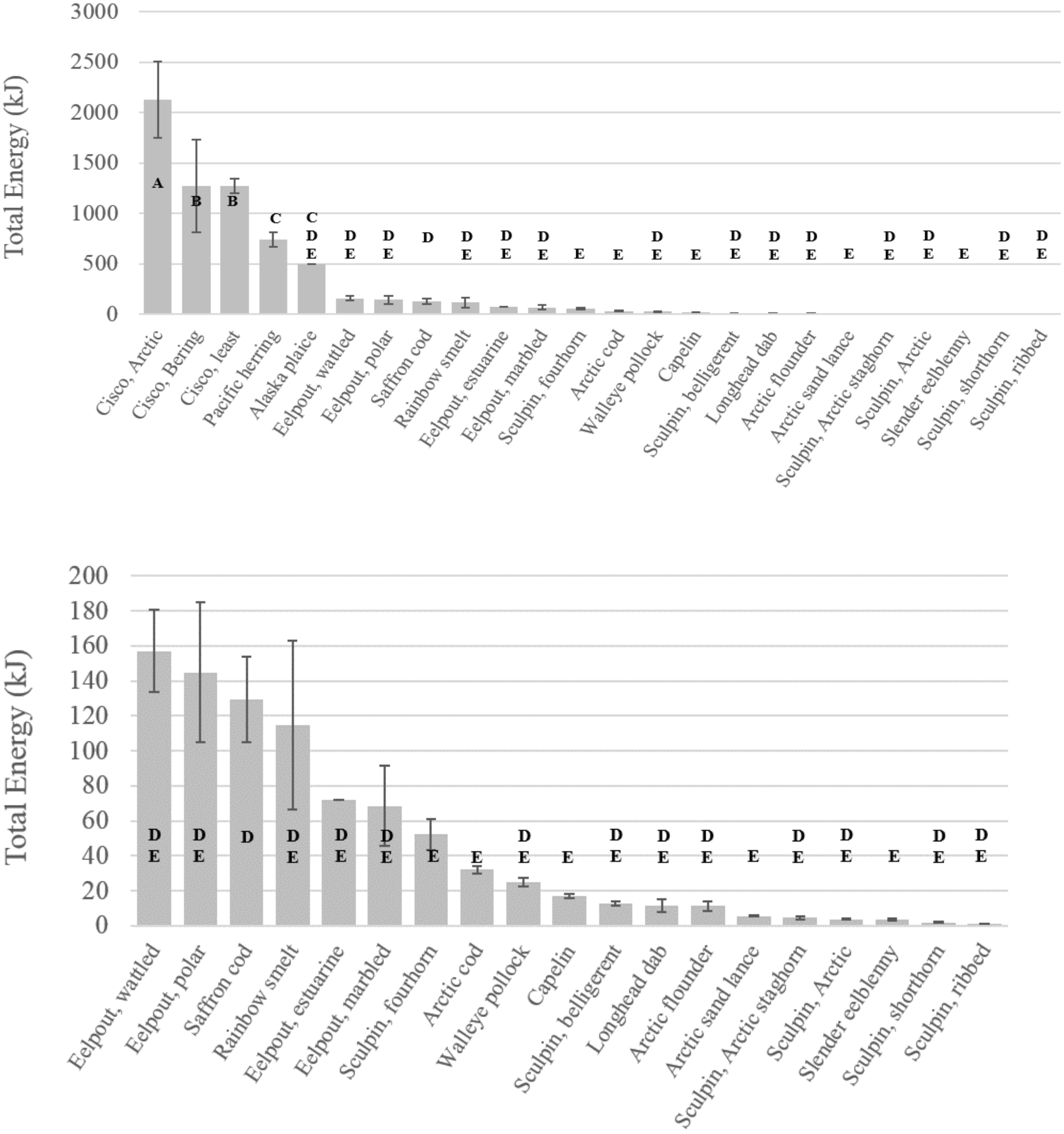

Figure 6. Average total energy content (kJ) of all sampled Arctic fish species. Like letters indicate statistical similarity determined by ANOVA. The top panel includes all 24 species evaluated and the bottom panel excludes the top 5 species with the greatest energy content.

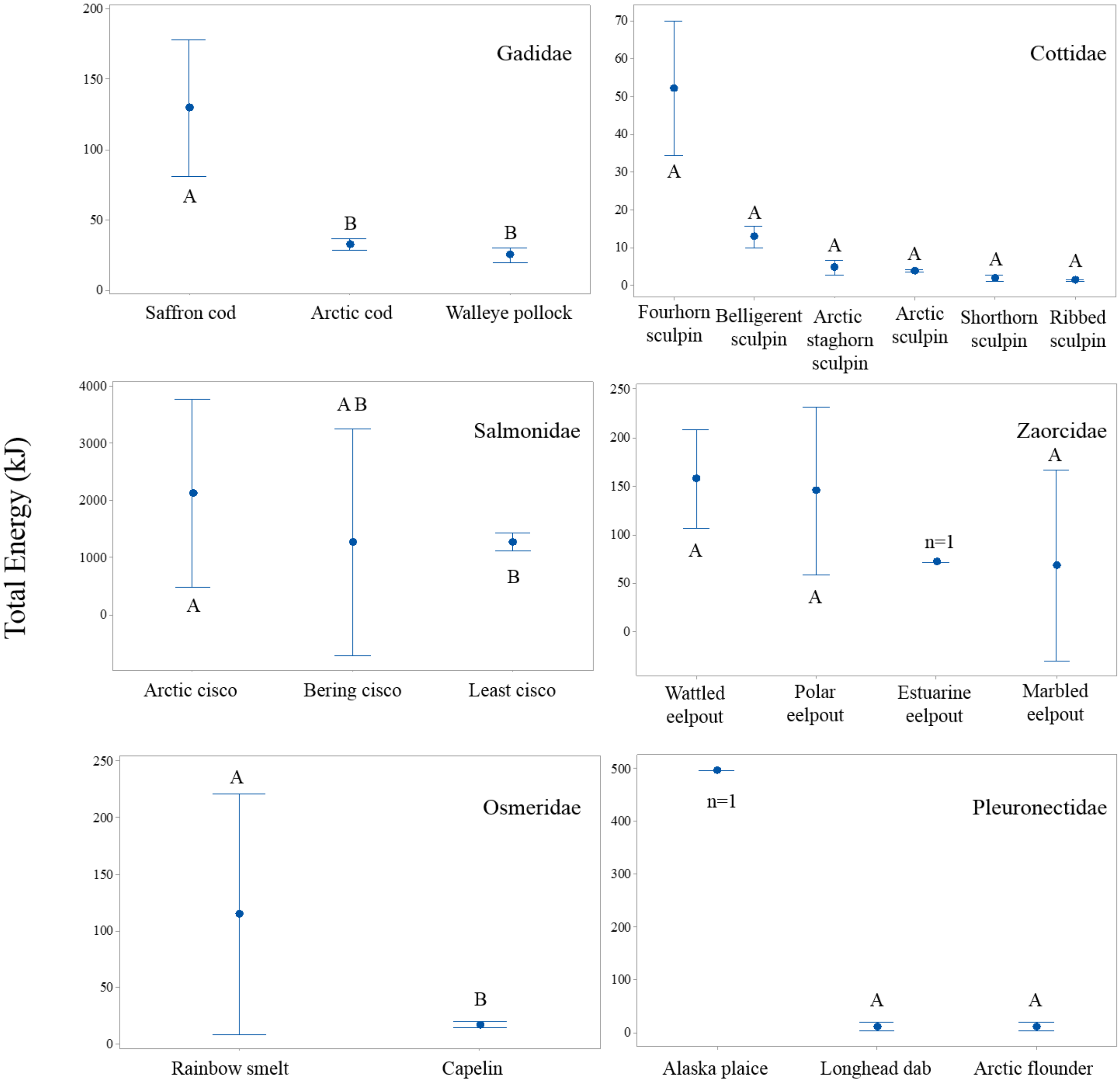

Figure 7. Average total energy (kJ) by family of Arctic fish species. Like letters indicate statistical similarity determined by ANOVA.

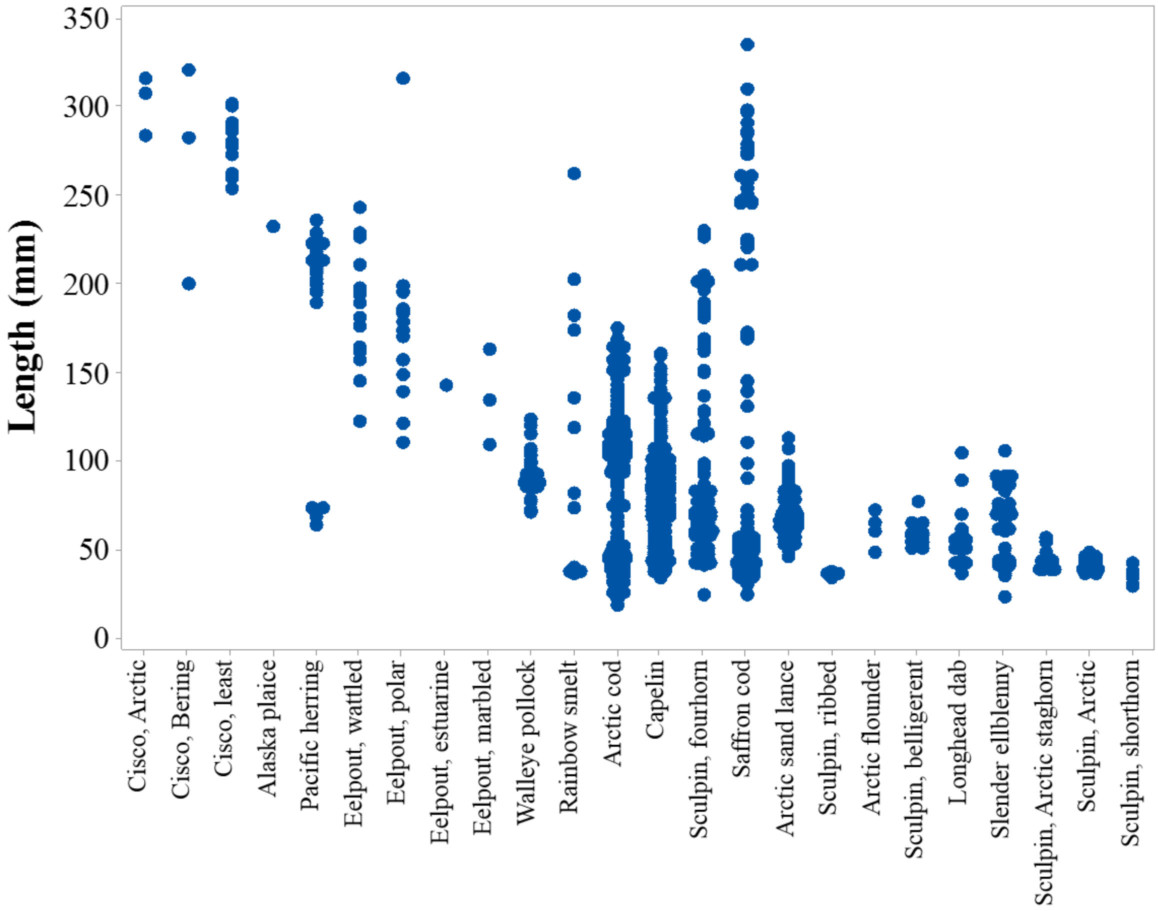

Figure 8. Individual value plot of lengths (mm) of Arctic fish evaluated for energetics.

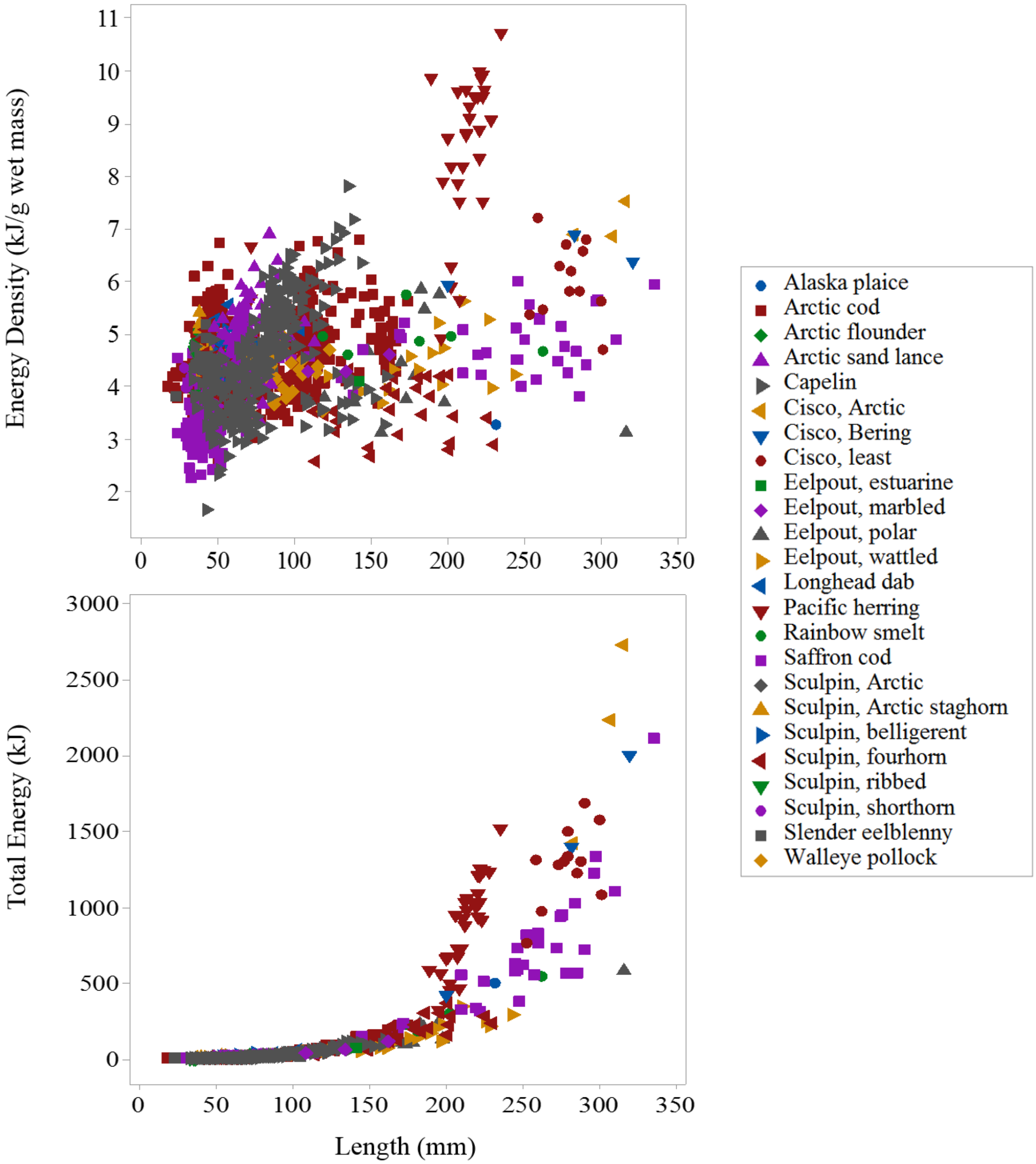

Figure 9. Energy density (kJ/g wet mass) in relation to length (mm) (top panel) and total energy content (kJ) in relation to length (bottom panel) of all Arctic species.

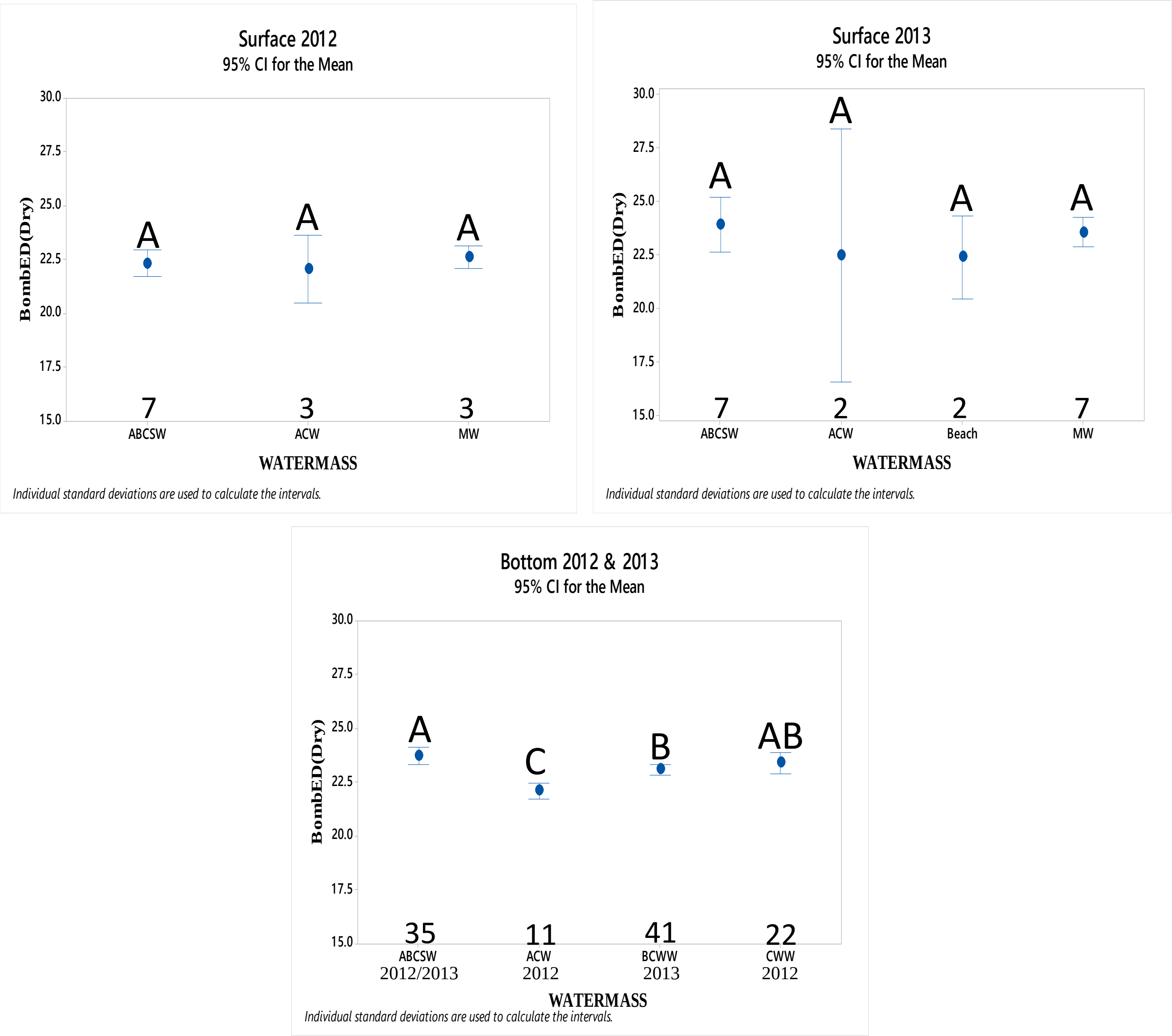

Figure 10. Energy density (kJ/g dry mass) of Arctic cod caught in different water masses from surface and bottom trawls and beach seines in 2012 and 2013. ABCSW = Anadyr, Bering, Chukchi Shelf Water; ACW = Alaska Coastal Water; BCWW = Bering, Chukchi Winter Water; CWW = Chukchi Shelf Winter Water; Beach-C = Beach Chukchi Sea. Like letters indicate statistical similarity determined by ANOVA. Sample sizes are listed along the x-axis.

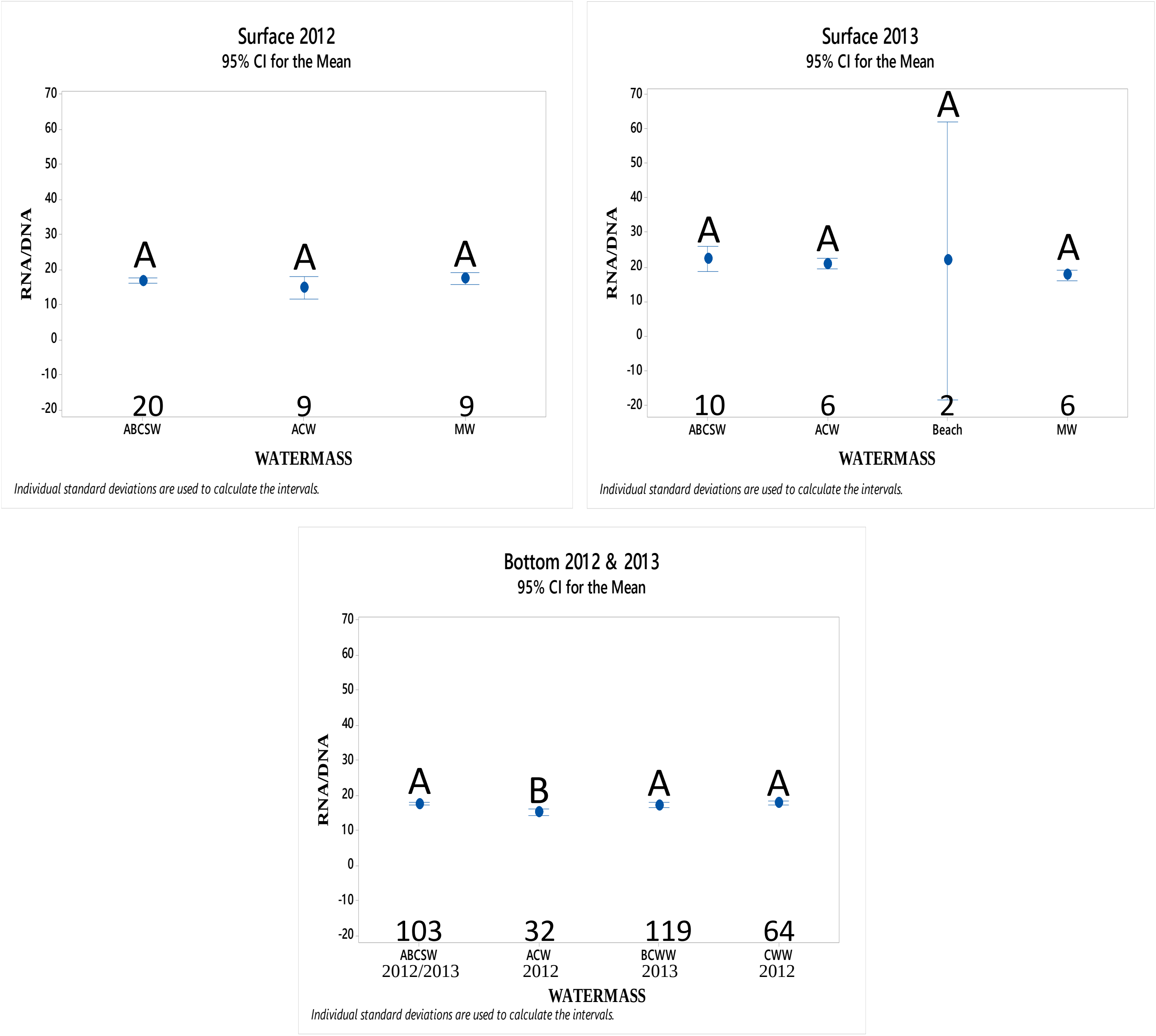

Figure 11. RNA/DNA of Arctic cod caught in different water masses from surface and bottom trawls and beach seines in 2012 and 2013. ABCSW = Anadyr, Bering, Chukchi Shelf Water; ACW = Alaska Coastal Water; BCWW = Bering, Chukchi Winter Water; CWW = Chukchi Shelf Winter Water; Beach-C = Beach Chukchi Sea. Like letters indicate statistical similarity determined by ANOVA. Sample sizes are listed along the x-axis.

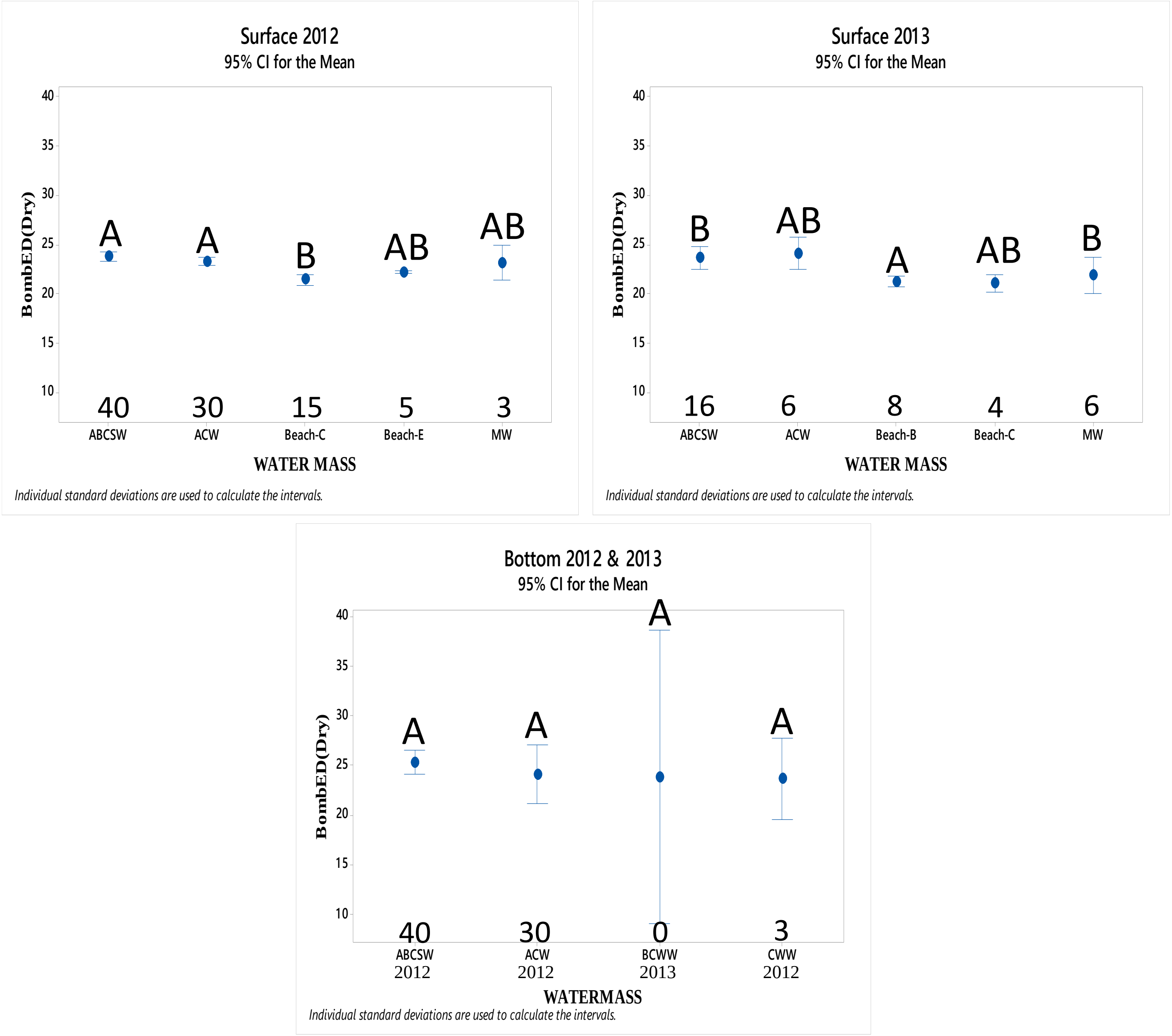

Figure 12. Energy density (kJ/g dry mass) of capelin caught in different water masses from surface and bottom trawls and beach seines in 2012 and 2013. ABCSW = Anadyr, Bering, Chukchi Shelf Water; ACW = Alaska Coastal Water; BCWW = Bering, Chukchi Winter Water; CWW = Chukchi Shelf Winter Water; Beach-B = Beach Beaufort Sea; Beach-C = Beach Chukchi Sea; Beach-E = Beach Elson Lagoon. Like letters indicate statistical similarity determined by ANOVA. Sample sizes are listed along the x-axis.

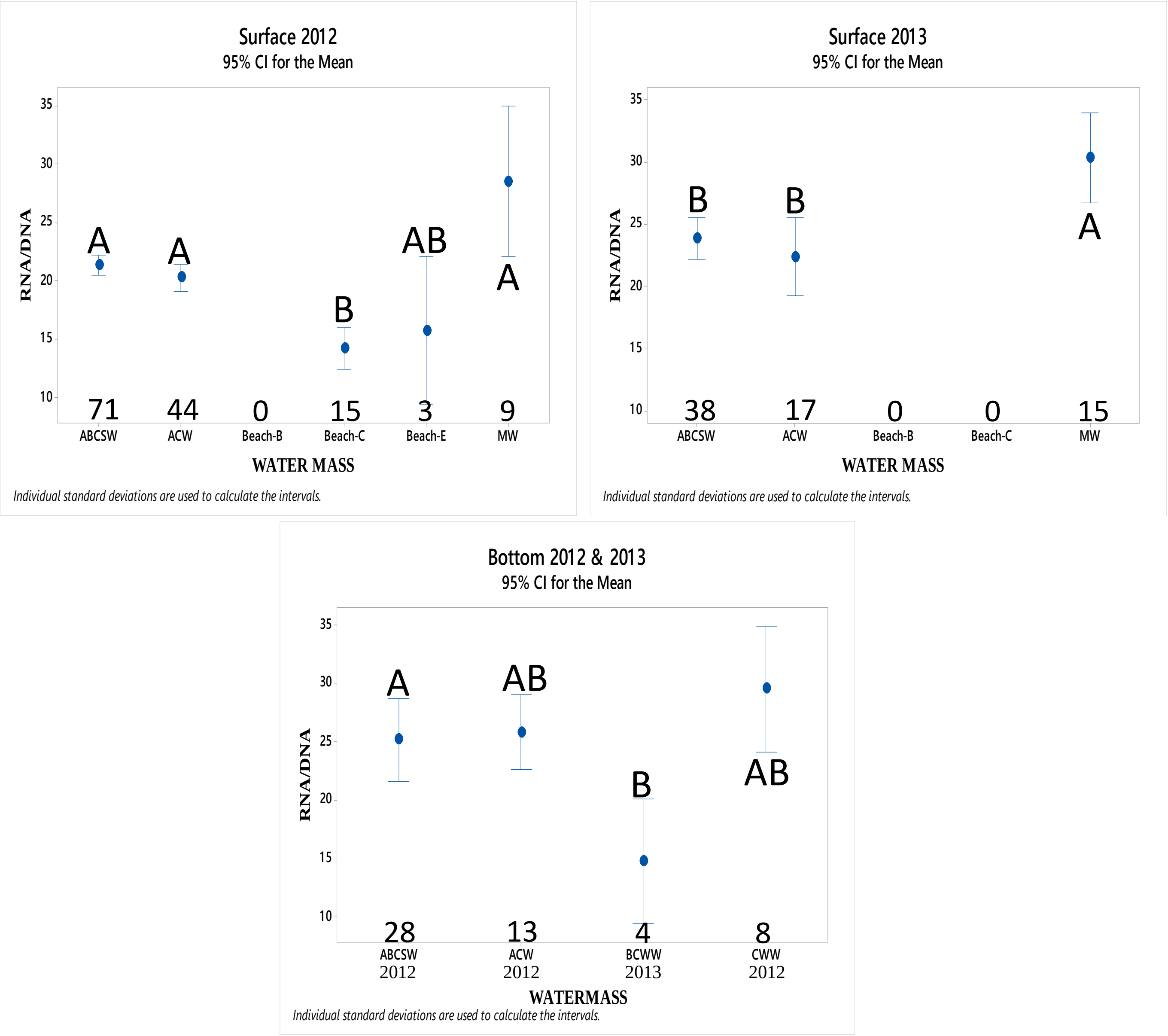

Figure 13. RNA/DNA of capelin caught in different water masses from surface and bottom trawls and beach seines in 2012 and 2013. ABCSW = Anadyr, Bering, Chukchi Shelf Water; ACW = Alaska Coastal Water; BCWW = Bering, Chukchi Winter Water; CWW = Chukchi Shelf Winter Water; Beach-B = Beach Beaufort Sea; Beach-C = Beach Chukchi Sea; Beach-E = Beach Elson Lagoon. Like letters indicate statistical similarity determined by ANOVA. Sample sizes are listed along the x-axis.

Appendix V.

Growth and Condition of Juvenile Chum and Pink Salmon in the Northeastern Bering Sea

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December 4, 2015

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
AIC	Akaike’s Information Criterion
ACW	Alaska Coastal Water
BSW	Bering Sea Water
CTD	Conductivity-Temperature-Depth
IGF-1	Insulin-like Growth Factor 1
NEBS	Northeastern Bering Sea
SEBS	Southeastern Bering Sea
SSS	Sea-surface salinity
SST	Sea-surface temperature
TSMRI	Ted Stevens Marine Research Institute

List of Oral and Poster Presentations

*indicates student author

Prechtl, M*. Patterns in size, growth, and condition of juvenile chum and pink salmon in the northeastern Bering Sea. M.S. Thesis Defense, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks. Juneau, AK. 16 October 2014.

Prechtl, M*, B Beckman, A Beaudreau, and M McPhee. The effects of climate variability on juvenile pink and chum salmon growth and condition in the northeastern Bering and Chukchi seas. Alaska Marine Science Symposium, Anchorage, AK, 20 Jan; and the 15th Salmon Ocean Ecology Meeting, Santa Cruz, CA, 14 Mar 2014.

Prechtl, MP*, B Beckman, and MV McPhee. The effects of climate variability on juvenile pink and chum salmon growth and condition in the Northeastern Bering and Chukchi seas. 28th Lowell Wakefield Fisheries Symposium: Responses of Arctic Marine Ecosystems to Climate Change, Anchorage, 26 Mar 2013.

Prechtl, MP*, MV McPhee, and B Beckman. Impact of Arctic climate warming on juvenile salmon abundance and condition in the northeastern Bering and Chukchi seas. Western Alaska Interdisciplinary Science Conference, Nome, AK, 21 Mar 2013.

Prechtl, MP*, MV McPhee, and B Beckman. Impact of Arctic climate warming on juvenile salmon abundance and condition in the northeastern Bering and Chukchi seas. Alaska Marine Science Symposium, Anchorage, 18 Jan 2013.

Prechtl, MP*, MV McPhee, and B Beckman. Impact of Arctic climate warming on juvenile salmon abundance and condition in the northeastern Bering and Chukchi seas. 39th Annual Meeting of the Alaska Chapter of the American Fisheries Society, Kodiak, AK, 24 Oct 2012.

Proposed Objectives and Study Chronology

The objective of this salmon ecology component of Arctic Eis was to characterize the size, growth, and condition of juvenile pink and chum salmon and their relation to biophysical features in the northeast Bering and Chukchi seas over two years. Data were collected during the two surface/midwater trawl and oceanographic survey cruises in summers of 2012 and 2013. Very few juvenile salmon were captured in the Chukchi Sea during these cruises, which sampled the Chukchi Sea earlier in the year than did a previous NOAA survey in 2007 that captured substantial numbers of juvenile salmon in the Chukchi Sea. In 2013, a broken water line (providing seawater coolant to a shipboard generator) flooded the midship deck, resulting in the loss of many biological samples, including the blood samples we collected to measure insulin-like growth factor in juvenile salmon. Despite these challenges, we were able to combine the data we collected during the Arctic Eis surveys to previous NOAA surveys from 2003 – 2011 (excluding 2008), in order to provide a baseline description of the ecology of juvenile pink and chum salmon in the northeastern Bering Sea. This work is an important contribution to understanding the ocean ecology of Pacific salmon, as the region is likely to see greater use by salmon with increased warming. The data we describe in this report will be available to the public through the Alaska Ocean Observing System (AOOS).

1. Abstract

As the Arctic continues to warm, abundances of juvenile Pacific salmon (*Oncorhynchus* spp.) in the northern Bering Sea are expected to increase. However, information regarding the growth and condition of juvenile salmon in these waters is limited. The first objective of this study was to describe relationships between size, growth, and condition of juvenile chum (*O. keta*) and pink (*O. gorbuscha*) salmon and environmental conditions using data collected in the northeastern Bering Sea (NEBS) from 2003-2007 and 2008-2012. Stations with greater bottom depths and cooler sea-surface temperatures were associated with greater length and lower condition (weight-length residuals) in both species, as well as greater energy density in chum salmon. Chlorophyll-a explained little variation in any measure of size or physiological condition. We used insulin-like growth factor-1 (IGF-1) concentrations as an indicator of relative growth rate for fishes sampled in 2009-2012 and that found fish exhibited higher IGF-1 concentrations in 2010-2012 than in 2009, although these differences were not clearly attributable to environmental conditions across years. Our second objective was to compare size and condition of juvenile chum and pink salmon in the NEBS between warm and cool spring thermal regimes of the southeastern Bering Sea (SEBS), based on the strong role of sea-ice retreat in the spring for production dynamics in the SEBS and prevailing northward currents, suggesting that feeding conditions in the NEBS are influenced by production in the SEBS. Chum and pink salmon were shorter and chum salmon exhibited greater energy density in years with cool springs; however, no other aspects of size and condition differed significantly between spring thermal regimes. Finally, we compared indicators of energy allocation between even and odd brood-year stocks of juvenile pink salmon to test the hypothesis that odd-year stocks allocate more energy to growing in length while even-year stocks allocate more energy to fat storage. In support of the hypothesis, even stocks of juvenile pink salmon were more energy dense, while odd stocks exhibited higher IGF-1 levels. Overall, our results support the idea that sea-ice dynamics influence energy allocation and growth of juvenile salmon in both the southern and northern Bering Sea and provide a foundation for further understanding of how environmental conditions influence juvenile salmon at the northern edge of their range.

2. Introduction

Chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon provide vital ecological, economic, and subsistence resources to the peoples of western Alaska. Chum and pink salmon are broadly distributed across the Pacific Ocean and inhabit the most northern range extent of Pacific salmon, with a few populations natal to Alaska's North Slope rivers (Irvine et al. 2009). The cold-water tolerance of these species and their minimal use of freshwater habitat have enabled populations to colonize sub-Arctic and Arctic regions (Craig and Haldorson 1986; Irvine et al. 2009). These characteristics make chum and pink salmon likely candidates for future northern range expansion as Arctic climate continues to warm (Nielsen et al. 2012). In recent years, populations of chum and pink salmon in the North Pacific Ocean have increased, due primarily to increased hatchery production but also enhanced marine survival (Ruggerone et al. 2010). Furthermore, significant abundances of juvenile chum and pink salmon have been observed in the northeastern Bering Sea (NEBS) and southern Chukchi Sea (Moss et al. 2009). These observations parallel reported increases in the abundance of salmon by subsistence users in Arctic and sub-Arctic habitats in northwestern Alaska (Eggers et al. 2011; Carothers et al. 2013) and highlight the need for research on juvenile salmon at higher latitudes. In northern habitats, growth and condition are likely key factors that provide insight into marine survival.

Changing ocean conditions may affect marine survival of juvenile salmon, through effects on growth and nutritional condition. Marine survival of salmon may be dependent on growth accrued over the first summer in the ocean (Beamish and Mahnken 2001; Farley et al. 2007). Marine survival during their first winter may also be dependent on juvenile salmon reaching threshold levels of nutritional condition (from hereafter referred to as ‘condition’) (Beamish and Mahnken 2001). There is a strong correlation between salmon growth and temperature, given that nutritional needs are met and temperatures are within the thermal limits of the organism (Larsen et al. 2001; Beckman et al. 2004a,b; Andrews et al. 2009). However, temperature has been shown to have contrasting effects on growth and condition of juvenile salmon (Andrews et al. 2009; Davis et al. 2009; Heintz 2009). For example, Andrews et al. (2009) found that juvenile pink salmon in the NEBS were longer during warm years, but less energy dense. Conversely, juvenile pink salmon sampled during cool years were shorter, but more energy dense (Andrews et al. 2009). While it is likely that the relationship between temperature and condition is due to a combination of physiological and environmental variables, lab studies have shown that cooler temperatures facilitate lipid storage in juvenile salmon (Heintz 2009). To further investigate relationships between physiological and environmental variables, this study describes relationships between juvenile chum and pink salmon growth, condition, and environmental variables measured within the NEBS.

While sea ice extent and timing of sea ice retreat has remained relatively consistent in the NEBS, sea ice conditions in the southeastern Bering Sea (SEBS) have alternated between periods of early and late sea ice retreat (Hunt et al. 2011). Anomalously warm May spring sea surface temperatures and early sea ice retreat occurred in 2002-2005. From 2006-2013, the region was characterized by anomalously cool May spring sea surface temperatures and late sea ice retreat (Andrews et al. 2009; Farley and Trudel 2009; Overland et al. 2012). Warm years were found to support open-water spring blooms that led to a 70% increase in primary production (Brown and Arrigo 2013). However, in the SEBS, these open water blooms supported warm-water species of zooplankton that were lipid-poor, reducing the amount of energy available to higher trophic levels (Coyle and Pinchuk 2002; Coyle et al. 2011; Hunt et al. 2011). Conversely, ice-associated blooms that occurred during years of late ice-retreat supported lipid-rich, cold-water species of zooplankton, increasing the amount of energy available to higher trophic levels (Coyle and Pinchuk 2002; Coyle et al. 2011; Hunt et al. 2011). Thus, it has been interpreted that ice-associated blooms provide an energy-rich prey source for pelagic fishes, such as juvenile walleye pollock and salmon. As prevailing currents advect waters from the SEBS northward into the NEBS (Johnson et al., 2004), we hypothesized that fundamental differences in production between early and late ice retreat in the SEBS would have downstream consequences for fish consumers in the NEBS, such as salmon and their prey.

Environmental variables may influence growth and condition of juvenile salmon, but there may also be an important genetic influence on juvenile pink salmon. Pink salmon have a unique two-year life cycle, with even and odd stocks (with 'even' or 'odd' referring to the year of spawning) being genetically distinct (Apsinwall 1974; Beacham and Murray 1988; Beacham et al. 2012). Genetic differences between even and odd stocks may include differences in metabolic strategy (Beamish 2012). The short life cycle of pink salmon has corresponded with the evolution of rapid marine growth (Ricker 1976; Brett 1979). In recent years, odd stocks of pink salmon in the Fraser River system, British Columbia, have increased, while even stocks have remained fairly constant (Beamish 2012). Beamish (2012) attributed this to genetic differences in metabolic strategy during the first marine summer between stocks, with odd stocks allocating more energy to growing in length and even stocks allocating more energy to fat storage. This difference in energy allocation would allow odd stocks to benefit from the increased prey production during late fall that has been attributed to warming off the coast of British Columbia, and thus could explain why odd stocks have increased in abundance in that region while even stocks have not (Beamish 2012).

We used data from late summer, integrated ecosystem surveys conducted in the northeastern Bering Sea from 2003 to 2013 (see Farley et al. 2009) to examine how spring thermal regime and summer ocean conditions influence size, growth, and condition of juvenile chum and pink salmon in the NEBS. Specifically, our objectives were to 1) describe how size (length), condition, and growth were related to environmental variables measured at time of capture, 2) determine whether size and condition in the NEBS differed between warm and cool spring thermal regimes of the SEBS, and 3) to test odd/even year energy allocation strategy (growth vs. storage) hypothesis (Beamish 2012) for western Alaska pink salmon. For objectives 1 and 2, we hypothesized that juvenile pink and chum salmon would be smaller but in better condition during the cool spring thermal regime based on expected trophic consequences of ice-associated bloom in the SEBS. Our results provide a foundation for understanding how climate-induced changes in ecosystem structure may affect condition and growth of juvenile pink and chum salmon in the NEBS.

3. Methods

3.1 Field sampling

Surveys were conducted each September from 2003 to 2013 (except 2008, due to insufficient funding) in the northeastern Bering Sea. Over the time frame of our analysis, the mean geographic position of the entire NEBS survey tended to shift northward and eastward (further inshore), and also tended to occur earlier. For these reasons, we only included stations sampled between 59.92°N to 64.06°N and -174.00°W to -165.95°W in our analyses (Fig. 1). Additionally, the direction of sampling varied among years, with sampling occurring from south to north in 2003, 2007, 2009-2011 and from north to south in 2004-2006 and 2012-2013.

Juvenile salmon were collected following methods described in Murphy et al. (2003) and Farley et al. (2009). All sampling was done during daylight hours, from approximately 0700 AKDT to 2300 AKDT. Oceanographic data were collected at each trawl station immediately prior to deploying the trawl. Vertical profiles of temperature, salinity, chlorophyll-a fluorescence, light transmission, and photosynthetic available radiation (PAR) were measured with a Sea-Bird Electronics Inc. SBE 25 (2003- 2005) and SBE 911/17 (2005-current) Sealogger Conductivity-Temperature-Depth profiler (CTD).

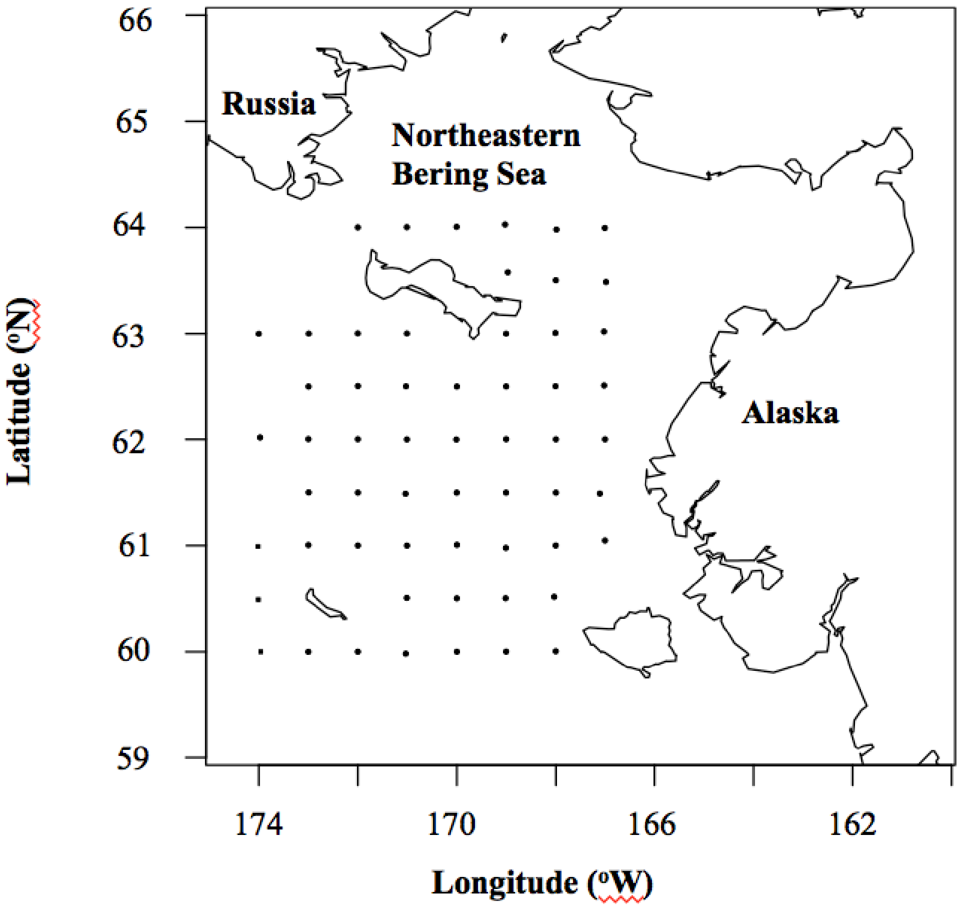

Figure 1. Map of study area showing only stations included in statistical analyses. Standard grid survey with sampling stations approximately every 30 nautical miles in the northeastern Bering Sea between 2003-2007; 2009-2013.

3.2 Biological measurements

We characterized juvenile salmon growth and condition in the NEBS using body length, weight-length residuals, insulin-like growth factor-1 (IGF-1), and energy density. Weight-length residuals provide a simple method for assessing body mass while controlling for variation in body length (Jakob et al. 1996). The growth-regulating hormone IGF-I is an indicator of feeding level and somatic growth over the most recent 2-4 weeks (Beckman, 2011). Energy density, measured as calories/g-wet weight in our study, provides a measure of protein and lipid content and is therefore an indicator of how much energy a fish has stored (Higgs et al., 1995; Trudel et al., 2005). While the importance of size for marine survival of juvenile fish is often emphasized (Sogard 1997), it is hypothesized that energy density plays an additional role in overwinter marine survival, when prey resources are reduced (Beamish and Mahnken 2001).

Fork length (to the nearest mm) and weight (to the nearest g) were measured in up to 50 (target sample size) individuals per species collected at each station (Appendix I). Linear regressions of natural log-transformed weight (g) against natural log-transformed length (mm) were performed for each species separately, and pooled over stations and years within species. Length-weight residuals were calculated from the fitted models and used as an index of body condition (Farley et al. 2005).

Beginning in 2009, IGF-1 concentrations were measured in blood samples from up to 10 individuals (target sample size) of each species from each station (Appendix I). A heparinized syringe was used to draw blood from the ventral side of the caudal peduncle. Bleeding of fish <130 mm in length was accomplished by cutting the tail off at an angle at the caudal peduncle and collecting the blood in a microhematocrit tube. Samples were kept on ice (up to 4 hours) until centrifugation. Samples were spun at 3000 x g (~5000 rpm) for 5 minutes and plasma was removed. Centrifuged plasma samples were kept on ice until they were frozen at -20 °C. Plasma samples were sent to the Northwest Fisheries Science Center in Seattle, WA where plasma IGF-1 concentrations were quantified by means of time-resolved fluorescence immunoassay, following the methods of Ferriss et al. (2014). In 2013, flooding aboard the vessel resulted in the loss of juvenile pink and chum salmon whole-body and blood samples. Two individuals per species and station were randomly sampled for energy density (Appendix I). Whole bodies of juvenile salmon were stored at -20°C and shipped to Ted Stevens Marine Research Institute (TSMRI) in Juneau, AK, at the end of the cruise. At TSMRI, juvenile chum and pink salmon energy densities were determined using bomb calorimetry, following the method described by Andrews et al. (2009).

In some cases, target sample sizes were exceeded or not met; actual sample sizes are reported in Appendix I.

3.3 Modeling relationships between environmental variables and size, condition, and growth

We used linear mixed-effects models (Zuur et al. 2009) to determine relationships between environmental variables and size, condition, and growth of juvenile chum and pink salmon, for stations where juvenile salmon were captured. Separate analyses were run for each species and response variable [ln(length), weight-length residuals, ln(energy density), and insulin-like growth factor-1 (IGF-1; proxy for instantaneous growth rate)]. Preliminary analyses (not shown) were conducted for each response in order to determine random and fixed effects structure (based on AICc) of the full model, which included all potential fixed effects and reasonable interactions. Full models for all response variables included year to account for inter-annual variability, Julian day to account for effects of growth over the duration of the surveys (Andrews et al. 2009), SST, SSS, bottom depth, and length (in chum salmon energy density) as fixed effects (Table 1). For all response variables, the best random-effect structure was to allow the model intercept to vary among stations, with station held as random effect.

We assessed multi-collinearity among environmental variables using Pearson's correlation tests. The only instance of significant correlation between environmental variables was between SST and SSS over the shorter time series (2009-2012) when juvenile chum and pink salmon were sampled for IGF-1 (correlation coefficient = -0.56, p-value = 2.2e-16; correlation coefficient = -0.78, p-value = 2.2e-16). Previous studies have shown temperature to be strongly correlated with growth and IGF-1 concentration (Larsen et al. 2001; Beckman et al. 2004b); therefore, SST was used in the models. For all other response variables, both SST and SSS were retained in the full model. Bottom depth was included as a proxy for distance from shore, which provides information on how long a juvenile salmon may have been in the marine environment (Bi et al. 2007, 2011; Burke et al. 2013). We assumed that direct environmental effects were consistent among years and therefore did not include interaction terms with environmental variables.

Table 1. Full models evaluated in the study for juvenile salmon length, weight-length residuals, and energy density by species and objective.

Species	Response	Fixed Effects	Random Effect
Objective 1. Environmental variation			
Chum Salmon	Length	Year * Julian day + SST + SSS + Depth	Station
	Weight-length residual	Year * Julian day + SST + SSS + Depth	Station
	Energy Density	Year + ln(Length) + Julian day + SST + SSS + Depth	Station
	IGF-1	Year + Julian day + SST + Depth	Station
Pink Salmon	Length	Year * Julian day+ SST + SSS + Depth	Station
	Weight-length residual	Year * Julian day + SST + SSS + Depth	Station
	Energy Density	Year * Julian day + SST + SSS + Depth	Station
	IGF-1	Year * Julian day + SST + Depth	Station
Objective 2. Spring thermal regime			
Chum Salmon	Length	Thermal regime * Julian day	Year/Station
	Weight-length residual	Thermal regime	Year/Station
	Energy Density	Thermal regime + ln(Length)	Year/Station
Pink Salmon	Length	Thermal regime * Julian day	Year/Station
	Weight-length residual	Thermal regime	Year/Station
	Energy Density	Thermal regime + ln(Length)	Year/Station

Chlorophyll-a levels were used to assess primary production (Brodeur et al. 2004; Bi et al. 2007, 2011; Peterson et al. 2010; Burke et al. 2013). However, chlorophyll-a was included in a separate analysis because chlorophyll-a data was collected at only a subset of stations.

Candidate models describing relationships of juvenile salmon size (length), condition (weight-length residuals and energy density), and growth (IGF-1 concentration) with environmental factors were compared using an information-theoretic (I-T) model selection approach (Burnham and Anderson 2002). The benefit of this approach allows candidate models to be evaluated based on Akaike's information criterion (AIC) (Burnham and Anderson 2002; Hobbs and Hilborn 2006). Additionally, using this approach allows for an evaluation of individual explanatory variables by their Akaike parameter weights (Burnham and Anderson 2002; Arnold 2010).

We used Akaike's information criterion, bias-corrected for small sample size (AICc), to compare candidate models. Models with the lowest AICc value were considered to best represent the data. To compare models, ΔAICc was calculated for each model as the difference of its AICc from the lowest AICc. However, models with ΔAICc within 2 of the minimum AICc are often considered equivalent (Burnham and Anderson 2002). Biological inferences were drawn from the set of best models ($\Delta\text{AICc} \leq 2$) and importance of explanatory variables was evaluated by their parameter weights (Burnham and Anderson 2002; Arnold 2010). Diagnostic residual and probability plots were generated for each model to assess nonconstant variance and nonlinearity (Zuur et al. 2009).

3.4 Testing for differences in size and condition between spring thermal regimes

Years were classified as warm (2003-2005) or cool (2006-2007; 2009-2013) based on positive or negative May SST anomalies in the SEBS (hereafter referred to as 'spring thermal regime'), as documented in Farley et al. (2009). This classification was chosen because we were focusing on the productivity effects of early vs. late ice retreat in the eastern Bering Sea (see Introduction). May SST in the SEBS is well correlated with the timing of sea-ice retreat in the eastern Bering Sea (http://www.beringclimate.noaa.gov), whereas much of the NEBS is under ice during May.

Linear mixed-effects models (Zuur et al. 2009) were used to determine if juvenile salmon size and condition in the NEBS significantly differed between SEBS spring thermal regimes after accounting for random variation among years and correlation among individuals within a station (Table 1). Separate analyses were run for each species and response variable (length, weight-length residuals, and energy density). The full model included spring thermal regime, Julian day, and length (energy density models only) as fixed effects. For all analyses, we tested for an interaction between Julian day and spring thermal regime to evaluate whether growth rate differed between spring thermal regimes (Table 1). Length was included as a covariate in the energy density models as it has been shown to correlate strongly with energy density in juvenile salmon (Andrews et al. 2009). To achieve normality, juvenile salmon energy density and length were natural log-transformed. Station nested within year was included as a random effect. All statistical analyses were run using the open source statistical program R (R Core Team 2013).

3.5 Testing for differences in growth and condition of juvenile pink salmon between even and odd brood years

For pink salmon, we added stock as a categorical variable (even or odd) to the size, condition, and growth models with the lowest AICs score (see 3.2-3.5) to determine if there were significant differences in length, weight-length residuals, or energy density between even and odd stocks of juvenile pink salmon.

4. Results

4.1 Juvenile salmon distribution in relation to station and environmental variables

There were annual differences in juvenile chum and pink salmon distribution with respect to the distribution of the survey stations (Fig. 2). The average latitudinal distribution of pink salmon tracked that of the survey during the warm spring regime years (2003-2005) and again in 2006, 2011 and 2013, but they were captured further south than the average survey latitude in 2007, 2010 and 2012, and further north than the survey in 2009 (Fig. 2a). The average latitudinal distribution of chum salmon was further south than that of the survey except in 2003 and 2007 (similar to the survey average), and 2009 and 2011 (further north; Fig.2a). On average, both species were captured further east (inshore) than the average survey longitude, with chum salmon showing a more easterly (inshore) average distribution than pink salmon (Fig. 2b). Pink salmon tended to be captured at stations further offshore (as indicated by bottom depth) than chum salmon, although differences in average bottom depth between the species diminished after 2007 (Fig. 2c). Only in 2012 did the mean sampling date of stations where salmon were caught differ from the mean sampling date of all stations (Fig. 2d).

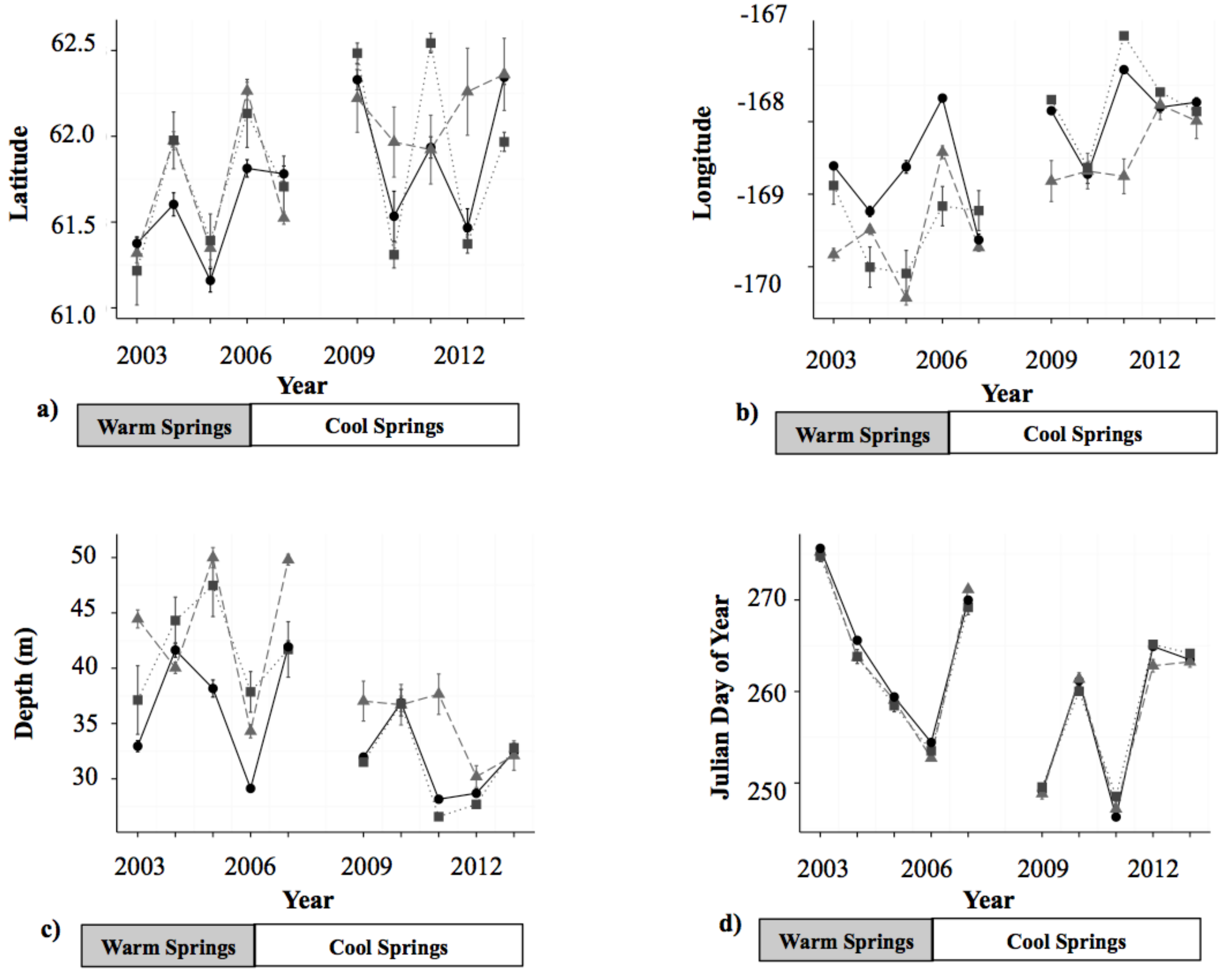

Fig. 2. Differences in station location and sampling time between 2003-2007 and 2009-2013 from all stations (ovals), stations where chum salmon present (squares), and stations where pink salmon present (triangles)**.** Error bars represent standard deviation (where not visible they were smaller than the size of the symbol). (a) Mean station latitude, (b) mean station longitude, (c) mean station depth, and (d) mean Julian day of sampling. Bars on year axes indicate spring thermal regime.

SST, SSS, and chlorophyll-a varied among years at survey stations (Fig. 3). There was a general decrease in SST over the survey years (Fig. 3a). In 2006, juvenile pink and chum salmon were caught at distinctly lower average salinities when compared to the average salinity across all stations in that year, as well as when compared to the average salinity of stations where pink and chum salmon were caught in the other sample years (Fig. 3b). A similar decrease was observed in chlorophyll-a levels in 2006 (Fig. 3c). Compared to juvenile pink salmon, juvenile chum salmon tended to be found in warmer, shallower, and less saline waters, illustrating their tendency to be caught closer to shore (Fig. 2, 3).

4.2 Relationships between length and environmental variables

The best explanatory models for length of both chum and pink salmon included SST, SSS, and depth (Tables 2 and 3 for chum and pink salmon, respectively). Chum and pink salmon lengths were negatively related to SST and positively related to bottom depth. Chum salmon length was negatively related to SSS, while pink salmon length was positively related to SSS. The most important predictors of length for both species were SST and depth (parameter weights: 0.91-1.0; Table 4). SSS was a less important predictor of salmon length, based on relatively low parameter weights of 0.35 and 0.36 for chum and pink, respectively (Table 4).

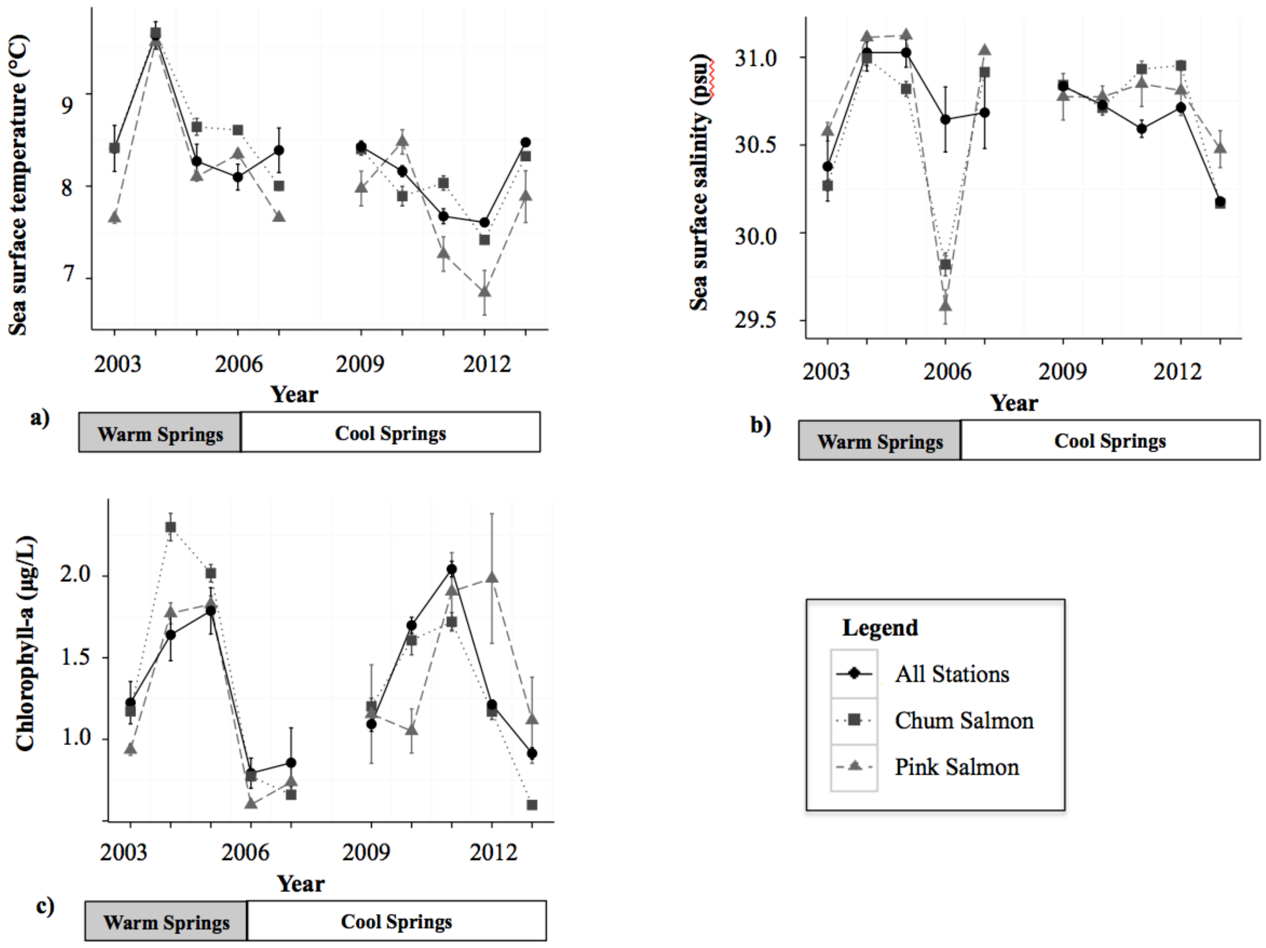

Fig. 3. Plots of environmental variables from all stations. Average values from all stations (ovals), stations where chum salmon present (squares), and stations where pink salmon present (triangles). Error bars represent standard deviation (where not visible they were smaller than the size of the symbol). (a) Sea surface temperature (°C), (b) sea surface salinity (psu), and (c) chlorophyll-a concentration (µg/L). Bars on year axes indicate spring thermal regime.

4.3 ***Relationships between weight-length residuals and environmental variables***

Chum and pink salmon weight-length residuals were negatively related to bottom depth and salinity, and positively related to SST (Table 2; Table 3). Multiple models performed nearly equivalently (ΔAICc ≤ 2) in explaining variation in weight-length residuals for both species. Temperature and depth were only moderately important predictors of chum salmon weight-length residuals (Table 4). Depth was the most important predictor of pink salmon weight-length residuals (Table 2; Table 3). Parameter weight of SSS was considerably lower than the other explanatory variables, providing support for its exclusion from chum and pink models (Table 4). Additionally, the low parameter weight of SST provided support for its exclusion from the pink salmon weight-length residual model (Table 4).

(a) 4.4 Relationships between energy density and environmental variables

Energy density of chum and pink salmon was negatively related to SST and positively related to depth (Table 2; Table 3). SSS was negatively associated with chum salmon energy density (Table 2). SST and SSS were important predictors of chum salmon energy density, but bottom depth was relatively unimportant (Table 4). SST was the most important predictors of pink salmon energy density and there was little support for inclusion of SSS and bottom depth in the best model (Table 4).

Table 2. Model coefficients (and standard deviations) and Akaike weights of chum salmon environmental models with ΔAICc ≤ 2. Random effects include standard deviation of salmon response between (A) and within stations (B). Dash: explanatory variable was not included in models with ΔAICc ≤ 2; NA: explanatory model was not included in the full candidate model.

			Fixed effects (coefficients)					**Random effects (SD)**	
Response	**ΔAICc**	**Intercept**	**SST**	**SSS**	**Depth**	**Julian day**	**Ln(Length)**	**σ^2A**	**σ^2B**
Length	0	-1227.146 (242.291)	-1.996 (0.824)	---------	0.344 (0.076)	5.199 (0.869)	NA	9.761	12.483
	1.13	-1109.283 (275.656)	-2.383 (0.931)	-1.191 (1.325)	0.355 (0.079)	4.912 (0.926)	NA	9.771	12.483
Weight-length residual	0	-1.672 (0.923)	0.007 (0.003)	-----------	-----------	0.006 (0.003)	0.039	0.062	0
	0.24	-1.162 (1.002)	0.005 (0.003)	-----------	-0.001 (0.001)	0.004 (0.004)	0.039	0.062	0.24
	0.44	-0.619 (0.926)	-----------	-----------	-0.001 (0.001)	0.002 (0.003)	0.039	0.062	0.44
	1.41	-0.334 (0.974)	-----------	-0.005 (0.005)	-0.001 (0.001)	0.002 (0.003)	0.039	0.062	1.41
Energy density	0	4.699 (0.437)	-0.017 (0.004)	-0.102 (0.003)	----------	-0.006 (0.001)	0.825 (0.045)	5.366-06	0.078
	0.51	4.836 (0.450)	-0.015 (0.004)	-0.010 (0.003)	0.001 (0.001)	-0.006 (0.001)	0.824 (0.045)	5.295e-06	0.078
IGF-1	0	175.319 (31.866)	0.922 (0.411)	NA	----------	-0.556 (0.1209)	NA	2.038	6.050

Table 3. Model coefficients (and standard deviations) and Akaike weights of pink salmon environmental models with ΔAICc ≤ 2. Random effects include standard deviation of salmon response between (A) and within stations (B). Dash: explanatory variable was not included in models with ΔAICc ≤ 2; NA: explanatory model was not included in the full candidate model.

			Fixed effects (coefficients)				**Random effects (SD)**	
Response	**ΔAICc**	**Intercept**	**SST**	**SSS**	**Depth**	**Julian day**	**σ^2A**	**σ^2B**
Length	0	-502.403 (291.572)	-2.852 (0.959)	-----------	0.387 (0.081)	2.543 (1.047)	10.041	12.294
	1.260	-618.840 (324.748)	-2.530 (1.037)	1.292 (1.583)	0.370 (0.084)	2.816 (1.099)	10.051	12.295
Weight-length residual	0	-1.296 (1.349)	-----------	-----------	-0.001 (0.001)	0.005 (0.005)	0.047	0.070
	1.299	-0.949 (1.421)	-----------	-0.005 (0.007)	-0.001 (0.001)	0.004 (0.005)	0.039	0.062
	1.581	-1.613 (1.446)	0.003 (0.005)	-----------	-0.001 (0.001)	0.006 (0.005)	0.039	0.062
Energy Density	0	9.649 (0.829)	-0.036 (0.010)	-----------	0.002 (0.001)	-0.008 (0.003)	0.080	0.085
	1.237	9.112 (0.779)	-0.039 (0.010)	-----------	-----------	-0.006 (0.003)	0.081	0.085
IGF-1	0	124.893 (34.421)	-----------	NA	-----------	-0.336 (0.137)	1.896	5.632
	1.607	120.618 (35.950)	-----------	NA	0.045 (0.083)	-0.325 (0.141)	1.955	5.635

4.5 Relationships between IGF-1 concentration *and environmental variables*

IGF-1 concentrations of both species were greater in 2010-2012 compared to 2009 (Fig. 4d). Mean IGF-1 concentration of juvenile salmon increased between 2010 and 2012, and juvenile chum salmon had higher IGF-1 concentration values compared to juvenile pink salmon (Fig. 4d). Chum salmon IGF-1 concentrations were positively associated with SST and juvenile pink salmon IGF-1 concentrations were positively associated with bottom depth (Table 2; Table 3). SST was the most important factor explaining variation in chum salmon IGF-1 (Table 4). Depth and SST were mostly unimportant predictors of pink salmon IGF-1 (Table 4).

Table 4. Predictor parameter weights from models of juvenile salmon response variables versus environmental variables.

Species	Response	SST	SSS	Depth
Chum salmon	Length	0.91	0.36	1.00
	Weight-length residual	0.60	0.35	0.57
	Energy density	0.88	0.88	0.44
	IGF-1	0.83	NA	0.28
Pink salmon	Length	0.96	0.36	1.00
	Weight-length residual	0.34	0.39	0.93
	Energy density	0.71	0.25	0.18
	IGF-1	0.38	NA	0.36

4.6 *Inclusion of chlorophyll-a*

Including chlorophyll-a in an analysis of only those stations where chlorophyll was sampled did not qualitatively change the results described in sections 3.1- 3.5. Chlorophyll-a was never included in the model with the lowest AICc value. However, it was included in the set of best models (ΔAICc ≤ 2) for length, weight-length residuals, and IGF-1 in chum salmon, where it was negatively correlated with all of these response variables (Appendix II). In pink salmon, chlorophyll-a was included in the best explanatory models for length (negatively correlated) and energy density (positively correlated; Appendix 3). The highest parameter weight for chlorophyll-a among all of the models tested was 0.42, suggesting it had low explanatory value for juvenile pink and chum salmon size, condition, and growth in our study.

4.7 Differences in size and condition between spring thermal regimes

Variation in chum and pink salmon length was related to the interaction between Julian day and spring thermal regime ($p < 0.001$ for both species). After accounting for this interaction, length was significantly greater during the warm regime for both chum ($t = 4.788$, $p = 0.001$) and pink ($t = 3.897$, $p = 0.005$) salmon (Table 5; Fig. 4a). There were no significant differences in weight-length residuals between regimes in the NEBS for either species (Table 5; Fig. 4b). Energy density was lower in warm-regime years for both species (Fig. 4c), but only statistically significant for chum salmon ($t = -3.373$, $p = 0.012$ vs. $t = -1.850$, $p = 0.107$ for pink salmon; Table 5).

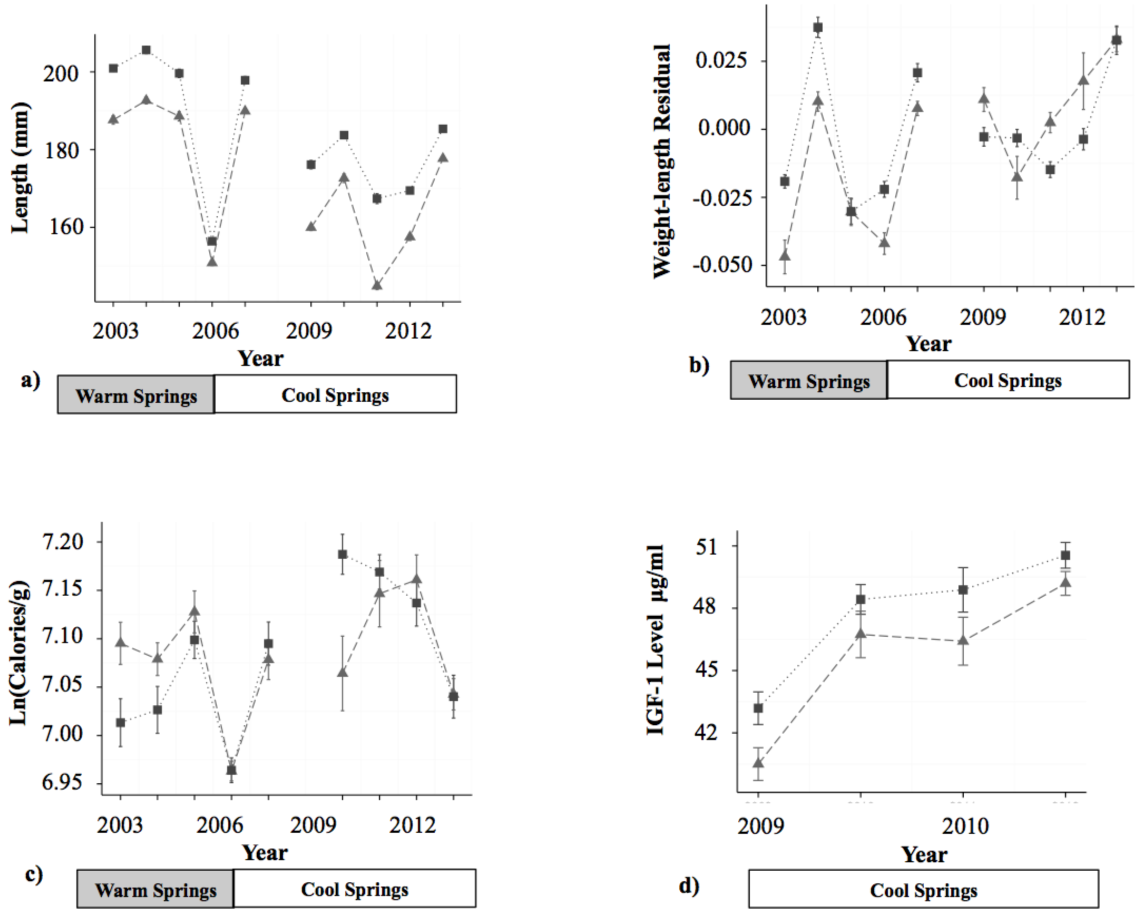

Fig. 4. Mean (± standard deviation) for physiological measures of juvenile chum (black triangles) and pink (grey circles) salmon. Error bars represent standard deviation (where not visible they were smaller than the size of the symbol). (a) Salmon length (mm); (b) salmon weight-length residuals; (c) energy density [ln(calories/g)], no data available for 2013; and (d) salmon IGF-1 level, data only available 2009-2012. Bars on year axes indicate spring thermal regime.

4.8 Differences in growth and condition between even and odd brood year stocks of juvenile pink salmon

Results of comparisons between even and odd stocks of pink salmon are summarized in Table 6. There were no significant differences in length or weight-length residuals between even and odd brood year stocks of juvenile pink salmon. However, odd stocks had significantly greater IGF-1 concentration than even stocks (*t* = 3.865, *p* = 0.001). Consistent with the hypothesis of greater energy allocation to fat storage in even stocks, we found that even stocks had greater energy density (*t* = -2.060, *p* = 0.042).

Table 5. Coefficients (and standard deviations) for fixed effects in models relating physiological responses to spring thermal regime after accounting for Julian day (and length in the case of energy density). The t- and p-values (significant values in bold) for the effect of thermal regime are given, as well as the standard deviations for the random effects: among years (A), among stations (B), and within stations (C).

		Fixed effects				**Regime test**		**Random effects**		
Response	**Intercept**	**Warm regime**	**Julian day**	**Julian *regime**	**ln(Length)**	***t***	***P***	**σ^2A**	**σ^2B**	**σ^2C**
Chum salmon										
Length	-435.388 (68.504)	490.842 (102.506)	2.369 (0.264)	-1.818 (0.388)	NA	4.788	**0.001**	13.087	12.218	12.487
Weight-length residual	-0.007 (0.009)	-0.006 (0.015)	NA	NA	NA	-0.359	0.419	0.020	0.044	0.062
Energy density	2.996 (0.217)	-0.118 (0.032)	NA	NA	0.789 (0.042)	-3.670	**0.008**	0.042	0.016	0.079
Pink salmon										
Length	-186.278 (52.605)	328.165 (84.203)	1.359 (0.203)	-1.178 (0.32)	NA	3.897	**0.005**	5.393	11.260	12.300
Weight-length residual	-0.002 (0.008)	-0.022 (0.013)	NA	NA	NA	-1.706	0.126	0.014	0.051	0.07
Energy density	3.195 (0.251)	-0.064 (0.035)	NA	NA	0.756 (0.049)	-1.850	0.107	0.043	0.066	0.056

Table 6. Coefficients (and standard deviations) and t- and p-values (significant values in bold) from models testing for differences in juvenile pink salmon responses between even and odd brood-year stocks.

		Fixed effects				**Even/odd test**		**Random effects**	
Response	**Intercept**	**Odd brood-year**	**SST**	**Depth**	**Julian day**	**t-value**	**p-value**	**σ^2A**	**σ^2B**
Length	-165.923 (36.008)	-1.328 (2.219)	2.809 (0.880)	0.502 (0.079)	1.148 (0.134)	-0.598	0.550	14.439	12.285
Weight-length Residuals	0.035 (0.127)	-0.004 (0.008)	----------	-0.001 (0.001)	0.001 (0.001)	-0.469	0.639	0.051	0.070
Energy Density	7.188 (0.350)	-0.043 (0.021)	-0.016 (0.008)	0.001 (0.001)	0.001 (0.001)	-2.060	**0.042**	0.091	0.085
IGF-1	149.533 (41.686)	11.691 (3.025)	----------	----------	-0.425 (0.167)	3.865	**0.001**	2.769	5.583

(b)

5. Discussion and implications

(c) ***5.1 Relationships between physiological measures and environmental variables***

A major focus of our study was describing the variation in juvenile chum and pink salmon size and condition in response to among-station variation in oceanographic parameters such as SST and SSS. While these factors have direct and indirect effects on salmon physiology that influence condition of juvenile salmon (Andrews et al. 2009; Heintz et al. 2013; Morita et al. 2001), it is likely that our results reflected spatial variation in size and condition of juvenile salmon, particularly in terms of distance from shore. Water masses that flow through the NEBS can be characterized according to SST and SSS, with the warmer and less saline Alaska Coastal Water (ACW), comprised of riverine inputs and northward advection of the Alaska Coastal Current, and the cooler and more saline Bering Sea Water (BSW) flowing further offshore (Eisner et al. 2012). The cooler SSTs of the BSW are associated with higher densities of lipid-rich species of zooplankton (Richardson 2008; Hunt et al. 2011; Eisner et al. 2012; Stabeno et al. 2012a), whereas the warmer waters of the ACW are nutrient limited in the summer (Grebmeier et al. 2006). Thus, cooler SSTs may serve as an indicator of better feeding conditions for juvenile salmon in the NEBS.

We found that juvenile salmon length and energy density increased with station bottom depth and cooler water temperatures, while weight-length residuals were correlated with warmer temperatures and shallower station bottom depths. These results likely reflected the offshore movement of salmon as they grew. Weight-length residuals provide an index of condition that accounts for length, but they do not provide specific information on energy content, and greater weight-length residuals do not necessarily translate to higher fat reserves (Trudel et al. 2005). In our study, weight-length residuals indicated that fish caught closer to shore weighed more for a given length. However, the corresponding increase in energy density with length (chum salmon) or time (pink salmon) suggests that during the course of our study, fish were allocating energy to both length and fat storage. We caution that the energy density results were based on limited sample sizes and possibly biased toward larger fish, if larger fish were more readily selected on the sorting table. The degree to which this potential bias may have influenced our results would depend on how consistent the bias was from year to year or station to station, which was not quantified. However, we limited the degree to which our inferences were based on the energy density data by themselves.

Although IGF-1 increased with SST (chum salmon) and station depth (pink salmon), the distinctly lower concentrations of IGF-1 in 2009 compared to 2010-2012 (Fig. 4d) were not explained by the environmental variables (Fig. 3) or aspects of the sampling design (Fig. 2). High IGF-1 concentration may be an indicator of prey availability, as growth can only occur if nutritional needs are met (Beckman 2011). Thus, these results may reflect differences in food availability or quality over time. Indeed, data on quality and quantity of prey, distributional overlap between salmon and prey, and SST effects on prey field and salmon metabolism would likely be necessary to fully understand variation in IGF-1 concentration.

While previous studies have used chlorophyll-a level as a measure of energy available to higher trophic levels (Brodeur et al. 2004; Bi et al. 2007, 2011; Peterson et al. 2010; Burke et al. 2013), it is important to recognize that low chlorophyll-a level may reflect increases in grazing pressure (e.g., Strom et al. 2007). The reduced chlorophyll-a levels associated with longer lengths may reflect grazing by secondary consumers, thus a greater prey availability for juvenile salmon. However, the negative relationship between chlorophyll-a and chum salmon weight-length residuals and IGF-1 concentration and the positive relationship with pink salmon energy density make it difficult to discern between direct and indirect effects of chlorophyll-a level on salmon production. Furthermore, variability in the overall timing of the spring bloom likely has implications for growth and condition of juvenile salmon that our models did not account for.

All three measures of juvenile salmon size and condition responses were diminished in 2006. While 2006 is considered a cool year based on spring thermal regime in the SEBS, ice extent in the Bering Sea during this year was comparable to years of the warm spring thermal regime (Stabeno et al. 2012b). Winds can have a strong influence on water masses in the NEBS region (Cooper et al. 2006). In 2006, strong easterly and northeasterly winds may have spread the ACW further offshore, contributing to the large influence of the fresh, nutrient poor waters of the ACW in the NEBS (Cooper et al. 2012). In addition, Cooper et al. (2012) found reduced winter brine formation in 2006, a consequence of reduced sea ice, and the authors suggested this might have limited nutrient availability within the NEBS. Our observation of clear declines between 2005 and 2006 in salinity and chlorophyll-a, as well as salmon length and energy density, support these findings (Fig. 3b,c).

(d) 5.2 Differences in size and condition between spring thermal regimes

Larger salmon often have increased marine survival during their first year at sea (Beamish and Mahnken 2001; Farley et al. 2007; Moss et al. 2009) and it has been presumed that larger salmon would have greater lipid reserves needed to survive their first winter (Beamish and Mahnken 2001; Farley and Trudel 2009**)**. Andrews et al. (2009) compared juvenile pink salmon length and condition in the NEBS among years with warm (2004 and 2005) and cool (2006 and 2007) spring and summer SSTs and found that juvenile pink salmon were longer, but of reduced condition during warm years. Our findings confirmed that of Andrews et al. (2009) for greater pink salmon length during warm years over a longer time series, and support the extension of their results to chum salmon as well. Our results also bolster the prediction of Farley et al. (2009) that warm spring SSTs lead to greater growth of juvenile salmon from western Alaska; we unfortunately did not have the data to evaluate Farley et al.’s (2009) prediction that larger juvenile size would translate into higher survival rates.

While we found that juvenile chum and pink salmon in the NEBS were longer during the warm regime and juvenile chum salmon more energy dense during the cool regime, we did not observe a concomitant increase in weight-length residuals during years with a cool spring thermal regime. These results may reflect real differences in the effect of the SEBS spring thermal regime on energy allocation in juvenile pink and chum salmon in the NEBS. However, salmon responses were highly variable between years within both spring thermal regimes (Fig. 4), suggesting that differences in salmon size and energy density in the NEBS cannot be attributed to spring thermal regime alone. Furthermore, weight-length residuals provide limited information on body composition (Trudel et al. 2005), and may not be an adequate measure of energetic status when comparing between warm and cool regimes.

5.3 Coherence of pink and chum salmon responses

Although it was not a predefined objective of our study, we observed striking coherence between pink and chum salmon in inter-annual variation of length and condition (Fig. 4). These results indicated that both species respond in similar ways to ocean conditions during their first summer in the NEBS, highlighting ecological similarity of the two species. Previous studies have described interactions between pink salmon and other salmon species (Azumaya and Ishida 2000; Ishida et al. 2002; Ruggerone et al. 2010; Ruggerone et al. 2012; Agler et al. 2013), including competitive effects manifested as even/odd differences in chum salmon diet and growth (Tadokoro et al. 1996, Kaga et al. 2013). However, despite the apparent ecological similarities between pink and chum salmon in the NEBS, even/odd differences were not evident in chum salmon in our study, perhaps because juvenile pink salmon abundances in the NEBS are not large enough to result in the kinds of effects observed in chum salmon in the western North Pacific.

5.4 *Differences in growth and condition between even and odd brood year stocks of juvenile pink salmon*

Beamish (2012) hypothesized that odd stocks of juvenile pink salmon allocate more energy to growing in length and even stocks allocate more energy to fat storage. Our results partially supported the hypothesis (Fig. 5), with odd stocks being lower in average energy density and higher in IGF-1 concentrations, which may reflect a greater allocation of energy towards growth in length, rather than fat storage. These results are consistent with the hypothesized differences in metabolic strategy between even and odd stocks of juvenile pink salmon within the NEBS. More years of data would help determine whether the failure of our length and condition results to support the hypothesis reflects a true inconsistency with the hypothesis or the lack of statistical power.

5.5 Conclusions

The goal of our study was to describe relationships between growth and condition of juvenile pink and chum salmon and physical conditions of the NEBS. This study represents the most comprehensive examination of juvenile pink and chum salmon in the northeast Bering Sea to date. While our results provide a foundation for future efforts to better understand how juvenile pink and chum salmon will respond to changing environmental conditions, our model results should be viewed as descriptive and rather than predictive.

Overall, this study highlighted differences in size and condition of juvenile salmon as they moved offshore, provided further support for differing energy allocation between spring thermal regimes (*sensu* Andrews 2009), and supported the hypothesis of stock-specific differences in energy allocation in pink salmon (Beamish 2012). While pink and chum salmon were longer during the warm regime and chum salmon had greater energy density during the cool regime, variability in physiological measures among years within thermal regimes suggested that differences in salmon size and condition within the NEBS cannot be attributed to spring thermal regime alone. Although our environmental modeling included bottom depth and Julian day, more spatially and temporally explicit analyses could help disentangle how intraannual (i.e., among-station) and inter-annual variation in environmental conditions influenced juvenile salmon size and condition over the study period.

Differences in energy allocation between even and odd stocks of juvenile pink salmon have implications for how these two genetically distinct lines of salmon may respond to changes in climate. Beamish (2012) attributed the increase of odd pink salmon along the central coast of British Columbia to their ability to take advantage of greater fall and winter zooplankton production resulting from warmer winters. Currently, odd stock abundances are relatively low in western Alaska (Ruggerone et al. 2003; Beacham et al. 2012). However, as sub-Arctic and Arctic climate continues to warm, increased production in the region may support the growth of these stocks.

While current climate patterns have facilitated cooling temperatures in the NEBS, future decreases in seasonal sea ice and continued Arctic warming can be expected to increase the frequency of warm spring thermal regimes within the Bering Sea. Anomalous years, such as 2006, point to the unpredictability of climate change and underscore the importance of ecosystem assessment surveys such as the one described in this study. By monitoring different aspects of juvenile salmon size, recent growth (as captured by IGF-I), and energetic status, a better understanding of the drivers of salmon productivity will emerge.

6. Acknowledgements

This project incorporated data collected from the Bering Aleutian Salmon International Surveys (BASIS) and the Arctic Ecosystem Integrated Surveys (Artic Eis). We are enormously grateful for the many scientists and crew who participated in the data collection and for all the scientists involved in sample processing. In particular, E. Farley, J. Murphy, and W. Strasburger were instrumental in making the data available. We also thank F. Mueter and B. Mecum for statistical and R coding advice and J. Weems for assistance with project management. The report was improved by the comments and suggestions of two anonymous reviewers and E. Farley. This project could not have been completed without the financial support of our funding sources, to which we are extremely appreciative: the Bureau of Ocean Management, the Coastal Impact Assistance Program, and the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative.

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Appendix I. Sample size by year, species and response variable. For response variables, the number outside parentheses represents the number of stations sampled. The numbers in parentheses represent number of individuals sampled (minimum/maximum/mean per station). All stations where juvenile salmon were caught were measured for length and weight, so the number of stations sampled for that variable represents the number of stations where the species was caught.

		Chum salmon			**Pink salmon**		
Year	**Total # stations**	**Length/weight**	**Energy density**	**IGF-1**	**Length/weight**	**Energy density**	**IGF-1**
2003	24	23 (2/50/27)	17 (1/5/2)	--	21 (1/47/10)	18 (1/2/2)	--
2004	55	42 (1/50/11)	14 (1/2/2)	--	46 (1/50/14)	25 (1/3/2)	--
2005	42	27 (2/50/10)	26 (1/2/2)	--	29 (1/50/10)	29 (1/2/2)	--
2006	43	26 (1/52/21)	14 (2/2/2)	--	21 (1/50/17)	11 (1/2/2)	--
2007	36	24 (1/50/23)	21 (1/2/2)	--	24 (3/60/32)	20 (1/2/2)	--
2008	--	--	--	--	--	--	--
2009	36	13 (2/50/32)	6 (2/2/2)	8 (6/11/9)	14 (2/50/32)	3 (2/2/2)	6 (1/12/8)
2010	39	23 (1/50/16)	11 (2/2/2)	11 (2/16/9)	20 (1/19/6)	5 (1/2/2)	5 (4/10/8)
2011	43	12 (1/60/39)	11 (1/2/2)	8 (2/10/7)	15 (1/50/27)	6 (1/2/2)	7 (2/9/6)
2012	27	13 (1/53/33)	13 (1/2/2)	13 (1/10/9)	9 (1/46/11)	8 (1/2/2)	8 (1/10/7)
2013	29	20 (1/51/20)	--	--	20 (1/63/26)	--	--

Appendix II. Model coefficients (and SD) and Akaike weights of chum salmon models (ΔAICc ≤ 2). Random effects include SD of salmon response between (A) and within stations (B). Dash: explanatory variable was not included in models with ΔAICc ≤ 2; NA: explanatory model not included in the full candidate model.

			Fixed Effects					Random Effects	
Response	**ΔAICc**	**Intercept**	**SST**	**SSS**	**Depth**	**Chl.a**	**Julian day**	**σ^2A**	**σ^2B**
Length	0	-1221.049 (242.862)	-2.014 (0.829)	---------	0.338 (0.078)	---------	5.178 (0.870)	9.777	12.487
	0.77	-1079.074 (277.101)	-2.478 (0.936)	-1.428 (1.341)	0.351 (0.079)	---------	4.832 (0.929)	9.779	12.486
	0.93	-1192.681 (244.516)	-2.129 (0.837)	---------	0.335 (0.078)	-0.809 (0.823)	5.082 (0.876)	9.775	12.487
	1.72	-1052.492 (278.429)	-2.587 (0.943)	-1.413 (1.341)	0.348 (0.079)	-0.780 (0.823)	4.741 (0.943)	9.778	12.486
Weight-length residual	0	-1.693 (0.926)	0.007 (0.003)	---------	---------	---------	0.006 (0.003)	0.039	0.062
	0.30	-1.188 (1.007)	0.005 (0.003)	---------	-0.001 (0.001)	---------	0.004 (0.004)	0.039	0.062
	0.35	-1.029 (1.013)	0.004 (0.003)	---------	-0.001 (0.001)	-0.005 (0.003)	0.004 (0.003)	0.039	0.062
	0.67	-0.619 (0.930)	---------	---------	-0.001 (0.001)	---------	0.002 (0.003)	0.039	0.062
	1.36	-0.274 (0.979)	---------	-0.004 (0.005)	-0.001 (0.001)	-0.005 (0.003)	0.001 (0.003)	0.039	0.062
	1.67	-0.327 (0.981)	---------	-0.005 (0.005)	-0.001 (0.001)	---------	0.002 (0.003)	0.039	0.062
	1.77	-1.385 (1.112)	0.006 (0.004)	-0.003 (0.005)	---------	---------	0.005 (0.004)	0.039	0.062

Appendix II (continued). Model coefficients (and SD) and Akaike weights of chum salmon models (ΔAICc ≤ 2). Random effects include SD of salmon response between (A) and within stations (B). Dash: explanatory variable was not included in models with ΔAICc ≤ 2; NA: explanatory model not included in the full candidate model.

			Fixed Effects					Random Effects	
Response	**ΔAICc**	**Intercept**	**SST**	**SSS**	**Depth**	**Chl.a**	**Julian day**	**σ^2A**	**σ^2B**
IGF-1	0	175.319 (31.866)	0.922 (0.411)	---------	---------	---------	-0.556 (0.121)	2.038	6.050
	0.994	170.571 (32.366)	0.817 (0.427)	---------	---------	-0.585 (0.600)	-0.531 (0.124)	2.055	6.048

Appendix III. Model coefficients (and standard deviations) and Akaike weights of pink salmon environmental models, including chl-a, with ΔAICc ≤ 2. Random effects include standard deviation of salmon response between (A) and within stations (B). Dash: explanatory variable was not included in models with ΔAICc ≤ 2; NA: explanatory model was not included in the full candidate model.

			Fixed effects					**Random effects**	
Response	**ΔAICc**	**Intercept**	**SST**	**SSS**	**Depth**	**Chl.a**	**Julian day**	**σ^2A**	**σ^2B**
Length	0	-540.357	-2.70	-----------	0.412	----------	2.673	10.144	12.266
		(295.031)	(0.978)		(0.084)		(1.059)		
	0.97	-511.976	-2.783	-----------	0.409	-0.753	2.576	10.119	12.268
		(296.179)	(0.981)		(0.084)	(0.838)	(1.062)		
	1.12	-672.345	-2.329	1.445	0.394	----------	2.985	10.149	12.267
		(330.512)	(1.064)	(1.629)	(0.087)		(1.116)		
	1.91	-653.981	-2.384	1.584	0.389	-0.824	2.908	10.118	12.268
		(330.275)	(1.063)	(1.631)	(0.087)	(0.841)	(1.116)		
Energy Density	0	9.115	-0.038	-----------	----------	----------	-0.006	0.081	0.085
		(0.783)	(0.010)				(0.003)		
	0.53	9.695	-0.035	-----------	0.001	0.006	-0.009	0.080	0.085
		(0.836)	(0.010)		(0.001)	(0.009)	(0.003)		
	0.80	10.007	-0.038	-0.009	0.002	----------	-0.009	0.080	0.085
		(1.087)	(0.011)	(0.017)	(0.001)		(0.003)		

Appendix W.

Trophic structure of the eastern Chukchi Sea: An updated mass balance food web model

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March 11, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

List of Oral and Poster Presentations

Whitehouse, GA and K Aydin. 2014. An updated trophic model of the eastern Chukchi Sea. Poster presentation. Alaska Marine Science Symposium, January 20-24, 2014, Anchorage, Alaska.

Whitehouse, GA and K Aydin. 2016. Resilience of the eastern Chukchi Sea food web to mortality based perturbations and identification of ecologically important species. Poster presentation. AGU Ocean Sciences Meeting, February 21-26, 2016, New Orleans, Louisiana.

Proposed Objectives and Study Chronology

The objective of this component of the Arctic Eis project was to update and further develop a pre-existing mass balance food web m odel of the eastern Chukchi Sea previously developed by scientists from the Resource Ecology and Ecosystem Modeling Program of the AFSC. There were no field collections explicitly associated with this component of the Arctic Eis. This study utilized data gathered from other component projects within the Arctic Eis (e.g., fish food habits) and from other recent studies, to update and improve the overall quality of the pre-existing mass balance food web model. Following the completion of the fieldwork and laboratory analysis components of the Arctic Eis, new data and rates were acquired from other PI's and incorporated to the updated mass balance food web model. Specifically, data from the Arctic Eis included, information on fish food habits, the age and growth of Arctic gadids, and biomass estimates for trawl caught organisms were added to the model. Informal workshops and email correspondence with other collaborators at the AFSC and elsewhere were instrumental to the process of balancing the updated model. We experienced no significant problems or delays throughout the duration of this project. This report documents the updated model, including all of the model parameters and data sources. This final report is based on our manuscript prepared for submission to the NOAA Technical Memorandum series of documents.

1. Abstract

This is a 2010s update of the previous 1990s Ecopath trophic mass balance model of the eastern Chukchi Sea. In the time since the original 1990s model was developed, a number of datasets have been produced and several reports and journal articles published documenting the findings of recent field studies in the eastern Chukchi Sea, including the completion of the BOEM funded Arctic Ecosystem Integrated Survey (Arctic Eis). In this report we use published and unpublished datasets from many of these recent studies to update several input parameters from the preliminary 1990s Ecopath model of eastern Chukchi Sea, so it is more representative of the current (2010s) state of the eastern Chukchi Sea food web. Overall, 93 input parameters were updated and the data quality was improved for 34 parameters. A total of 9 new functional groups were added, 6 for seabirds and 3 for fish. Here we document all model parameters that we were able to update with improved information, including estimates of biomass, production, consumption, and diet composition. Changes in the included species, the species composition of functional groups, and their related parameters resulted in higher biomass for marine mammals, seabirds, fish and zooplankton, and decreased biomass for benthic invertebrates, jellies, microbes, and phytoplankton. Additionally, we calculate several ecosystem level metrics for both models and compare the results between the original model and our updated model. In both models, benthic invertebrates represent the dominant portion of total ecosystem biomass, and energy flow is dominated by benthic resources. Total energy flow, total production, total biomass, and net primary production decreased from the preliminary model to the updated model. A key result common to both the preliminary model and the updated model is that trawl survey derived estimates of demersal fish biomass were insufficient to balance the model. Fish biomass needed to be several times greater to meet the modeled trophic demand from predators. Changes in the ecosystem metrics are the reflection of the updated and improved (higher quality) model inputs, and do not necessarily reflect any change in ecosystem state between the two model time periods. Given the number of updated parameters and improved data quality in the updated model (2010s), we recommend using the updated model over the preliminary model (1990s) for future modeling studies and as a baseline of this system’s food web.

2. Introduction

The effects of climate change and sea ice decline are becoming increasingly apparent in the Arctic, with the nine lowest annual sea ice minima over the satellite record (1979-present) occurring in the last nine years, 2007^{-2}015 (Comiso 2012, Stroeve et al. 2012, http://nsidc.org). Evidence of climate impacts on Arctic marine ecosystems is accumulating (Wassmann et al. 2011) and these systems may face additional stresses from increasing anthropogenic activity due to easier access following sea ice declines. The continental shelves of the Arctic possess large petroleum reserves (Gautier et al. 2009) and industrial activities related to petroleum extraction are expected to increase in the Alaska Arctic (Shell Gulf of Mexico Inc. 2015). In response, several intensive ecological investigations of oil and gas lease sites in the Alaska Arctic have recently been undertaken (Day et al. 2013, Dunton et al. 2014). The recent declines in sea ice coverage have also helped to increase interest in establishing new shipping lanes through the Arctic (Ho 2010, Lasserre and Pelletier 2011, Smith and Stephenson 2013), and prompted research on the impacts this vessel traffic may have on Arctic ecosystems (Jing et al. 2012, Reeves et al. 2012). Interest in Arctic tourism has also risen and related vessel traffic may increase as well in the near future (Williams 2014). What the cumulative impacts of climate change and increasing commercial development will be on Arctic marine ecosystems is unknown, but will likely be important. The Arctic is home to several species of marine mammals and fishes which are important resources for indigenous and non-indigenous residents of the Arctic (Craig 1987, Hovelsrud et al. 2008, Zeller et al. 2011). At present in the Alaska Arctic, the development of new commercial fisheries is prohibited until such a time that a sufficient amount of research and data become available to support the sustainable management of new commercial fisheries (NPFMC 2009). In consideration of the multiple, and potentially conflicting human interests in the Arctic marine environment, there is a growing need to provide stakeholders, resource managers, and decision makers with sufficient information to support an ecosystem-based approach to managing Arctic resources (Clement et al. 2013).

Ecosystem models are an effective tool in support of an ecosystem based approach to managing marine resources (Christensen and Walters 2004, Link et al. 2012) and can be used to investigate ecosystem scale processes and the relative effects different stressors may have on ecosystems (e.g., Gaichas et al. 2011). An ecosystem model is a plausible representation of an ecosystem, or an ecosystem process, that can be used to make comparisons with real world observations and be used to evaluate hypotheses (Hilborn and Mangel 1997). Ecosystem models permit the user to conduct experiments that would otherwise be impractical in the real world, such as the manipulation of mortality rates or the strength of predator-prey interactions (e.g., Harvey et al. 2012). The results and insights from such exercises may provide valuable strategic guidance for resource managers and stakeholders (Samhouri et al. 2009).

A mass balance ecosystem model describing the food web of the eastern Chukchi Sea in Alaska has previously been developed. Whitehouse (2013) (hereinafter referred to as W13) compiled information on biomass levels, diet composition, rates for production and consumption, and harvest/fishery removals, and used this information to develop an Ecopath trophic mass balance model (http://ecopath.org/, Christensen and Pauly 1992) of the eastern Chukchi Sea. Whitehouse et al. (2014) used this model to describe the general structure and function of this ecosystem. They found the ecosystem to be dominated in terms of biomass by benthic invertebrates and found that the majority of mass flows amongst consumer groups (trophic level ≥ 2.0) were through benthic oriented organisms as opposed to pelagic organisms (e.g., zooplankton). Additionally, they found biomass estimates of fish groups, derived from trawl survey data, were insufficient to meet the trophic demands from predators and, thus, trawl surveys were likely underestimating fish densities.

The preliminary mass balance food web model of the eastern Chukchi Sea was constructed in an effort to provide a comprehensive view of the ecosystem using the data and rates available at that time, primarily centered on the years surrounding 1990, as many of the data needed to parameterize the preliminary model were available from that time period. Having a base time period of 1990 was an important limitation of this preliminary model, given the more recent observations of shrinking and thinning sea ice coverage. It is not clear whether food web conditions in the Chukchi Sea have undergone any changes since the 1990s. In the time since the preliminary model was developed a number of interdisciplinary ecological studies of the Chukchi Sea have been completed and published, adding to the knowledge about this ecosystem (e.g., Bluhm et al. 2010 [RUSALCA], Day et al. 2013 [CSESP], Dunton et al. 2014 [COMIDA-CAB]). The Arctic Ecosystem Integrated Survey (Arctic Eis, https://web.sfos.uaf.edu/wordpress/arcticeis/) is continuing to build upon this growing knowledge base by conducting a comprehensive assessment of the oceanography, plankton, and fishes of the northern Bering Sea and Chukchi Sea. The information collected during the Arctic Eis will help enable resource managers to evaluate the potential effects of climate and human activities on this ecosystem.

In this study we improved upon the preliminary food web model by incorporating data and information from recent studies to more closely represent the current ecological conditions in the eastern Chukchi Sea. Specifically, we incorporated data gathered during the BOEM funded Arctic Eis, including updated biomass estimates of trawl caught organisms and the diet composition of fishes. Additionally, we updated other model parameters where current or otherwise improved estimates were available in the literature. We compared the original and updated models and examined how the new data and rates may have affected model outputs and discuss whether any changes in ecosystem properties may be a reflection of the new data or actual changes in ecological conditions.

3. Methods

3.1 Study system

The Chukchi Sea is a marginal Arctic Sea that is seasonally covered by ice. The broad and shallow continental shelf, with most depths shallower than 60 meters (Jakobsson 2002), is the only connection between the Pacific and Arctic oceans (Carmack and Wassmann 2006). The Chukchi Sea has a strong advective regime, where a net northward flow of Pacific origin water passes through the Bering Strait and continues in a net northward direction across it’s continental shelf (Coachman et al. 1975, Roach et al. 1995, Weingartner et al. 2005, Woodgate et al. 2005). The Pacific origin water flowing into the Chukchi Sea is rich with nutrients and fuels high levels of primary production throughout the ice free season, particularly in the southern Chukchi Sea (Sambrotto et al. 1984, Hansell and Goering 1990, Springer and McRoy 1993). Only a small portion of the primary production is consumed by zooplankton (Cooney and Coyle 1982, Coyle and Cooney 1988, Campbell et al. 2009, Sherr et al. 2009) and most of it eventually sinks out of the water column to the sea floor, where it supports an abundant benthic food web (Grebmeier et al. 1988, Dunton et al. 2005). The thriving benthic community in turn supports benthic foraging specialists including gray whales (*Eschrichtius robustus*), Pacific walrus (*Odobenus rosmarus*), and bearded seals (*Erignathus barbatus*). Several marine mammal species are regular occupants of the Chukchi Sea and many of these species, such as bowhead whales (*Balaena mysticetus*) and ringed seals (*Phoca hispida*), are important subsistence resources for the residents of Alaskan coastal villages(Hovelsrud et al. 2008).

The Chukchi Sea is an international sea, shared by the United States and the Russian Federation, and is approximately bisected by the U.S.-Russia Maritime Boundary. We focused our study on the eastern Chukchi Sea within the territorial waters of the U.S. There is no ecosystem basis for only modeling the eastern Chukchi Sea. This decision is a reflection of the general unavailability of datasets providing an adequate description of the western Chukchi Sea, and we felt it was inappropriate to extrapolate our parameters for the eastern region to the entire extent of the Chukchi Sea. The model describes the continental shelf waters of the eastern Chukchi Sea between the 20 m and 70 m isobaths, covering approximately 192,000 km^{-2} (Figure 1). Waters outside this depth boundary are beyond the range of most trawl surveys and may incorporate near shore and deep water processes and species that are not included in this or the original model. The only exception to the 70 m depth limit is the portion of Barrow Canyon north and west of Pt. Barrow, where the maximum depth is approximately 150 m. The model area is bordered by the Bering Strait to the south, Pt. Barrow to the east, the U.S. Russia Maritime Boundary to the west, and a combination of the Exclusive Economic Zone (EEZ, 200 mile limit) and 70 m isobath to the north. Near shore the model is bounded by the 20 m isobath.

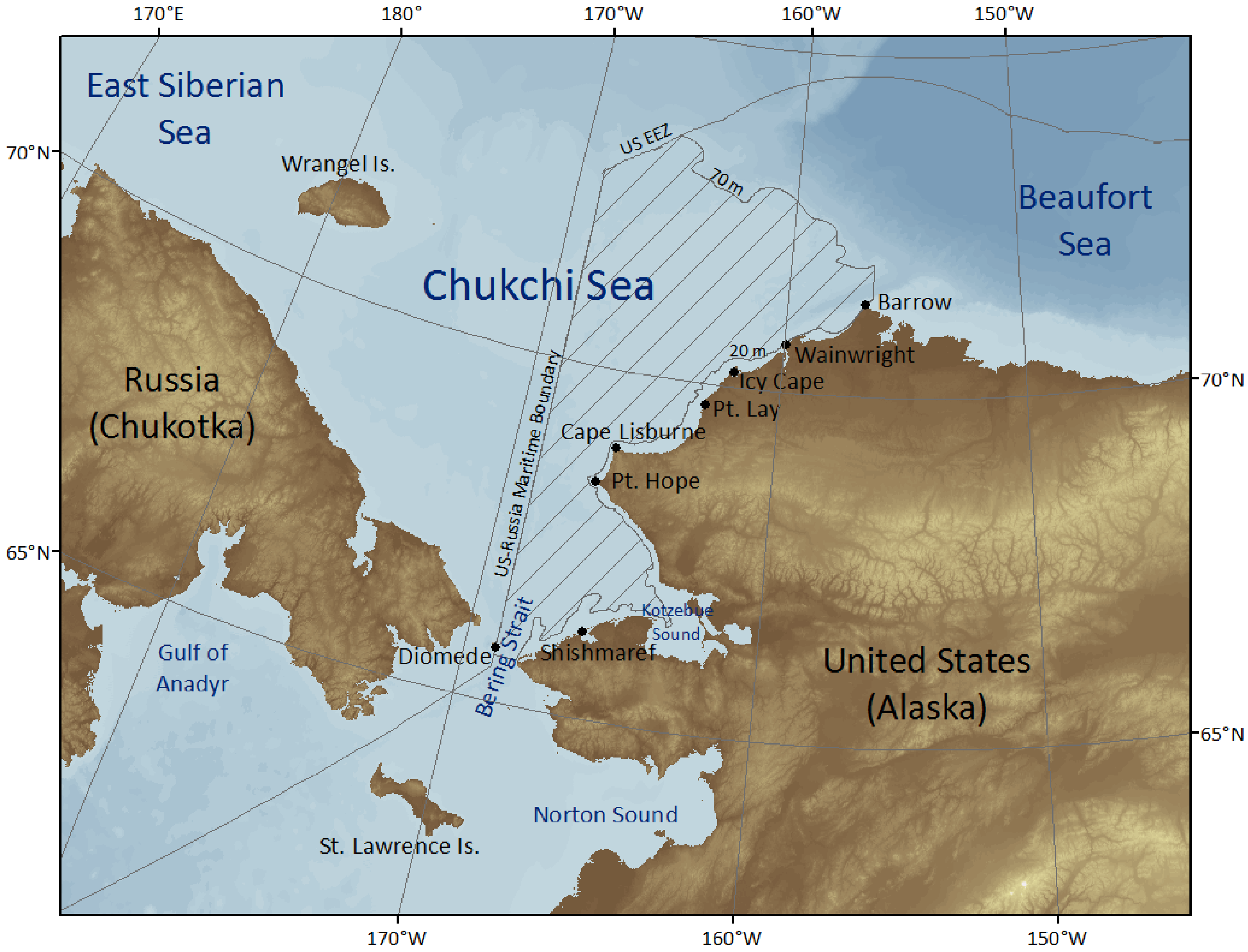

Figure 1: The model area in the eastern Chukchi Sea (filled with hatched lines).

3.2 General methodology for the model update

The primary purpose of this report is to update the existing preliminary trophic mass balance model of the eastern Chukchi Sea (W13) so that it better represents current conditions in this ecosystem. The preliminary model had a base time period of the early 1990s because much of the data needed to parameterize the preliminary model was available from that time period, even though some more recent parameter values may have been available. This model update revised many of the model parameter values by incorporating data from more recent studies, so as to provide a more accurate and current representation of the eastern Chukchi Sea food web. Primarily we will be incorporating data gathered as part of the BOEM funded Arctic Eis trawl surveys of the eastern Chukchi Sea during the summer of 2012. Additionally, we have updated other model parameters as data permitted and as required by the model balancing process.

3.3 Modeling framework

Using the Ecopath with Ecosim (EwE, version 6) modeling framework (Christensen et al. 2008), we update the earlier eastern Chukchi Sea model. Ecopath is a static, mass balance food web model originally developed by Polovina (1984) to describe a coral reef ecosystem and has since been used to study ecosystems around the globe, including high latitude marine ecosystems (e.g., Cornejo-Donoso and Antezana 2008, Pedersen et al. 2008, Gaichas et al. 2009, Morissette et al. 2009, Whitehouse et al. 2014, Lovvorn et al. 2015). Ecopath is a biomass compartment model where each compartment represents a species or functional group of multiple species and describes the material flows between compartments in a food web. The mass balance requirement ensures that production by a compartment is sufficient to match removals by predators and fisheries catch. The balanced model provides a snapshot of ecosystem structure and can be used to calculate a number of metrics which describe key ecosystem attributes. Under equilibrium conditions, the interactions between functional groups are described by a set of linear equations. For each group (i) with predators (j), this relationship is expressed as:

$$B_i \left(\frac{P}{B}\right)_i * EE_i = \sum_j B_j * \left(\frac{Q}{B}\right)_j * DC_{ij} - C_i \;, \qquad (1)$$

where, B is biomass density (t km^{-2}) in wet weight, P/B (yr^{-1}) is the production to biomass ratio, Q/B (yr^{-1}) is the consumption to biomass ratio, DC_{ij} is the proportion of prey *i* in the diet of predator *j*, and C is subsistence harvest or fisheries catch (t km^{-2}) of group i. Ecotrophic Efficiency (EE) is the proportion of production (B_i*[P/B]$_i$) that is consumed by predators and removed by fisheries/subsistence harvests included in the model and must be ≤ 1.

Mass balance is achieved by solving this set of linear equations for one missing parameter for each functional group. DC must be entered into the model and typically B, P/B, Q/B, and C are also entered, and the equation is solved for EE. When reliable estimates of model parameters are unavailable, EE can be set to an arbitrary value and the equation solved for the missing parameter. This is usually done for B, and is commonly referred to as a “top-down balance” because the model is estimating biomass based on top-down removals from predators and fisheries. EE is difficult to measure in nature and is generally unknown but is thought to be close to 1 for prey groups subject to heavy predation and/or fishing pressure and close to zero for top predators that experience little predation and fishing pressure (Christensen et al. 2005). All top-down balancing performed in the original model was done with EE set to 0.8, and for consistency, we take the same approach here. Setting EE to 0.8 implies that the model explains 80% of the total mortality through the predation and fisheries removals explicitly included in the model. Other sources of mortality not included in the model but accounting for the remaining 20% of total mortality (1-EE) include disease, senescence, starvation, and possible outmigration. This non-predation mortality is generally not measurable, and applying a uniform percentage to this unexplained mortality (20%) allows for a standardized analysis and is generally consistent with dynamic fits of unexplained mortality across a range of species (Aydin et al. 2007).

The energy balance within a functional group must also be maintained, and the total production, plus the costs for maintenance and metabolism (respiration), plus the fraction of food that is not assimilated must not exceed their total consumption. This is ensured for each functional group i with the following equation:

$$Q_i = P_i + R_i + U_i \tag{2}$$

Where Q_i is total consumption (i.e., $B_i*[Q/B]_i$), P_i is total production (i.e., $B_i*[P/B]_i$), R_i is respiration, and U_i is the portion of consumption that is unassimilated and is egested or excreted as feces and urine, and is directed to detritus. Estimates of Q, P, and U are generally more available than R, thus equation 2 is used to estimate R. Measurements of the portion of consumed food that is unassimilated (i.e., 1-assimilation efficiency) are highly variable, and are influenced by biological and environmental factors including the predator species, prey quality, the amount consumed, temperature, and gut passage time (Winberg 1960, Conover 1966, Bayne et al. 1988, Gaudy et al. 1991, Hop et al. 1997, Bochdansky et al. 1999). We use the default value of 0.2 for the unassimilated fraction of food (U/Q) for most functional groups, meaning 20% of total consumption is not useful for production or respiration (Christensen et al. 2008). For benthic detritivores (DC at least 50% benthic detritus) the unassimilated fraction is assumed to be higher (Welch 1968) and we use a default of 0.4 (Christensen et al. 2008).

Model balancing is the process of solving the system of linear equations set up by Ecopath, to ensure mass balance is achieved. Normally, initial attempts to balance an Ecopath model are unsuccessful and a number of functional groups will be out of balance (EE > 1). This sometimes alerts the model developer to an error that may have been made during model development (e.g., misplaced decimal point, typo, etc.), but more often highlights instances where a collection of the model inputs are incompatible (e.g., predator consumptive requirements in excess of prey production). When input parameters are determined to be incompatible, the parameters in question, and all related parameters, need to be re-evaluated to determine how to best reconcile the conflicting parameters. This can involve selecting a different parameter from the published literature or recalculating a parameter based on the new information, using Ecopath to solve for the parameter in doubt, making a manual adjustment to the input parameter value, or reconfiguring functional groups.

3.4 Data sources and data quality

The development of an ecosystem-scale food web model necessitates the synthesis of a large body of literature and requires the inclusion of data and rates of varying quality, from a variety of sources. Some data and rates can be directly inserted to the model, while others may require some modification to account for the temporal and spatial limitations of the model framework. We graded all model parameters and/or data for quality and uncertainty using a data pedigree previously described by Christensen et al. (2005), with specific data quality definitions from Aydin et al. (2007). Model parameters and data were assigned a data pedigree (grade) based upon the data source, collection methodology, temporal and spatial coverage of the dataset, and taxonomic relevance.

In this model update, we used the same data pedigree (Table 2) as that used in the development of the preliminary model (W13). Where input parameters (B, P/B, Q/B, DC, C) have been updated for the current analysis we have provided in the Results section a detailed description of parameter development, data sources, and parameter adjustments. Parameters from the preliminary model that remain unadjusted in the updated model will not be described in detail here, and instead the reader is referred to the preliminary model documentation (W13). The full suite of basic model parameters is presented in Table 1 and the diet matrix can be found in Appendix A. Input parameters that have been updated from the original model are highlighted with red text in Table 1. Additionally, the data pedigree for basic model parameters can be found in Appendix B.

Table 1. The basic model parameters for the updated eastern Chukchi Sea Ecopath model. Parameters that are input to the model are in bold and italicized. Input parameter values that are different from the preliminary model are additionally highlighted in red. New functional groups added to the updated model are also highlighted in red. TL is Trophic Level, B is Biomass, P/B is production to biomass ratio, Q/B is consumption to biomass ratio, EE is ecotrophic efficiency, GE is growth efficiency, and U/Q is the unassimilated fraction of consumed food. B is in t km^{-2}; P/B, Q/B, and GE are in year^{-1}, and EE and U/Q are dimensionless.

Table 1.

Group	TL	B	P/B	Q/B	EE	GE	U/Q	Removals
Beluga	4.6	***0.01159***	***0.11***	***14.50***	0.211	0.008	***0.2***	***6.34E-05***
Gray whale	3.5	***0.18795***	***0.06***	***8.87***	0.000	0.007	***0.2***	
Bowhead whale	3.5	***0.39848***	***0.01***	***5.26***	0.299	0.002	***0.2***	***0.00120***
Polar Bear Chukchi	5.5	***0.00040***	***0.06***	***4.00***	0.663	0.015	***0.2***	***1.61E-05***
Polar Bear S Beaufort	5.5	***0.00012***	***0.06***	***4.00***	0.304	0.015	***0.2***	***2.26E-06***
Pacific walrus	3.4	***0.05909***	***0.07***	***21.66***	0.757	0.003	***0.2***	***0.00308***
Bearded seal	3.9	***0.03905***	***0.08***	***12.94***	0.912	0.006	***0.2***	***0.00177***
Ringed seal	4.7	***0.05587***	***0.09***	***19.23***	0.896	0.005	***0.2***	***0.00212***
Spotted seal	4.8	***0.00579***	***0.07***	***18.70***	0.385	0.004	***0.2***	***0.00015***
Procellarids	3.7	***0.00193***	***0.07***	***187.93***	0.000	0.0004	***0.2***	
Cormorants	4.4	***1.47E-06***	***0.16***	***142.62***	0.000	0.001	***0.2***	
Scolopacids	3.5	***7.77E-05***	***0.16***	***374.31***	0.000	0.0004	***0.2***	
Larids	4.5	***9.31E-05***	***0.11***	***205.67***	0.000	0.001	***0.2***	
Alcids piscivorous	4.8	***0.00116***	***0.10***	***178.38***	0.741	0.001	***0.2***	
Alcids planktivorous	3.5	***0.00014***	***0.14***	***247.51***	0.000	0.001	***0.2***	
Large-mouth flatfish	4.2	0.11142	***0.40***	***1.78***	***0.800***	0.225	***0.2***	
Small -mouth flatfish	3.4	0.09015	***0.31***	***1.54***	***0.800***	0.201	***0.2***	
Large-mouth sculpin	4.3	0.59984	***0.40***	***2.00***	***0.800***	0.200	***0.2***	
Other sculpin	3.6	0.85526	***0.46***	***2.42***	***0.800***	0.190	***0.2***	
Eelpout	3.7	0.38218	***0.40***	***2.00***	***0.800***	0.200	***0.2***	
Pelagic forage fish	3.7	1.19059	***0.54***	***2.92***	***0.800***	0.186	***0.2***	
Misc. shallow fish	3.5	6.49835	***0.40***	***2.00***	***0.800***	0.200	***0.2***	
Other Snailfish	3.8	0.13509	***0.40***	***2.00***	***0.800***	0.200	***0.2***	
Variegated snailfish	4.3	0.09874	***0.40***	***2.00***	***0.800***	0.200	***0.2***	
Alaska skate	4.4	***0.00536***	***0.21***	2.10	0.000	***0.100***	***0.2***	
Walleye pollock	4.2	***0.00054***	***0.87***	***3.01***	0.0001	0.289	***0.2***	
Pacific cod	4.0	***3.79E-05***	***0.55***	***2.80***	0.744	0.195	***0.2***	
Saffron cod	4.0	0.97905	***0.55***	***2.80***	***0.800***	0.195	***0.2***	
Arctic cod	3.7	1.04491	***0.87***	***3.01***	***0.800***	0.289	***0.2***	
Salmon outgoing	3.5	***0.00052***	***1.28***	***13.56***	0.000	0.094	***0.2***	
Salmon returning	3.5	***0.00521***	***1.65***	***11.60***	0.027	0.142	***0.2***	
Cephalopods	3.9	0.01058	***1.77***	8.85	***0.800***	***0.200***	***0.2***	
Bivalves	2.3	***90.28777***	***0.76***	3.78	0.289	***0.200***	***0.4***	
Snails	3.3	***1.38446***	***1.77***	8.85	0.254	***0.200***	***0.2***	
Snow crab	3.1	***3.16997***	***1.00***	***2.75***	0.082	0.364	***0.2***	
Other crabs	3.1	***3.06715***	***0.82***	4.10	0.330	***0.200***	***0.2***	
Shrimps	2.9	7.49216	***0.58***	***2.41***	***0.800***	0.239	***0.2***	
Sea stars	3.3	***2.18016***	***0.34***	1.70	0.032	***0.200***	***0.2***	
Brittle stars	2.7	***5.64425***	***0.49***	2.43	0.197	***0.200***	***0.4***	
Basket stars	3.5	***0.50986***	***0.34***	1.70	0.002	***0.200***	***0.2***	
Urchins, dollars, cucumbers	2.0	***36.28965***	***0.70***	3.48	0.050	***0.200***	***0.4***	
Sponge	2.3	***0.52716***	***1.00***	5.00	0.047	***0.200***	***0.4***	
Benthic urochordate	2.3	***1.16008***	***3.58***	17.90	0.033	***0.200***	***0.4***	
Anemones	3.1	***0.38413***	***1.00***	5.00	0.387	***0.200***	***0.2***	
Corals	2.3	***0.02568***	***0.05***	0.23	0.006	***0.200***	***0.4***	
Benthic amphipods	2.5	20.52616	***1.00***	5.00	***0.800***	***0.200***	***0.4***	
Polychaetes	2.5	***27.80796***	***2.92***	14.58	0.209	***0.200***	***0.4***	
Worms etc.	2.5	***17.03959***	***2.23***	11.15	0.119	***0.200***	***0.4***	
Misc. crustaceans	2.5	***5.58099***	***2.01***	10.04	0.617	***0.200***	***0.4***	
Jellyfish	3.4	***0.37197***	***0.88***	***3.00***	0.002	0.293	***0.2***	
Copepods	2.5	2.04268	***6.00***	***27.74***	***0.800***	0.216	***0.2***	
Other zooplankton	2.5	1.22520	***5.48***	15.64	***0.800***	***0.350***	***0.2***	
Pelagic microbes	2.0	1.48870	***26.25***	75.00	***0.800***	***0.350***	***0.2***	
Benthic microbes	2.0	22.31165	***26.25***	75.00	***0.800***	***0.350***	***0.2***	
Phytoplankton	1.0	***27.8***	***75.00***		0.072			
Pelagic detritus	1.0	1427.98			0.047			
Benthic detritus	1.0	4879.12			0.9997			

Table 2. The criteria for the data pedigrees (or data quality grade) . B = biomass, P/B = production/biomass ratio, Q/B = consumption/biomass ratio, DC = diet composition, and C = fishery catch or subsistence harvest. (This table recreated from Aydin et al. 2007)

	Data pedigree and corresponding data characteristics		
	B, P/B, Q/B, DC, and C		
1	Assessment data is established and substantial, from more than one independent method (from which the best method is selected) with resolution on multiple spatial scales.		
2	Data is a direct estimate but with limited coverage/corroboration, or established regional estimate is available while subregional resolution is poor.		
3	Data is proxy, proxy may have known but consistent bias.		
4	Direct estimate or proxy with high variation/limited confidence or incomplete coverage.		
	B and C		**P/B, Q/B, and DC**
5	Estimate requires inclusion of highly uncertain scaling factors or extrapolation	5	Estimation based on same species but in "historical" time period, or a general model specific to the area.
6	Historical and/or single study only, not overlapping in area or time.	6	For P/B and Q/B, general life history proxies or other Ecopath model. For DC, same species in adjacent region or similar species in the same region.
7	Requires selection between multiple incomplete sources with wide range.	7	General literature review from a wide range of species, or outside the region. For DC, from other Ecopath model.
8	Estimated by Ecopath	8	Functional group represents multiple species with diverse life history traits. For P/B and Q/B, estimated by Ecopath.

3.5 Cetaceans

We include the dominant and most frequently observed species of cetaceans known to reside for some portion of the year in the eastern Chukchi Sea. Though other cetacean species have been sighted in the region on several occasions (e.g., humpback whale, fin whale, minke whale, killer whale; see Clarke et al. 2013) we only include those species for which the eastern Chukchi Sea comprised a well-established portion of their current range.

Changes to the parameters for cetacean groups are primarily updates from the historical abundance estimates to the most recent abundance estimates available. There were no changes to P/B, Q/B, or diet composition. For the model parameters not modified as a part of this model update (B, P/B, Q/B, DC, C), detailed functional group descriptions, including data sources, any parameter adjustments, and the diet matrix can be found in the preliminary model documentation (W13). We do provide a brief summary here of the methods used in the preliminary model for parameter development.

(i) Biomass (B)

The biomass density estimates of cetacean groups were calculated from published estimates of abundance, average individual body mass, and information regarding migration and seasonal occupancy of the eastern Chukchi Sea. Due to the seasonal sea ice coverage and known migration patterns of cetaceans, the abundance and biomass estimates were lowered to reflect time spent within the model area only. The general formula to calculate cetacean biomass density (t km^{-2}) for the model is to multiply population abundance estimates by published estimates of species-specific average individual body mass (Hunt et al. 2000), then reducing this biomass estimate by multiplying it by the proportion that reflects the amount of time within a year spent within the model area, and finally dividing this corrected biomass by the model area (km2). This results in a density estimate (B) in t km^{-2}.

(ii) Production (P/B)

The P/B ratios for cetaceans in this updated model are the same as those in the preliminary model. The P/Bs for cetaceans in the preliminary model were estimated with a variation of Siler's competing risk model (Siler 1979) as modified by Barlow and Boveng (1991). Under equilibrium conditions, P/B is assumed to be equal to the instantaneous mortality rate, Z (Allen 1971). This method uses surrogate life histories scaled by longevity to produce survivorship curves, which are used to estimate P/B.

(iii) Consumption (Q/B)

The cetacean Q/B's used in this model update are unchanged from the values used in the preliminary model. Q/B's were calculated using a generalized formula for calculating marine mammal daily energy requirements from Perez et al. (1990) and scaled up to an annual rate. Estimates of prey caloric density and average individual body mass were taken from Hunt et al. (2000).

(iv) Food habits (DC)

The diet compositions of cetacean groups are taken from a variety of literature sources.

3.6 Caniforms

The caniforms includes two stocks of polar bears (*Ursus maritimus*) and four species of pinnipeds, the Pacific walrus (*Odobenus rosmarus*), bearded seal (*Erignathus barbatus*), ringed seal (*Phoca hispida*), and spotted seal (*P. largha*). This group is limited to caniform species whose established range includes the eastern Chukchi Sea for some portion of the year. Ribbon seals (*Histriophoca fasciata*) in particular, were not included as only a small number of ribbon seals are thought to migrate north through Bering Strait (Burns 1970, 1981b, Boveng et al. 2008) and they are infrequently spotted near coastal villages in the southern Chukchi Sea, with sightings in the northern Chukchi Sea being rare (Burns 1981b).

Current or improved estimates of biomass are not presently available for polar bears or most ice-associated pinnipeds in the eastern Chukchi Sea. Biomass is only updated for Pacific walrus. There were no changes to P/B or Q/B for any of the caniforms, however we do summarize here the methodology used in the preliminary model to estimate these parameters. Diet composition was modified for bearded seals and spotted seals, reflecting changes in the species composition of fish functional groups. See the preliminary model documentation (W13) for detailed descriptions of caniform functional groups, including the development of model parameters that were not modified as a part of this model update (B, P/B, Q/B, DC, C), data sources, and any parameter adjustments.

(v) Biomass (B)

The biomass density estimates of caniform functional groups were calculated based on published species-specific abundance estimates, estimates of mean body mass (Derocher 1991, Trites and Pauly 1998), as well as data and information regarding migration, seasonal distribution, and time spent in the eastern Chukchi Sea. Due to the seasonal sea ice coverage and pinniped migration patterns, biomass estimates were lowered as needed to reflect the seasonal nature of their occupation of the model area. The general formula for caniform biomass density (t km^{-2}) is to multiply the abundance estimate by a species-specific mean body mass, then multiply this number by the proportion of time in one year spent occupying the model area. Finally, the biomass (t) is divided by the model area (km^{-2}) to result in the biomass density estimate.

(vi) Production (P/B)

The P/B's for pinniped groups were estimated in the preliminary model (W13) with a variation of Siler's competing risk model (Siler 1979) as modified by Barlow and Boveng (1991). Under equilibrium conditions, P/B is assumed to be equal to the instantaneous mortality rate, Z (Allen 1971). This method uses surrogate life histories scaled by longevity to produce survivorship curves, which are used to estimate P/B. The P/B's of the polar bear groups are approximated with an estimated annual intrinsic population growth rate for the southern Beaufort Sea stock of polar bears (Amstrup 1995).

(vii) Consumption (Q/B)

Pinniped Q/B's are estimated with a generalized formula from Perez et al. (1990) for calculating marine mammal energy requirements, and scaling up to an annual rate. Estimates of pinniped average individual body mass are from Trites and Pauly (1998), and estimates of prey caloric density are from

Hunt et al. (2000). The polar bear Q/B's are estimated using the basal metabolic rate from Best (1977), prey caloric density from Stirling and McEwan (1975), and with information on individual body mass from Derocher (1991).

(viii) Food habits (DC)

The diet compositions of caniform groups are derived from a variety of literature sources. The diet compositions of bearded seals and spotted seals were not updated but were modified to conform to the reconfiguration of some fish functional groups. Bering flounder was moved from the small-mouth flatfish group and added to the large-mouth flatfish group. This is relevant to bearded and spotted seals because flatfish have been identified as part of their diets (Lowry et al. 1980a, Burns and Frost 1983, Lowry et al. 1983, Bukhtiyarov et al. 1984, Perez 1990, Dehn et al. 2007), however species level identifications of flatfish prey are not available. Lacking species-specific information, we decided to evenly proportion the amount of flatfish consumed by bearded and spotted seals between the small and large mouth flatfish groups.

3.7 Seabirds

We focused on the dominant and most frequently observed seabirds of the eastern Chukchi Sea, for which the pelagic environment is their primary habitat. We recognize the presence of many other bird species that make use of the pelagic environment of the eastern Chukchi Sea (>20m depth) as regular transients or occasional visitors but have a different primary habitat, such as waterfowl (e.g., eiders, loons, scoters, etc.) and shorebirds (e.g., sandpipers, dowitchers, etc.), we have excluded these species from the analysis. There are 6 total functional groups representing 20 species of seabirds.

(e) New seabird functional groups

In this model update we include an additional 8 species of seabirds and maintain the same number of seabird functional groups-6 from W13. To accomplish this we have reconfigured the seabird functional groups (Table 5) to reflect family relationships (e.g., Laridae, Procellaridae) or grouped by diet similarities within family (e.g., Alcidae piscivorous, Alcidae zooplanktivorous). A notable shortcoming of the seabird groups in the preliminary model (Whitehouse et al. 2014), was the omission of pelagic migrants and nonbreeders that do not occupy or maintain coastal colonies within the eastern Chukchi Sea region (e.g., short-tailed shearwaters [*Puffinus tenuirostris*], phalaropes [*Phalaropus* spp.]). These pelagic migrants may be among the most numerous birds found offshore in the Chukchi Sea during the ice-free season (Divoky 1987, Gall et al. 2013, Hunt et al. 2013). Therefore, we have added two new functional groups: 1) the Procellarids, which contains northern fulmars (*Fulmaris glaciallis*) and short-tailed shearwater (*Puffinus tenuirostris*), and 2) the Scolopacids, which contains the red-necked phalarope (*Phalaropus lobatus*) and Red phalarope (*P. fulicarius*). The complete reconfiguration of the seabird functional groups necessitated that all model input parameters were recalculated for all seabird functional groups.

(i) Biomass (B)

The preferred method of calculating biomass density for seabirds was to use colony count data multiplied by individual species specific body mass. Though, colony count data may underestimate the abundance of seabirds in the area by not accounting for non-breeders, the colony counts are used here as a best conservative estimate of seabird abundance because it is assumed the colony counts reflect consistent annual occupation of the study area. A previous study of seabirds breeding in the northern Bering/southern Chukchi sea region found that species population estimates derived from colony counts were of similar orders of magnitude as pelagic estimates (Piatt and Springer 2003). However, only using colony data excludes pelagic migrants and non-breeders. To include these species in our current work necessitated the use of pelagic estimates of seabird density. In this model update we have attempted to include the most abundant pelagic migrants by utilizing unpublished population estimates of seabirds occupying the eastern Chukchi Sea during the period of maximum annual seabird abundance (late summer/early fall) (Divoky 1987). The regional scale of the estimates reported in Divoky (1987), effectively describe seabird use of the entire eastern Chukchi Sea (approximately equivalent to the total area described by our model, 192,054 km2). This was seen as an advantage over more recent pelagic seabird density estimates focused on three oil and gas lease sites, covering only about 9,000 km2 in the northeastern Chukchi Sea (Gall et al. 2013). The basic methods for the population estimates reported by Divoky (1987) are briefly reviewed here. Average seabird density estimates were derived from pelagic surveys that were conducted throughout the eastern Chukchi Sea from 1970 to 1986 on nine separate cruises, during the ice-free season. The coarse population estimates reported in Divoky (1987) were calculated by multiplying the average seabird density (birds km^{-2}) for the study region by the total area (km2) of the study region.

We calculated density estimates from the coarse population estimates of Divoky (1987) for Procellarids (northern fulmars and short-tailed shearwaters) and Scolopacids (red-necked phalarope and red phalarope). The population estimates were converted to biomass density estimates (t km^{-2}) by dividing the total population estimate by the total area of our study region, then multiplying by a species-specific mean body mass, taken from Hunt et al. (2000). Species-specific abundance estimates are not available for phalaropes, so a mean body mass for the two species is used. The biomass estimates were reduced further to accommodate the model’s annual time frame and account for the birds seasonal occupation of the model area (~ 4 months), by multiplying the density estimate times one-third.

Biomass estimates of nesting seabirds were derived from colony counts made at seabird colonies found within the model area and along the coast of Alaska between the model’s southern boundary at Bering Strait (65°40’ N) and eastern Boundary at Pt. Barrow (156°25’ W). Colony counts of nesting seabirds were obtained from the North Pacific Seabird Colony Database (Seabird Information Network 2011); an online interactive database which contains current and historical records of censused seabird colonies in the north Pacific, including Alaska and the Russian Far East. In the previous edition of this food web model (W13), colony counts were obtained from a predecessor to the North Pacific Seabird Colony Database, the Beringian Seabird Colony Catalog (USFWS 2003).

The colony counts selected for use in this model were conducted over many years, from 1959 to 1998, by different observers, and to our knowledge are the most current and best colony counts available. The preferred method for calculating seabird biomass density was to multiply the total number of seabirds from the colony counts by the respective species-specific mean body mass found in Hunt et al. (2000). Biomass estimates were added together for species within the same functional group. The estimated biomass was then divided by the total model area to arrive at the functional group biomass density (t km^{-2}). The biomass density estimate was then reduced further to account for the model's annual time frame and the seabird's seasonal occupation of the model area (~4 months), by multiplying times one-third (Table 5).

Mean individual body masses were compiled from the literature by Hunt et al. (2000) for all species except the black guillemot (*Cepphus grylle*) and unidentified murres. The mean individual body mass for black guillemots was calculated as the average of male and female body masses reported by Berzins et al. (2009). The mean individual body mass used for unidentified murres is the average of the mean individual body masses for common murres and thick-billed murres, weighted by their estimated biomass within the study region.

(ii) Production (P/B)

There are few published estimates of P/B for seabirds. Because seabirds are largely unexploited we use estimated survival rates (S) in their place, and set P/B equal to the negative logarithm of the survival rate (P/B = -ln[S]). Species specific survival rates were preferred but when they were unavailable an order level, average survival rate was used, except for puffins (Table 6). All survival rates are from Schreiber and Burger (2001). Where annual survival rates were given as a range, the midpoint of that range was used in calculations. Survival rates for horned and tufted puffins were unavailable, so in their place we use the Atlantic puffin (*Fratercula arctica*) survival rate. The functional group P/B is an average of the species-specific (and/or order level) P/B's, weighted by biomass.

(iii) Consumption (Q/B)

Estimates of Q/B had to be developed for all seabird species due to the reconfiguration of the seabird functional groups. In the preliminary eastern Chukchi Sea model all estimates of seabird Q/B were taken from taxonomically equivalent functional groups in an Ecopath model of the eastern Bering Sea. A different approach is taken here and Q/B is calculated from daily allometric energy requirements for seabirds presented in Hunt et al. (2000). These daily energy requirements were calculated for each species individually using the allometric equation of Birt-Friesen et al. (1989):

$$\log Y = 3.24 + 0.727 * \log M \tag{2}$$

Where Y = the daily energy requirements in kj, and M is the body mass in kg.

The average prey energy density (kj g^{-1}) for generalized seabird prey groups has previously been described by Hunt et al. (2000). We determined the energy density of seabird prey in our model by assigning each prey functional groups to one of the generalized prey categories, with its corresponding energy density, described in Hunt et al. (2000) (Table 3). Average prey energy density was calculated for each predator as the average energy density weighted by the prey's proportion in the predator's diet. The functional group Q/B is an average Q/B weighted by the estimated biomass of the group's constituent species within the model area (Table 7).

(iv) Food habits (DC)

The diet compositions of seabirds are taken from a variety of literature sources. The diets of multi-species functional groups are an average diet weighted by biomass.

Table 3. Approximate energy density (kj g^{-1}) of functional groups found as prey in the diet of seabirds. Energy densities and corresponding prey categories are taken from Hunt et al. (2000).

Prey functional group	Prey category from Hunt et al. (2000)	energy density (kj/g)
Alcids piscivorous	Birds and mammals	7.0
Large-mouth flatfish	Fish low density	3.0
Small -mouth flatfish	Fish low density	3.0
Large-mouth sculpin	Fish low density	3.0
Other sculpin	Fish low density	3.0
Eelpout	Fish low density	3.0
Pelagic forage fish	Fish med density	5.0
Misc. shallow fish	Fish low density	3.0
Walleye pollock	Fish low density	3.0
Pacific cod	Fish low density	3.0
Saffron cod	Fish low density	3.0
Arctic cod	Fish low density	3.0
Snow crab	Misc. inverts	4.0
Bivalves	Misc. inverts	4.0
Snails	Misc. inverts	4.0
Crabs	Misc. inverts	4.0
Shrimps	Misc. inverts	4.0
Brittle stars	Misc. inverts	4.0
Urchins, dollars, cucumbers	Misc. inverts	4.0
Jellyfish	gel. Zooplankters	3.0
Cephalopods	sm. Cephalopods	3.5
Benthic amphipods	Misc. inverts	4.0
Polychaetes	Misc. inverts	4.0
Worms etc.	Misc. inverts	4.0
Misc. crustaceans	Misc. inverts	4.0
Copepods	Crust zoop	4.0
Other zooplankton	Crust zoop	4.0

3.8 Fish

In this model update the number of fish functional groups has expanded from 13 to 16. This expansion is a reflection of the catch data from the 2012 Arctic Eis bottom trawl survey and additionally, the result of incorporating updated region- and species-specific diet data for fishes, also collected during Arctic Eis trawl surveys (Whitehouse et al. *Accepted*). The biomass density and diet composition have been updated for all fish functional groups, except salmonids for which all parameters remain unchanged.

(v) Biomass (B)

Initial fish biomass density estimates were derived from the catch data of the 2012 Arctic Eis bottom trawl survey of the eastern Chukchi Sea. The survey was conducted during August and September aboard the chartered fishing vessel Alaska Knight. The fish were sampled with an 83-112 Eastern bottom trawl (EBT) with 25.3 m headrope and 34.1 m foot rope with a 4.5 mm cod end liner, towed for 15 min. at 3 knots. Station locations were determined using a systematic grid design with 30 x 30 nautical mile grid cells, and trawls were attempted at the center of each grid square. Bottom trawls were conducted successfully at 71 stations between Bering Strait and Pt. Barrow (Figure 2). Station depth ranged from 12 to 90 m and the distance fished ranged from 0.5 to 1.5 km. All EBT bottom trawls were performed in accordance with standard NOAA trawling procedures (Stauffer 2004), see Goddard et al. (2014) for complete details. Biomass density (t km^{-2}) estimates were calculated using the area-swept method (Wakabayashi et al. 1985). The net-width was multiplied by the distance fished to determine the area trawled (km2) for each haul. The weight of the catch for each species (t) was divided by the area trawled to determine the biomass density (t km^{-2}) at each station. The mean biomass density for the entire survey area was calculated as the sum of the station density estimates divided by the total number of stations sampled.

Catch data, which included fishes, were also available from beam trawls that were conducted at 40 of the same sample stations during the 2012 trawl survey of the eastern Chukchi Sea. However, the EBT data was selected as the initial biomass inputs for the fish functional groups rather than the beam trawl data due to differences in sampling coverage and gear performance. We will briefly review the key differences in gear performance here as it relates to the selection of the EBT as our starting fish biomass estimates, but see Britt et al. (2013) for a more complete discussion and comparison of catch data from the two gear types.

In terms of gear performance, the four key differences between these two gears are area-swept, tow speed, vertical opening, and mesh size (Britt et al. 2013). The total area swept by the EBT is much larger than the area-swept by the beam trawl. This is due to a combination of factors: trawls with the EBT are of longer duration (15 min) than the beam trawl (2-5 min), the EBT is towed at a higher speed (3 knots) than the beam trawl (1.5 knots), and the EBT is a much larger net than the beam trawl (see Britt et al. 2013 for the complete dimensions of both nets). The average area-swept by the EBT during a single haul was greater than the total area-swept by all 40 successful beam trawls combined during the 2012 survey (Britt et al. 2013). Bottom trawls were successfully completed with the EBT at 71 sampling stations and at 40 stations for the beam trawl. Overall, the total number of stations sampled and the total area-swept was far greater for the EBT than for the beam trawl.

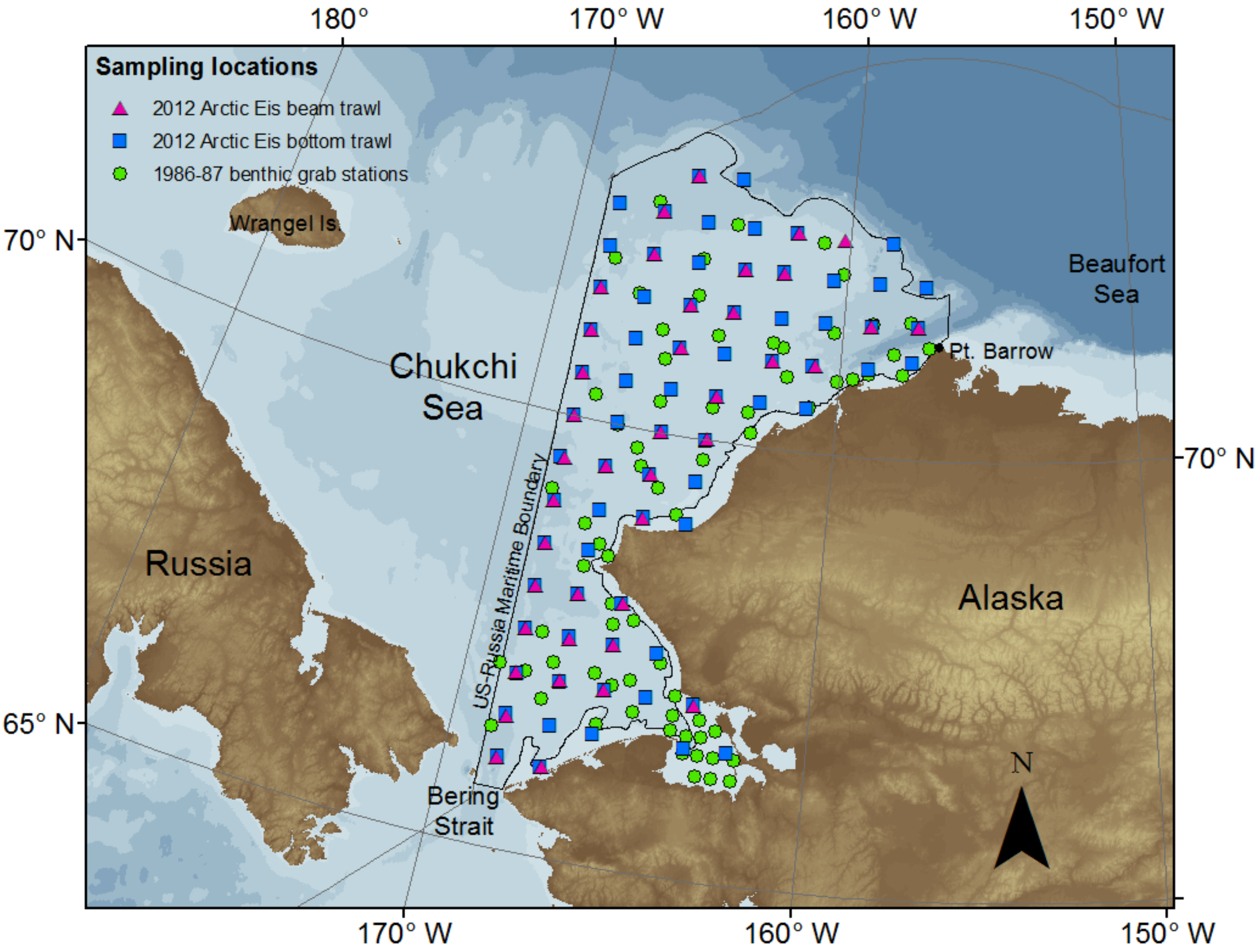

Figure 2: The sampling locations for the 2012 Arctic Eis bottom trawl and beam trawl stations (Britt et al. 2013). Arctic Eis bottom trawl stations are based on a 30 nautical mile (nmi) square grid pattern, with trawling locations at the center of each grid cell (Goddard et al. 2014). Also shown are the locations of benthic van Veen grab stations (Feder et al. 1994b, Feder et al. 2007).

After considering all the differences in gear design, performance, number of stations sampled, and total area-swept, we felt the EBT gave us the best overall estimates of fish biomass and therefore, selected the EBT catch data as our initial biomass inputs for the fish groups. However, we note that the beam trawl may be more efficient at catching smaller and more slender fishes (Britt et al. 2013).

(vi) Production (P/B) and consumption (Q/B)

Under the assumption of steady-state conditions, P/B can be approximated by Z, the instantaneous mortality rate (Allen 1971). Following this relationship we use the regression estimator of the instantaneous natural mortality rate (M) developed by Hewitt and Hoenig (2005) as a proxy for the P/B of fish groups. This method requires a minimum amount of information, just an estimate of maximum age (t_{max}) from the stock in question.

Estimates of P/B and Q/B have been updated for all 4 species of the family Gadidae; Arctic cod (*Boreogadus saida*), Pacific cod (*Gadus macrocephalus*), walleye pollock (*Gadus chalcogrammus*), and saffron cod (*Eleginus gracilus*). We acquired estimates of maximum age for Arctic cod and saffron cod from Helser et al. (*Accepted*). The specimens used in Helser et al. (*Accepted*) were collected during Arctic Eis trawl surveys; the same trawl surveys from which the data used for initial biomass estimates were calculated, and were collected concurrent with the fish specimens collected for diet analysis (Whitehouse et al. *Accepted*).

The Q/B of fishes was calculated following the methods of Aydin (2004). This method requires an estimate of Z, the instantaneous mortality rate, and the von Bertalanffy growth parameter *k*. Estimates of the instantaneous mortality rate for Arctic cod and saffron cod were acquired from the previous calculation of P/B using the regression estimator of M developed by Hewitt and Hoenig (2005). Estimates of the von Bertalanffy *k* parameter for Arctic cod and saffron cod were acquired from Helser et al. (*Accepted*).

Region-specific data to support calculations of P/B and Q/B for walleye pollock (*Gadus chalcogrammus*) and Pacific cod (*G. macrocephalus*) within the Chukchi Sea are not available. Maximum observed sizes for both walleye pollock and Pacific cod have generally been much smaller (<20 cm) in the Chukchi Sea (Wolotira et al. 1977, Barber et al. 1997, Norcross et al. 2010) than what is typically observed in the eastern Bering Sea. Therefore we did not feel it was appropriate to apply the P/B's and Q/B's previously calculated for the more southerly stocks found in the eastern Bering Sea (Aydin et al. 2007) to the corresponding groups in the Chukchi Sea model. Instead we apply the Chukchi Sea-specific estimates of P/B and Q/B for Arctic cod to walleye pollock and apply the Chukchi Sea-specific estimates for saffron cod to Pacific cod. Though there are many differences between Arctic cod and walleye pollock, both of these gadid species can be found occupying demersal and pelagic habitats, both feed on a variety of prey including zooplankton (Whitehouse et al. *Accepted*). Therefore, we felt the Chukchi Sea-specific P/B and Q/B were our best approximation of these parameters for walleye pollock. Similarly, during post-juvenile stages both saffron cod and Pacific cod are found primarily in the demersal environment and both predominantly feed on benthic and demersal prey (Wolotira 1985, Lang et al. 2005, Whitehouse et al. *Accepted*). We made the assumption that in the absence of region-specific data for Pacific cod, the region-specific saffron cod P/B and Q/B were a best approximation of the Pacific cod parameters.

(vii) Food habits (DC)

Stomachs were collected from fish caught during the 2012 Arctic Eis surface and bottom trawl surveys of the eastern Chukchi Sea. A total of 2,073 stomachs were collected and analyzed from 39 species of fish (Table 4). The collected specimens were preserved in buffered 10% formalin at sea following capture, and prepared for transport back to the Food Habits Lab in Seattle at the NOAA Alaska Fisheries Science Center (AFSC). The total contents of each stomach were weighed to the nearest 0.00001 g, then the contents were sorted and identified to the lowest practical taxon. Each prey taxa was counted, weighed, and appropriate life history code identified. The diet data is maintained in the Resource Ecology and Ecosystem Modeling Program's (REEM) Food Habits Database at the AFSC. The predator diet compositions were acquired by querying the REEM food habits database (a detailed description of the database can be found at, http://www.afsc.noaa.gov/REFM/REEM/Data/Default.htm) with their Diet Analysis Tool (Lang 2004). The diet compositions were calculated as the mean percent weight of each prey item in the predator's total stomach contents.

Nearly all prey items were assigned to existing model functional groups. However, some prey items could not be assigned to a model functional group (e.g., unidentified eggs, unidentified organic matter, etc.). These prey items, which seldom accounted for more than 1% (by weight) of a predator's total diet, were removed from the final diet. Because the Ecopath modeling framework requires predator diets to sum to one, these diets were renormalized to one after removal of the unidentified prey.

Table 4. Fish stomachs collected during Arctic Eis trawl surveys and analyzed to establish diet composition. Family totals are in bold and the same row as family name.

Family	Species name	Common name	Bottom trawl total	Off-bottom Chukchi total
Clupeidae (herrings)			**23**	**34**
	Clupea pallasi	Pacific herring	23	34
Osmeridae (smelts)			**41**	**134**
	Mallotus villosus	capelin	9	124
	Osmerus mordax	rainbow smelt	32	10
Gadidae (cods)			**812**	**82**
	Boreogadus saida	Arctic cod	714	82
	Eleginus gracilis	saffron cod	84	
	Gadus macrocephalus	Pacific cod	1	
	Gadus chalcogrammus	walleye pollock	13	
Hexagrammidae (greenlings)			**5**	
	Hexagrammos stelleri	whitespotted greenling	5	
Cottidae (sculpins)			**287**	
	Artediellus scaber	hamecon	22	
	Enophrys diceraus	antlered sculpin	20	
	Gymnocanthus tricuspis	Arctic staghorn sculpin	107	
	Hemilepidotus papilio	butterfly sculpin	1	
	Icelus spatula	spatulate sculpin	21	
	Myoxocephalus jaok	plain sculpin	1	
	Myoxocephalus quadricornis	fourhorn sculpin	2	
	Myoxocephalus scorpius	shorthorn (warty) sculpin	64	
	Triglops pingeli	ribbed sculpin	48	
Hemitripteridae (sailfin sculpins)			**10**	
	Nautichthys pribilovius	eyeshade sculpin	10	
Agonidae (poachers)			**52**	
	Podothecus veternus	Veteran poacher	**5**	
	Ulcina olrikii	Arctic alligatorfish	47	
Liparidae (snailfishes)			**159**	
	Liparis gibbus	variegated snailfish	54	
	Liparis marmaratus	festive snailfish	7	
	Liparis tunicatus	kelp snailfish	98	
Zoarcidae (eelpouts)			**41**	
	Gymnelus hemifasciatus	halfbarred pout	1	
	Lycodes palearis	wattled eelpout	7	
	Lycodes polaris	Canadian eelpout	19	
	Lycodes raridens	marbled eelpout	10	
	Lycodes turneri	polar eelpout	2	
Stichaeidae (pricklebacks)			**175**	
	Lumpenus fabricii	slender eelblenny	148	
	Lumpenus medius	stout eelblenny	25	
	Stichaeus punctatus	Arctic shanny	2	
Ammodytidae (sand lances)			**5**	**53**
	Ammodytes hexapterus	Pacific sand lance	5	53
Pleuronectidae (flatfishes)			**163**	
	Hippoglossoides robustus	Bering flounder	114	
	Limanda aspera	yellowfin sole	13	
	Limanda proboscidea	longhead dab	7	
	Limanda sakhalinensis	Sakhalin sole	7	
	Liopsetta glacialis	Arctic flounder	13	
	Pleuronectes quadrituberculatus	Alaska plaice	8	
	Reinhardtius hippoglossoides	Greenland turbot	1	
Total stomachs collected for all families			**1770**	**303**
Grand total (bottom trawl and off-bottom collections)			**2073**	

(f) New and changed fish functional groups

Three fish functional groups were added in this model update, the Alaska skate (*Bathyraja parmifera*), variegated snailfish (*Liparis gibbus*), and other snailfish (other than *L. gibbus*). Additionally, the species composition of the flatfish functional groups changed as Bering flounder (*Hippoglossoides robustus*) was removed from the small-mouth flatfish group and added to the large-mouth flatfish group.

(i) Alaska skate

A single Alaska skate was caught in the south central Chukchi Sea during the 2012 bottom trawl survey of the eastern Chukchi Sea. This was the first live adult Alaska skate caught in the Chukchi Sea; previously, two beach cast specimens were found in 2010 near Pt. Hope and Kivalina (Mecklenburg et al. 2011). During the summer of 2010 several specimens of *B. parmifera* were caught in the northern Bering Sea during a NOAA bottom trawl survey (Lauth 2011, Stevenson and Lauth 2012). A steep increase in skate biomass (primarily *B. parmifera*) on the eastern Bering Sea continental shelf was observed between 1979 and 1990 and has remained steady since (Hoff 2006). Due to the observed increase of skate biomass in the eastern Bering Sea and the more recent records of Alaska skate in the northern Bering Sea and within the Chukchi Sea, we have added the Alaska skate to our eastern Chukchi Sea food web model as a single species functional group.

(ii) Variegated snailfish

In the original Ecopath model of the Chukchi Sea, the miscellaneous shallow fish functional group included poachers (Agonidae), wolffish (Anarhichadidae), lumpsuckers (Cyclopteridae), greenlings (Hexagrammidae), snailfish (Liparidae), and pricklebacks (Stichaeidae). In this updated model we have removed the variegated snailfish from the miscellaneous shallow fish functional group and it now forms its own single species functional group. The analysis of variegated snailfish stomachs collected during the 2012 eastern Chukchi Sea bottom trawl survey indicated that ~33% of their diet (by weight) consisted of other miscellaneous shallow fish. Approximately 13% of their diet was other liparids (*Liparis* sp.). To avoid the computational problems associated with functional group cannibalism, the variegated snailfish is now treated as a single species and not part of the larger miscellaneous shallow fish functional group.

(iii) Other Snailfish

The third new fish functional group is Snailfish, which includes all snailfish other than *L. gibbus*. These other snailfish species were formerly a part of the miscellaneous shallow fish functional group but were removed from it based on dietary differences. Approximately 18% of the snailfish diet consisted of fish, whereas none of the other species within the miscellaneous shallow fish group, for whom diet data was available, included any piscivory. Additionally, many of the non-snailfish species of the misc. shallow fish group were common prey items (especially stichaeids) in the diet of other piscivorous fishes. As the biomass estimate of the miscellaneous shallow fish group was top-down forced, their biomass increased commensurate with demand from predators. This had the effect of artificially increasing the biomass of the liparids because they were included in the same functional group with popular fish prey (e.g., stichaeids). As a result, the consumption of other fish by Liparids was also artificially increased. This looping of predator and prey ultimately resulted in inflated biomass levels for many of the fish functional groups, as most were top-down forced. The clear dietary distinctions between liparids and the rest of the miscellaneous shallow fish, in combination with the implications for top-down balancing of most fish functional groups, led us to the decision to separate snailfish from miscellaneous shallow fish into their own functional group.

(iv) Large-mouth flatfish and small-mouth flatfish

Bering flounder (*Hippoglossoides robustus*) was formerly included in the small-mouth flatfish group, along with yellowfin sole (*Limanda aspera*), longhead dab (*L. proboscidea*), Sakhalin sole (*L. sakhalinensis*), Arctic flounder (*Liopsetta glacialis*), starry flounder (*Platichthys stellatus*), and Alaska plaice (*Pleuronectes quadrituberculatus*), due to presumed similarities in diet and habitat requirements. Examination of the fish stomachs collected during the 2012 Arctic Eis surveys revealed that Bering flounders may be the only species in the small-mouth flatfish group that regularly preys on fish. We found that more than 50% of the Bering flounder diet composition (by weight) could be attributed to fish, while none of the stomachs collected for the other small-mouth flatfish species contained any fish prey. Due to this distinct difference in food habits we decided to remove Bering flounder from small-mouth flatfish and add them to large-mouth flatfish, which already includes two predators known to consume fish, Greenland turbot (*Rheinhardtius hippoglossoides*, also known as Greenland halibut) and Pacific halibut (*Hippoglossus stenolepis*).

3.9 Benthic Invertebrates

(v) Biomass (B)

Biomass density (t km^{-2}) estimates for benthic invertebrates were derived from two principal sources: beam trawls and benthic grab samples. For the larger epifaunal invertebrates, biomass estimates were calculated from the catch data of beam trawls conducted during the 2012 Arctic Eis trawl survey of the eastern Chukchi Sea. For smaller benthic invertebrates that are poorly sampled by trawls, biomass estimates were calculated from benthic grab samples collected throughout the eastern Chukchi Sea in the mid-1980s (Feder et al. 1994b, Feder et al. 2007). Recent studies have examined the benthic infauna of the northeastern Chukchi Sea (Schonberg et al. (2014) for COMIDA-CAB and Blanchard et al. (2013a) for CSESP) but are not included here as they only cover a limited portion of our study area. Combining benthic grab data from the more recent studies with the grab data collected during the 1980's was deemed unacceptable as the data sets are separated by 23 or more years and inclusion of the recent studies would introduce a spatial bias towards the northeastern Chukchi Sea.

The beam trawls were conducted during August and September of 2012 aboard the chartered fishing vessel Alaska Knight. Beam trawls were conducted at a selected number of stations where bottom trawls were also performed (see Britt et al. (2013) for complete details). Beam trawls were successfully performed at 40 stations between 66°N and 73°N in the eastern Chukchi Sea (Figure 2). The trawls were performed with a plumb staff beam trawl with a 5.1 m footrope, 4.1 m headrope and a 4 mm cod-end liner. The effective net width is 2.3 m and the fishing scope was approximately 3.5:1 (Norcross et al.

2010). The trawling speed was about 1.5 knots and trawl duration was approximately 5 minutes. The plumb staff beam trawl is designed to maintain consistent contact with the bottom along the entire length of the footrope and is effective at catching benthic fauna, including individuals that make shallow burrows (Gunderson and Ellis 1986). Biomass density (t km^{-2}) estimates were calculated using the area-swept method (Wakabayashi et al. 1985). The net width was multiplied by the distance fished to determine the area trawled (km2) for each haul. The weight of the catch for each species (t) was divided by the area trawled to determine the biomass density (t km^{-2}) at each station. The mean biomass density for the entire survey area was calculated as the sum of the station density estimates divided by the total number of stations sampled.

Quantitative benthic grab samples were collected with van Veen grabs (0.1 m^{-2}) at a total of 71 sampling stations across the eastern Chukchi Sea in 1986 and 1987 (Feder et al. 1994b, Feder et al. 2007). Two of the stations were excluded from our analysis due to incomplete data recording. Functional group density estimates (t km^{-2}) were averaged across all 69 sample stations (Figure 2).

(vi) Production (P/B) and Consumption (Q/B)

Estimates of P/B for benthic invertebrate groups that are both species-specific and specific to the Chukchi Sea are unavailable at this time. In the previous model, P/B estimates for related species from other regions or P/B estimates for taxonomically similar groups from other Ecopath models, were used in their place. These alternative P/B estimates were generally from studies conducted at lower latitudes, often in near shore (< 20 m depth) and intertidal waters. We updated the P/B estimates for many of the benthic invertebrates where improved estimates could be found in the literature. Estimates could be improved with greater geographic relevance (Arctic versus non-Arctic, data pedigree=5), taxonomic relevance (e.g., same species different region, data pedigree=5), or with estimates based on empirical methods (e.g., Cusson and Bourget 2005, data pedigree=6).

Input parameter estimates for Q/B and GE for benthic invertebrate functional groups remain unchanged from W13 . For several benthic invertebrate functional groups, reasonable estimates of Q/B are unavailable, and instead Q/B is calculated by Ecopath with an assumed GE of 0.2. GE usually ranges between 0.1 and 0.3 (Trites et al. 1999), and averages about 0.2 for benthic invertebrate groups in the eastern Bering Sea (Aydin et al. 2007). GE is calculated for most functional groups as P/B divided by Q/B. When a reasonable estimate of Q/B is unavailable, Q/B can be solved for by inserting an assumed GE value into the model. For those functional groups with updated P/B estimates and additionally have Q/B solved for with an assumed GE, Q/B is also be updated.

(vii) Food Habits (DC)

The diet compositions for benthic invertebrate functional groups remain unchanged from the preliminary model with the exception of snails. The diet composition of snails was updated with more specific diet data from the literature.

(viii) Unassimilated/consumption

The default value for the unassimilated fraction of consumption for carnivorous functional groups is 0.2. Unassimilated food is egested or excreted as feces and urine, and is directed to detritus. For herbivores and detritivores the unassimilated fraction is assumed to be higher and a default value of 0.4 is used.

3.10 Model Comparisons

We highlight similarities and differences between the preliminary model and our updated model by comparing the biomass of aggregated functional groups and with a selection of ecosystem-scale metrics, including, total energy flow, total production, and total biomass (excluding detritus).

We examined how biomass is distributed across broad taxonomic categories by contrasting the biomass of aggregated groups between the preliminary model and the updated model. For this set of comparisons we aggregate together related functional groups into eight aggregate groups, and calculate an aggregated biomass by summing the biomass estimates for member groups. The eight aggregated groups are mammals, seabirds, fish, benthic invertebrates, jellyfish, zooplankton, microbes, and phytoplankton.

Total energy flow was measured as total system throughput (TST), which is the sum of total mass flows (t km^{-2} year^{-1}) for consumption, respiration, flow to detritus, and export (Christensen et al. 2005). Total consumption is the sum of food intake (B*Q/B) by all predators. Respiration flow is the fraction of assimilated food that does not lead to production. The flow to detritus from each group is a combination of the unassimilated portion of food that egested and the portion of the group that is lost to other sources of mortality outside of the predation and fisheries mortality explicitly included in the model. We looked at the magnitude and direction of change in TST from the preliminary model to this model update.

Total ecosystem production is the sum of production (t km^{-2} year^{-1}) from all functional groups. Similarly, total biomass is the sum of biomass estimates (t km^{-2}) for all living groups. We examined how total production and total biomass have changed from the preliminary model to this model update and discussed possible explanations for those changes. Additionally, we calculate the ratio of total system production to total biomass (P/B). Whitehouse et al. (2014) also calculated the ratio of total ecosystem production to total biomass for the preliminary model and interpreted it as an overall measure of ecosystem turnover.

4. Results

a. Outline

Here we present descriptions of new input parameters and the output parameters that result from balancing the updated model (e.g., top-down balanced biomass). The results section is organized as follows. First, we present results of the updated model for each -functional group, in turn. For each functional group we note which basic input parameters (B, P/B, Q/B, DC, and C) were updated with new information and those parameters that remain unchanged from the preliminary model. For updated parameters we provide a detailed description of parameter development and data sources. An updated data pedigree can be found in Appendix B. For those model parameters that are not updated and remain unchanged from the preliminary model, they are not discussed at length here and instead the reader is directed to the preliminary model documentation (i.e., W13, Whitehouse et al. 2014). However, for those parameters not updated in this report we do include the parameter values and the core references informing those parameter estimates. Second, in the Model Balancing section we summarize the key adjustments to the model structure and input parameters that were made during the model balancing process. These are adjustments that were made after all input parameters were selected, but were necessary to bring the model into balance. Last, we present results for the ecosystem as a whole, in the Model Comparison section. There we present a collection of ecosystem scale metrics and compare these results with similar metrics calculated for the preliminary model.

4.2Cetaceans

(g) Beluga

Belugas (*Delphinapterus leucas*) are toothed whales (Odontoceti) from the family Monodontidae. Two stocks of belugas occur in the Chukchi Sea, the Chukchi Sea stock and the Beaufort Sea stock. Both stocks overwinter in the Bering Sea and migrate north through the Bering Strait and into the Chukchi Sea in spring when the sea ice begins to fracture (Frost et al. 1983, Moore et al. 1993).

(i) Updated parameters

None

(ii) Parameters from W13

The beluga biomass estimate **(B)** is based on population estimates for the eastern Chukchi Sea stock and the Beaufort Sea stock taken from Allen and Angliss (2010). The abundance estimate is multiplied by a mean adult beluga body mass from Hunt et al. (2000), then reduced to reflect seasonal occupancy of the model area and migration patterns, resulting in a biomass estimate of 0.01159 t km^{-2}. **P/B** was estimated to be 0.11 using a variant of Siler's competing risk model (Siler 1979), as modified by Barlow and Boveng (1991). A **Q/B** of 14.50 was estimated from daily caloric requirements scaled up to an annual rate and calculated following the methods of Perez et al. (1990). The diet composition **(DC)** of belugas is estimated to include primarily fish (~90%) and secondarily cephalopods and shrimp (~10%) (Seaman et al. 1982). The beluga subsistence harvest **(C)** is estimated as 6.34 * 10-5 t km^{-2} based on information in Allen and Angliss (2010).

(h) Gray whale

Gray whales (*Eschrichtius robustus*) are baleen whales (Mysteceti) that spend the winters in Baja California and migrate north to the northern Bering and Chukchi seas during summer (Braham 1984) where they feed on the abundant communities of benthic invertebrates (Highsmith and Coyle 1990, Highsmith et al. 2006).

(i) Updated parameters

Biomass (B): Updated gray whale biomass is calculated from an abundance estimate of 19,126 whales, corresponding to the years 2006-07 (Laake et al. 2009). This abundance estimate was reduced by half to account for seasonal occupation of the model area. It was reduced further to account for the fraction of whales migrating into the Chukchi Sea (~0.7) (Highsmith and Coyle 1992), and to account for the estimated proportion occupying the eastern Chukchi Sea (0.333). The remaining abundance estimate is multiplied by an average body mass of 16,177 kg (Hunt et al. 2000) then divided by the total model area (192,054 km^{-2}) to arrive at a gray whale model biomass of 0.188 t km^{-2}.

(ii) Parameters from W13

The **P/B** of 0.06 for gray whales was previously estimated by Aydin et al. (2007) using a variant of Siler's competing risk model (Siler 1979), as modified by Barlow and Boveng (1991). A **Q/B** of 8.87 was calculated by scaling the daily requirements listed in Hunt et al. (2000) up to an annual rate. The diet **(DC)** of gray whales primarily consists of benthic invertebrates, and is particularly dominated by benthic amphipods (Nerini 1984, Highsmith and Coyle 1990, 1992). Their diet is estimated to consist of 90% benthic amphipods with the remaining 10% divided among other benthic invertebrate prey.

(i) Bowhead whale

Bowhead whales (*Balaena mysticetus*) are baleen whales that migrate through the Chukchi Sea on their way between the northern Bering Sea where they spend the winter, and the Beaufort Sea where they spend the summer.

(i) Updated parameters

Biomass (B): Updated bowhead whale biomass is based on the most recent abundance estimate of 12,631, describing the population in 2004 (Koski et al. 2010). Biomass was calculated following the same methods as W13, using a mean body mass of 31,056 kg (Hunt et al. 2000) and accounting for seasonal use of the model area. The resulting bowhead biomass density in the model is 0.398 t km^{-2}.

Subsistence harvest (C): Bowhead whales are taken in subsistence harvests by Natives of Alaska, Russia, and Canada. Most recently, the annual average Native harvest over the years 2006 to 2010 was 38 whales (Allen and Angliss 2013). We use this estimated annual average harvest as a best estimate of bowhead whale harvest (C=0.00120 t km^{-2}).

(ii) Parameters from W13

The bowhead whale **P/B** of 0.01 was derived by Aydin et al. (2007) from survival estimates reported in Zeh et al. (2002). **Q/B** was estimated to be 5.26 by scaling the daily caloric requirements for bowheads listed in Hunt et al. (2000) up to an annual rate. Bowhead whales primarily consume pelagic invertebrates but small amounts of benthic invertebrates have also been recorded in stomach contents (Lowry and Burns 1980, Hazard and Lowry 1984, Lowry 1993, Moore et al. 2010). Their **DC** is estimated as 71% copepods, 24% other zooplankton, and 5% benthic invertebrates including other crabs, benthic amphipods, and other epifauna and infauna.

4.3 Caniforms

(j) Polar bear (Chukchi stock)

There are two stocks of polar bears (*Ursus maritimus*) found in Alaska, the Chukchi/Bering stock and the southern Beaufort Sea stock (USFWS 2010b, c). The distributions of the two stocks overlap with bears from the Chukchi stock found east of Pt. Barrow and bears from the southern Beaufort Sea stock found as far west as Icy Cape along the Chukchi Sea coast (Amstrup et al. 2005).

(i) Updated parameters

None

(ii) Parameters from W13

The biomass **(B)** of the Chukchi stock of polar bears is based on the best available population estimate of 2,000 bears, which is a revised estimate of this population based on an extrapolation of denning data from Wrangel Island (Lunn et al. 2002, Aars et al. 2006, Obbard et al. 2010, USFWS 2010b). The estimate was reduced to reflect occupancy of the model area and account for seasonal loss of sea ice and patterns in bear movement (Garner et al. 1990, Garner et al. 1994, Amstrup et al. 2005). The reduced abundance estimate was then multiplied by an average individual body mass (310 kg) derived from Derocher (1991), then divided by the model area to arrive at an estimated density of 4.04 * 10-4 t km^{-2}. The **P/B** of the Chukchi stock is estimated to be 0.06, which is based on an estimated annual intrinsic growth rate for the southern Beaufort Sea stock (Amstrup 1995) but is recommended as a best estimate for the Chukchi stock (USFWS 2010b). The **Q/B** of polar bears was calculated using information on the estimated polar bear basal metabolic rate (Best 1977) and daily metabolic rate (Best 1985), along with the estimated caloric density of their primary prey, ringed seals (*Phoca hispida*) (Stirling and McEwan 1975). When scaled up to an annual rate, this resulted in an estimated P/B of 4.00. The primary prey of polar bears, throughout their range, is ringed seals, and of secondary importance are bearded seals (*Erignathus barbatus*) (Stirling and Archibald 1977, Smith 1980, Derocher et al. 2002, Iverson et al. 2006, Bentzen et al. 2007). They are also known to consume belugas (Freeman 1973, Smith 1985, Lowry et al. 1987, Smith and Sjare 1990, Rugh and Shelden 1993), walrus (Kiliaan and Stirling 1978, Amstrup and DeMaster 1988, Calvert and Stirling 1990), and to opportunistically feed on whale carcasses either from subsistence hunts or beached whales (Kochnev 2006, Miller et al. 2006, Ovsyanikov 2010). The diet composition **(DC)** used here for both stocks of polar bears was derived through fatty acid analysis by Thiemann et al. (2008) and consists of approximately 65% ringed seal, 25% bearded seal, and 10% beluga. Polar bears from the Chukchi stock may be harvested for subsistence purposes or killed due to human interactions in both the United States and Russian portions of their range (Belikov 1995, DeBruyn et al. 2010, USFWS 2010b). The harvest of polar bears **(C)** was estimated from values reported in Schliebe and Evans (1995) and Belikov (1995) for a combined U.S. and Russian harvest of 1.61 * 10-5 t km^{-2}.

(k) Polar bear (Southern Beaufort stock)

There are two stocks of polar bears (*Ursus maritimus*) found in Alaska, the Chukchi/Bering stock and the southern Beaufort Sea stock (USFWS 2010b, c). Bears from the southern Beaufort Sea stock regularly occur in the Chukchi Sea and are found as far west as Icy Cape along the Chukchi Sea coast (Amstrup et al. 2005).

(i) Updated parameters

None

(ii) Parameters from W13

The estimated biomass **(B)** for the southern Beaufort stock of polar bears is based on an abundance estimate of 1,526 in the years 2004^{-2}006 (Regehr et al. 2006). This abundance estimate was reduced to represent the time spent in the model area and polar bear movement patterns (Amstrup 1995, Amstrup et al. 2005). The reduced abundance estimate was then multiplied by an average individual body mass (310 kg) derived from Derocher (1991), then divided by the model area to arrive at an estimated density of 1.2 * 10-4 t km^{-2}. The estimated **P/B** of 0.06 for the southern Beaufort stock of polar bears is based on an estimated annual intrinsic growth rate of 6.03% for this stock (Amstrup 1995). The **Q/B** of the southern Beaufort stock of polar bears was calculated exactly the same as for the Chukchi stock; using information on the estimated polar bear basal metabolic rate (Best 1977) and daily metabolic rate (Best 1985), along with the estimated caloric density of their primary prey, ringed seals (*Phoca hispida*) (Stirling and McEwan 1975). When scaled up to an annual rate, this resulted in an estimated Q/B of 4.00. The diet composition **(DC)** used for the southern Beaufort Sea stock of polar bears is exactly the same as the diet assumed for the Chukchi Sea stock of polar bears. We use the diet composition derived through fatty acid analysis by Thiemann et al. (2008) and includes 65% ringed seal, 25% bearded seal, and 10% beluga. Polar bears from the southern Beaufort Sea stock may be harvested for subsistence purposes or killed due to human interactions (DeBruyn et al. 2010, USFWS 2010c). The subsistence harvest (C) of polar bears from this stock was estimated to be 2.26 * 10-6 t km^{-2} from values reported in Schliebe and Evans (1995).

(l) Pacific walrus

The Pacific walrus (*Odobenus rosmarus divergens*) is the largest pinniped in the Alaskan Arctic and is easily recognized by their prominent large tusks. They overwinter in the northern Bering Sea and migrate north into the Chukchi Sea during spring, following the receding ice-edge (Fay 1982).

(i) Updated parameters

Biomass (B): We updated the Pacific walrus biomass estimate based on the most recent abundance estimate of 129,000 for 2006 (Speckman et al. 2011). The new biomass estimate was calculated following the methods of W13, accounting for seasonal occupation of the model area, and spatial distribution outside of the model area. Using body mass estimates from Trites and Pauly (1998), this resulted in a Pacific walrus model biomass density of 0.059 t km^{-2}.

(ii) Parameters from W13

A **P/B** of 0.07 was estimated for Pacific walrus using a variant of Siler's competing risk model (Siler 1979), as modified by Barlow and Boveng (1991). The **Q/B** of Pacific walrus was estimated using the prey caloric density and daily caloric requirements reported in Hunt et al. (2000). Scaling up to an annual rate resulted in a Q/B of 21.66. The primary prey of Pacific walrus throughout their range are bivalves but the exact composition of their diet varies with season and location (Fay 1982, Fay et al. 1986, Dehn et al. 2007, Sheffield and Grebmeier 2009). The estimated diet composition **(DC)** for Pacific walrus in the preliminary model is based on the generalized diet described by Perez (1990) and is dominated by bivalves (69.9%). Prey groups of lesser importance include sea cucumbers, anemones, tunicates, marine worms, benthic amphipods, crabs, snails, shrimp, and octopus. The subsistence harvest **(C)** is based on the average of harvest of 6,713 walrus by both the U.S. and Russia over the years 1960-2007 (USFWS 2010a)

(m) Bearded seal

The Bering-Chukchi seas stock of bearded seals (*Erignathus barbatus*) are found throughout the continental shelf waters (< 200 m depth) of the Pacific Arctic, including the Bering, Chukchi, East Siberian, and Beaufort seas (Cameron et al. 2010). Bearded seals are benthic foragers and the seasonal ice coverage, shallow depths, and large area of the continental shelf in the Pacific Arctic provides a large continuous expanse of habitat suitable for bearded seals (Burns and Frost 1983).

(i) Updated parameters

Food habits (DC): Bearded seals are benthic foragers with flexible diets that typically include brachyuran crabs, shrimp, mollusks, and fish (Kenyon 1962, Johnson et al. 1966, Lowry et al. 1980a, Lowry et al. 1983, Dehn et al. 2007). The bearded seal diet in the preliminary model was derived from food habits data reported in Lowry et al. (1980a) for bearded seals collected in the Chukchi Sea. The dominant prey groups are bivalves (33%), shrimp (25%), and snow crab (19.5%). The bearded seal diet from the preliminary model has been updated here reflecting the move of Bering flounder from the small-mouth flatfish group to the large-mouth flatfish group. Flatfish have been previously noted as prey to bearded seals (Lowry et al. 1980a, Burns and Frost 1983, Lowry et al. 1983, Antonelis et al. 1994), however species-level identifications of flatfish prey are not available. Antonelis et al. (1994) were able to identify *Hippoglossoides* sp. among the stomach contents of bearded seals collected near St. Matthew Island in the eastern Bering Sea. In the preliminary model small-mouth flatfish were the only flatfish included in the bearded seal diet. Lacking guidance on how to accurately attribute the flatfish portion of the bearded seal diet, in this model update we have divided this part of the diet evenly between both flatfish groups (2.1% each).

(ii) Parameters from W13

The biomass **(B)** of bearded seals within the model are was estimated to be 0.03905 t km^{-2} based on an average individual body mass from Trites and Pauly (1998), limited available information on population abundance from Burns (1981a), Cameron et al. (2010), and Ver Hoef et al. (2013), and uncertain information on migration patterns (Burns 1981a, Burns and Frost 1983). The **P/B** estimate of 0.08 was calculated with a generalized model for marine mammal survivorship (Barlow and Boveng 1991). The bearded seal **Q/B** of 12.94 was calculated with estimates of prey caloric density from Hunt et al. (2000) and daily caloric requirements calculated following the methods of Perez et al. (1990). The estimated subsistence harvest **(C)** of 0.00177 t km^{-2} was derived from annual harvest estimates from Allen and Angliss (2011).

(n) Ringed seal

Ringed seals (*Phoca hispida*) are found throughout the Arctic including the Bering, Chukchi, and Beaufort seas in Alaska (Kelly et al. 2010). They are year-round residents in ice-covered Arctic waters and are able to maintain breathing holes in the ice by scratching the ice with claws on their foreflippers (Johnson et al. 1966, Lowry et al. 1983, Kelly 1988).

(i) Updated parameters

None

(ii) Parameters from W13

The biomass estimate **(B)** of 0.05587 t km^{-2} for ringed seals is derived from abundance estimates in Bengtson et al. (2005), and estimates of average individual body mass from Trites and Pauly (1998). The estimated **P/B** of 0.09 for ringed seals was calculated with the generalized model for marine mammal survivorship from Barlow and Boveng (1991). The ringed seal **Q/B** of 19.23 was calculated with estimates of prey caloric density from Hunt et al. (2000) and daily caloric requirements calculated following the methods of Perez et al. (1990). Ringed seals have a diverse diet that includes both fishes and crustaceans. Arctic cod and saffron cod are the dominant fish prey, and shrimp are the dominant crustacean prey of ringed seals (Lowry et al. 1980b, Lowry et al. 1983). The diet composition **(DC)** used here is from Perez (1990), who compiled diet information for ringed seals from multiple studies in the eastern Chukchi, Beaufort, and northern Bering seas. The three most dominant prey types are Arctic cod (45%), saffron cod (33%), and shrimp (10%). The model harvest estimate **(C)** of 0.00212 t km^{-2} is based on estimated annual Alaska harvest from Allen and Angliss (2011).

(o) Spotted seal

In Alaska, the range of spotted seals includes the Chukchi, Bering, and Beaufort seas. They spend the winter in the Bering Sea near the southern edge of the ice pack among smaller ice floes, and migrate north and coastward into the northern Bering, Chukchi, and Beaufort seas during spring and summer when the sea ice breaks up (Burns 1970, Frost et al. 1983, Braham et al. 1984, Lowry et al. 2000, Simpkins et al. 2003).

(i) Updated parameters

Food habits (DC): The diet of spotted seals in the eastern Chukchi Sea and Bering Sea is dominated by fish, including Arctic cod, saffron cod, and pelagic forage fish (Lowry et al. 1983, Bukhtiyarov et al. 1984, Dehn et al. 2007). The diet composition used in W13 was based on the spotted seal diet composition presented in Perez (1990), which was compiled from multiple studies conducted throughout the species range in the Bering and Chukchi seas. The primary prey items in the spotted seal diet are pelagic forage fish (46%), Arctic cod (22%), large-mouth sculpins (12%), and saffron cod (9%). We have updated the spotted seal diet composition to reflect the move of Bering flounder from the small-mouth flatfish group to large-mouth flatfish. Previous diet studies have indicated flatfish are prey for spotted seals (Lowry et al. 1983, Bukhtiyarov et al. 1984, Dehn et al. 2007), however species-level identifications of flatfish prey are unavailable. In the absence of species-level guidance to properly attribute the flatfish portion of their diet, we have divided this part of their diet evenly between the two flatfish functional groups (0.85% each).

(ii) Parameters from W13

The spotted seal biomass estimate **(B)** of 0.00579 t km^{-2} was based on information from stock assessments (Allen and Angliss 2013), multiple studies on population abundance (Burns 1986, Reeves et al. 1992, Boveng et al. 2009, Ver Hoef et al. 2013), and information on migration patterns (Frost et al. 1993). The estimated average individual body mass was derived from information in Trites and Pauly (1998). The spotted seal **P/B** of 0.07 was estimated a general model for marine mammal survivorship (Barlow and Boveng 1991). The spotted seal **Q/B** of 18.70 was calculated with estimates of prey caloric density from Hunt et al. (2000) and daily caloric requirements calculated following the methods of Perez et al. (1990).The modeled spotted seal subsistence harvest **(C)** of 1.52*10-4 t km^{-2} was based on an estimated annual harvest of 5,265 seals (Allen and Angliss 2011).

4.4 Seabirds

(p) All seabirds

(i) Biomass (B)

We calculated biomass estimates for 20 species of seabirds known to occupy the eastern Chukchi Sea (plus unidentified murres [*Uria* sp.]). The biomass estimates for Procellarids and Scolopacids are based on population estimates from Divoky (1987) and the biomass estimates of Cormorants, Larids, Alcids piscivorous, and Alcids planktivorous are based on colony counts from the Seabird Information Network (2011) (Table 5).

(ii) Production (P/B)

We calculated estimates of P/B for all seabird functional groups (Table 6) based on adult survival rates (Schreiber and Burger 2001). The functional group P/B's are average P/B's weighted by the biomass of the functional group's species.

(iii) Consumption (Q/B)

Estimates of Q/B were calculated for all seabird functional groups based on average individual body mass, mean energy density of prey, and estimated daily energy requirements (Table 7).The Q/B of a seabird functional group is an average of the constituent species Q/B’s weighted by biomass.

Table 5. Biomass estimates for seabird functional groups. *Colony counts are from the Seabird Information Network (2011), and †Population estimates are from Divoky (1987). Estimates of mean individual body mass are from Hunt et al. (2000). $^{\Omega}$Density is calculated as either the colony count or population estimate multiplied by 1/3 to account for seasonal occupation, then divided by the total model area, 192,054 km^2.

Functional Group	Common name	Species	*colony count	†pop. Est.	$^{\Omega}$density (birds km^{-2})	mean body mass (t)	B (t km^{-2})	Group B (t km^{-2})
Procellarids								0.001927375
	Northern fulmar	*Fulmaris glacialis*		45,000	0.078103	0.000544	4.24881E-05	
	Short-tailed shearwater	*Puffinus tenuirostris*		2,000,000	3.471246	0.000543	0.001884887	
Cormorants								
	Pelagic cormorant	*Phalacrocorax pelagicus*	453		0.000786	0.001868	1.46869E-06	1.46869E-06
Scolopacids				1,000,000	1.735623	0.00004475	7.76691E-05	7.76691E-05
	Red-necked phalarope	*Phalaropus lobatus*				0.0000338		
	Red phalarope	*P. fulicarius*				0.0000557		
Larids								9.31276E-05
	Mew gull	*Larus canus*	20		0.000035	0.0004035	1.40065E-08	
	Glaucous gull	*L. hyperboreus*	3,534		0.006134	0.0014125	8.66384E-06	
	Black-legged kittiwake	*Rissa tridactyla*	119,323		0.207100	0.000407	8.42896E-05	
	Aleutian Tern	*Sterna aleutica*	393		0.000682	0.00012	8.1852E-08	
	Arctic Tern	*S. paradisaea*	410		0.000712	0.00011	7.82766E-08	
Alcids piscivorous								0.001155027
	Common murre	*Uria aalge*	82,470		0.143137	0.0009925	0.000142063	
	Thick-billed murre	*U. lomvia*	152,330		0.264387	0.000964	0.000254869	
	Unidentified murre	*Uria* spp.	435,305		0.755525	0.0009742	0.000736033	
	Tufted puffin	*Fratercula cirrhata*	508		0.000882	0.000779	6.86842E-07	
	Horned puffin	*F. corniculata*	19,670		0.034140	0.000619	2.11325E-05	
	Pigeon guillemot	*Cepphus columba*	109		0.000189	0.000487	9.21321E-08	
	Black guillemot	*C. grylle*	225		0.000391	0.0003832	1.49645E-07	
Alcids planktivorous								0.000139496
	Crested auklet	*Aethia cristatella*	219,000		0.380101	0.000264	0.000100347	
	Parakeet auklet	*A. psittacula*	20,000		0.034712	0.000258	8.95581E-06	
	Least auklet	*A. pusilla*	207,000		0.359274	0.000084	3.0179E-05	
	Dovekie	*Alle alle*	50		0.000087	0.000163	1.41453E-08	

Table 6. Seabird functional group P/B estimates. Species-specific annual survival rates and order level adult survival rates are from Schreiber and Burger (2001). The functional group P/B is an average P/B weighted by the estimated biomass of the constituent species within the model area. Where annual survival rates were given as a range, we used the midpoint of that range in calculations.

Functional group	Common name	Species	Annual survival rate	Order level adult survival rate	S	P/B=-ln(S)	Group P/B
Procellarids							0.0667
	Northern fulmar	*Fulmaris glacialis*	0.94-0.97		0.955	0.0460	
	Short-tailed shearwater	*Puffinus tenuirostris*	0.93-0.94		0.935	0.0513	
Cormorants							0.1625
	Pelagic cormorant	*Phalacrocorax pelagicus*		0.85	0.85	0.1625	
Scolopacids							0.1625
	Red-necked phalarope	*Phalaropus lobatus*		0.85	0.85	0.1625	
	Red phalarope	*P. fulicarius*		0.85	0.85	0.1625	
Larids							0.1057
	Mew gull	*Larus canus*		0.85	0.85	0.1625	
	Glaucous gull	*L. hyperboreus*		0.85	0.85	0.1625	
	Black-legged kittiwake	*Rissa tridactyla*	0.88-0.93		0.905	0.0998	
	Aleutian Tern	*Sterna aleutica*		0.85	0.85	0.1625	
	Arctic Tern	*S. paradisaea*	0.90		0.90	0.1054	
Alcids piscivorous							0.1041
	Common murre	*Uria aalge*	0.87-0.95		0.91	0.0943	
	Thick-billed murre	*U. lomvia*	0.89-0.9		0.895	0.1109	
	Unidentified murre	*Uria* spp.			†0.90037	0.1050	
	Tufted puffin	*Fratercula cirrhata*	*0.942		0.942	0.0598	
	Horned puffin	*F. corniculata*	*0.942		0.942	0.0598	
	Pigeon guillemot	*Cepphus columba*	0.80		0.80	0.2231	
	Black guillemot	*C. grylle*	0.87		0.87	0.1393	
Alcids planktivorous							0.1404
	Crested auklet	*Aethia cristatella*	0.89		0.89	0.1165	
	Parakeet auklet	*A. psittacula*		0.85	0.85	0.1625	
	Least auklet	*A. pusilla*	0.808		0.808	0.2132	
	Dovekie	*Alle alle*		0.85	0.85	0.1625	

†Average survival rate of thick-billed and common murres, weighted by biomass.

* Annual survival rate for Atlantic puffin (*Fratercula arctica,* Schreiber and Burger 2002)

Table 7. Q/B values for seabird functional groups. Mean body mass and daily energy needs are taken from Hunt et al. (2000). Mean prey energy density calculated with approximate energy densities reported in Table 3, weighted by diet composition (see diet matrix or functional group accounts for diet composition). Functional group Q/B is the average Q/B of the constituent species, weighted by their estimated biomass in the model area.

Functional group	Common name	Species	Mean body mass (kg)	Daily energy needs (kj)	Mean prey energy density (kj/g)	Q/B	Functional group Q/B
Procellarids							187.928
	Northern fulmar	*Fulmaris glacialis*	0.544	1116.299	3.5	213.996	
	Short-tailed shearwater	*Puffinus tenuirostris*	0.543	1114.806	4	187.341	
Cormorants							142.618
	Pelagic cormorant	*Phalacrocorax pelagicus*	1.868	2737.102	3.75	142.618	
Scolopacids							374.313
	Red-necked phalarope	*Phalaropus lobatus*	0.0338	148.089	4	399.796	
	Red phalarope	*P. fulicarius*	0.0557	212.930	4	348.830	
Larids							205.674
	Mew gull	*Larus canus*	0.4035	898.356	4.155	195.560	
	Glaucous gull	*L. hyperboreus*	1.4125	2233.786	4.5	128.272	
	Black-legged kittiwake	*Rissa tridactyla*	0.407	904.014	3.798	213.437	
	Aleutian Tern	*Sterna aleutica*	0.12	372.019	4.151	272.629	
	Arctic Tern	*S. paradisaea*	0.11	349.215	3.36	344.868	
Alcids piscivorous							178.383
	Common murre	*Uria aalge*	0.9925	1728.316	3.686	172.433	
	Thick-billed murre	*U. lomvia*	0.964	1692.092	3.526	181.721	
	Unidentified murre	*Uria* spp.	*0.974	1705.090	3.583	178.295	
	Tufted puffin	*Fratercula cirrhata*	0.779	1449.265	4	169.763	
	Horned puffin	*F. corniculata*	0.619	1226.194	4	180.760	
	Pigeon guillemot	*Cepphus columba*	0.487	1029.991	3.863	199.859	
	Black guillemot	*C. grylle*	†0.3832	865.267	3.07	268.460	
Alcids planktivorous							247.507
	Crested auklet	*Aethia cristatella*	0.264	659.942	4	228.105	
	Parakeet auklet	*A. psittacula*	0.258	649.004	3.7	248.153	
	Least auklet	*A. pusilla*	0.084	287.046	4	311.820	
	Dovekie	*Alle alle*	0.163	464.794	4	260.199	

†Mean body mass calculated from values reported by Berzins et al. (2009).

*Mean individual body mass calculated as average of values reported for common murre and thick-billed murre, weighted by estimated biomass within the model area.

(q) Procellarids

The Procellarid functional group is represented by two species, the northern fulmar (*Fulmaris glaciallis*) and the short-tailed shearwater (*Puffinus tenuirostris*), which are the most abundant Procellarids found in the eastern Chukchi Sea during the ice-free season (Divoky 1987, Gall et al. 2013).

(i) Updated parameters

Biomass (B): Density estimates for Procellarids were calculated from the coarse population abundance estimates reported by Divoky (1987). Divoky (1987) estimated there to be 45,000 northern fulmars and 2,000,000 short-tailed shearwaters at their peak abundance during the ice-free season. The abundance estimates were used in combination with estimates of average individual body mass from Hunt et al. (2000) to arrive at a group biomass of 0.0019 t km^{-2} (Table 5).

Production (P/B): The Procellarid P/B was calculated from species-specific annual survival rates (Table 6). The range of annual survival rate for northern fulmars is 0.94-0.97, and for short-tailed shearwaters it is 0.93-0.94. Using the midpoint of these survival rate ranges, we calculated a weighted (by biomass) group P/B of 0.067.

Consumption (Q/B): The Q/B for Procellarids was calculated assuming a mean body mass of 0.544 kg for northern fulmars and 0.543 kg for short-tailed shearwaters (Hunt et al. 2000). The Q/B for northern fulmars is 214 and 187 for short-tailed shearwaters. The functional group Q/B of 187.928 is an average Q/B weighted by the estimated biomass of the two species.

Food habits (DC): Northern fulmars feed on prey at the water’s surface and are capable of shallow dives, up to 3 m depth (Hobson and Welch 1992). In the eastern Bering Sea they are found in close association with commercial fishing vessels and are known to feed on offal (Hunt et al. 1981). Their diet in the eastern Bering Sea includes walleye pollock (55%, *Gadus chalcogrammus*), cephalopods (25%), other fish (10%), amphipods (5%), and euphausiids (5%); though the amount of walleye pollock that can be attributed to fishery discards as opposed to wild caught prey is difficult to interpret due to the fulmars known affinity for fishing vessels (Hunt et al. 1981). Phillips et al. (1999) reviewed the diet of northern fulmars at several high latitude locations and found their diet to generally consist of juvenile gadids, pelagic forage fish, and pelagic zooplankton. Birds from more southerly parts of their range had greater proportions of their diet attributed to fishery discards (Phillips et al. 1999). As there are no large scale commercial fisheries in the eastern Chukchi Sea, we assume there is no offal consumption by northern fulmars within our study area. In the Frans Josef Land archipelago (Russian Arctic), the dominant prey of northern fulmars by % weight were Arctic cod (50.7%) and *Myoxocephalus scorpius* (34.9%) (Weslawski et al. 1994). In the Canadian High Arctic, northern fulmars have been found to feed on fish (primarily Arctic cod), copepods, amphipods, other zooplankton, cephalopods, and polychaetes (Bradstreet and Cross 1982, Byers et al. 2010, Mallory et al. 2010). In pelagic waters of the marginal ice zone in eastern Svalbard, the most frequently encountered prey in northern fulmar stomachs were nereid polychaetes, squids, and Arctic cod (Mehlum and Gabrielsen 1993). In the northern Bering Sea, northern fulmars have been observed feeding in association with the mud plumes of benthic foraging gray whales, where they primarily consumed benthic amphipods (Obst and Hunt 1990, Grebmeier and Harrison 1992).

Additionally, there are observations of northern fulmars opportunistically scavenging on marine mammal remains from subsistence hunts (Bradstreet 1982, Haney 1988, Hobson and Welch 1992, Mallory et al. 2010) but this does not appear to be an important part of the diet. Lacking region specific data, and considering the available data, we are attributing 50% of the diet to Arctic cod, 20% to copepods, 20% to other zooplankton, and 10% to amphipods.

Short-tailed shearwaters forage for prey by seizing the prey at the water's surface, plunging or diving for prey underwater, hydroplaning, or opportunistically scavenging on floating remains (Ogi et al. 1980). Throughout the Bering Sea and north Pacific, their diet generally contains euphausiids, hyperiid amphipods, larval and juvenile fish, squid, and pteropods (Ogi et al. 1980, Hunt et al. 1981). In the eastern Bering Sea the most common fish prey species are walleye pollock, capelin, and Pacific sand lance (Ogi et al. 1980, Hunt et al. 1981, Hunt et al. 2002). Ogi et al. (1980) separately examined the diet of short-tailed shearwaters in the continental shelf area of the northeastern Bering Sea, from Cape Navalin (Russia) to the Pribilof Islands (USA). There they found the hyperiid amphipod *Themisto libellula* to be the dominant prey by frequency of occurrence (69.6%) and by weight, accounting for 69.1% of the total stomach contents by weight. We are unaware of any short-tailed shearwater diet studies specific to the Chukchi Sea, and in their absence we use a generalized diet adapted from the diet described by Ogi et al. (1980) for short-tailed shearwaters occupying the northeastern Bering Sea. There the fish prey was identified as walleye pollock and capelin. To adapt this diet to the Chukchi Sea, we replace the portion allocated to walleye pollock with Arctic cod. Walleye pollock is the dominant schooling, bentho-pelagic gadid in the eastern Bering Sea, while Arctic cod fulfills a similar role in the eastern Chukchi Sea. The final diet for short-tailed shearwaters consists of 88% other zooplankton (primarily hyperiid amphipods and euphausiids), 6% pelagic forage fish, and 6% Arctic cod.

The functional group diet composition is an average diet weighted by the biomass of the constituent species. The primary prey of the Procellarid group is other zooplankton (86.5%), followed by Arctic cod (7%), pelagic forage fish (5.9%), copepods (0.4%), and benthic amphipods (0.2%).

(r) Cormorants

Cormorants are represented by a single species, the pelagic cormorant (*Phalacrocorax pelagicus*), in colony counts from the eastern Chukchi Sea (Swartz 1966, Seabird Information Network 2011).

(i) Updated parameters

Biomass (B): The biomass of pelagic cormorants is estimated from colony count data (Seabird Information Network 2011) and a mean individual body mass of 1.868 kg (Hunt et al. 2000). The functional group biomass is 1.469 *10-6 t km^{-2}.

Production (P/B): In lieu of a species-specific annual survival rate, we used an Order level (Charadriiformes) estimated adult survival rate of 0.85 to calculate a group P/B of 0.1625.

Consumption (Q/B): The cormorant Q/B of 142.618 was calculated assuming a mean individual body mass of 1.868 kg and a daily energy requirement of 2737.102 kj (Hunt et al. 2000).

Food habits (DC): Pelagic cormorants forage by diving for prey, using their feet for propulsion under water (Hobson 1997). The diet of pelagic cormorants collected from the Pribilof Islands was dominated by fishes (74%), primarily sculpins (*Myoxocephalus* spp. and *Megalocottus laticeps*) (Preble and McAtee 1923). The remainder of the diet consisted of crustaceans, primarily shrimp (*Spirontocaris* spp.) and anomuran crabs. Ainley and Sanger (1979) summarized diet records of pelagic cormorants from multiple diet studies conducted in the northeast Pacific and Bering Sea, and found sculpins (Cottidae) and decapods to be major prey items throughout their range. Other prey items from Alaska included herring (*Clupea* sp.), cods (Gadidae), greenlings (Hexagrammidae), poachers (Agonidae), gunnels (Pholidae), Pacific sand lance (*Ammodytes hexapterus*), and flatfish (Pleuronectidae). In the eastern Chukchi Sea, Swartz (1966), examined two pelagic cormorant stomachs and found fish (Arctic cod [*Boreogadus saida*], Pacific sand lance, and Stichaeidae) and shrimp (Pandalidae and Crangonidae) to be the primary prey. Lacking a more detailed region-specific and species-specific diet description, we use the diet provided by Swartz (1966) as the basis for our pelagic cormorant diet. We divide the diet evenly (25% each) between Arctic cod, pelagic forage fish (Pacific sand lance), miscellaneous shallow fish (Stichaeidae), and shrimp.

(s) Scolopacids

Scolopacidae is a family of shorebirds that includes sandpipers, snipes, dowitchers, and phalaropes, among others. We focus our interest on two species of phalarope, the red phalarope (*Phalaropus fulicarius*) and red-necked phalarope (*P. lobatus*). These two species spend only the short breeding season on land, then spend the rest of the year (9 months or more) living at sea, and eating marine prey (Höhn 1969, Rubega et al. 2000, Schreiber and Burger 2001, Tracy et al. 2002). The red and red-necked phalaropes are the only shorebirds to spend such a significant portion of their lives at sea (Schreiber and Burger 2001). The two species are difficult to discern during at-sea observations and are frequently referred to collectively in the literature as phalaropes or *Phalaropus* sp. (e.g., Gall et al. 2013). Phalaropes are among the most abundant seabirds observed in the pelagic environment of the Chukchi Sea during the ice-free season (Divoky 1987, Piatt and Springer 2003, Gall et al. 2013).

(i) Updated parameters

Biomass (B): The biomass estimate for Scolopacids was calculated from the populations estimates in Divoky (1987). At peak abundance during the ice free season, Divoky (1987) estimated there to be about 1,000,000 phaloropes present. Because the abundance estimate is not species-specific we used a mean individual body mass of 44.75 g, calculated from species-specific body masses provided in Hunt et al. (2000). The estimated biomass of the Scolopacid group is 7.77*10-5 t km^{-2} (Table 5).

Production (P/B): Species-specific survival rates were not available for this group and instead we use an Order level (Charadriiformes) estimated adult survival rate of 0.85 (Schreiber and Burger 2001). The functional group P/B is 0.1625.

Consumption (Q/B): Q/B was estimated for the red-necked and the Red phalarope assuming mean individual body masses of 33.8 g and 55.7 g, respectively. The functional group Q/B of 374.313 is an average of the two species-specific Q/Bs.

Food habits (DC): In the open ocean, phalaropes feed in surface waters where oceanographic conditions concentrate their prey within their reach at the ocean surface. They feed by pecking their bill into the water and use the surface tension of water to deliver the prey into their mouth (Rubega and Obst 1993). They predominantly feed on copepods, euphausiids, fish eggs, other meroplankton, and other crustacean zooplankton (Briggs et al. 1984, Divoky 1984, Mercier and Gaskin 1985, Brown and Gaskin 1988). They have also been observed to feed on benthic amphipods in the mud plumes brought to the surface by benthic foraging gray whales in the northern Bering Sea (Obst and Hunt 1990, Grebmeier and Harrison 1992). The density of phalaropes has been positively correlated with whale density in the northern Bering Sea, indicating association with whales may be an important food source for phalaropes in this region (Obst and Hunt 1990). Divoky (1984) presented diet data on red phalaropes collected in the pelagic and near shore Beaufort Sea, Alaska and found the stomachs to most frequently contain amphipods, copepods, and other zooplankton. Lacking diet information specific to the Chukchi Sea or a more general region-wide diet description, we attribute 10% of the diet to benthic amphipods and evenly divide the rest of the diet among copepods (45%) and other zooplankton (45%).

(t) Larids

The Larids functional group consists of species from the family Laridae. In the eastern Chukchi Sea this group is dominated numerically and by weight by the black-legged kittiwake (*Rissa tridactyla*), followed by the glaucous gull (*Larus hyperboreus*). Also present in colony counts, but in much lower abundance are Arctic terns (*Sterna paradisaea*), Aleutian terns (*S. aleutica*), and mew gulls (*L. canus*). Other species known to occur in the eastern Chukchi Sea include ivory gull (*Pagophila eburnean*), sabine's gull (*Xema sabini*), ross's gull (*Rhodostethia rosea*), and herring gull (*L. argentatus*) (Swartz 1966, Divoky 1987, Gall et al. 2013).

(i) Updated parameters

Biomass (B): The estimated biomass of the Larid group is calculated with colony counts (Seabird Information Network 2011) and species-specific estimates of mean individual body mass (Hunt et al. 2000). The estimated functional group biomass is 9.313 *10 -5 t km^{-2} (Table 5).

Production (P/B): Species-specific annual survival rates were available for black-legged kittiwake (0.88-0.93) and Arctic terns (0.90). An order level (Charadriiformes) adult survival rate of 0.85 was assumed for mew gull, glaucous gull, and Aleutian tern. The functional group P/B of 0.1057 is a mean P/B weighted by the estimated biomass of the constituent species.

Consumption (Q/B): The Q/B of Larids (Table 7) is calculated assuming species-specific mean individual body masses and daily energy needs taken from Hunt et al. (2000). The functional group Q/B of 205.67 is an average Q/B weighted by the estimated biomass of the constituent species.

Food habits (DC): Glaucous gulls are generalist feeders whose diet includes fish, zooplankton, other crustaceans, birds, mammals, and insects (Weiser and Gilchrist 2012). In the Beaufort Sea glaucous gulls consumed Arctic cod, other seabirds, and amphipods (Divoky 1984). The seabird prey was identified as phalaropes and accounted for 75% of the total prey weight (Divoky 1984). In the eastern Chukchi Sea, the diet of glaucous gulls collected near seabird colonies included Arctic cod, sand lance, *Myoxocephalus quadricornis*, murres, kittiwakes, anemones, crabs, unidentified crustaceans, insects, and mammals (Swartz 1966). The carcasses of birds that have died from rockfalls and the eggs of other bird species, may form an important part of the glaucous gull diet in the eastern Chukchi Sea (Swartz 1966). The remains of murre chicks occurred in 50% of the glaucous gull stomachs examined (excl. nestlings) (Swartz 1966). The diet of glaucous gulls nesting on the coast of the eastern Bering Sea most frequently included fish (primarily saffron cod [*Eleginus gracilis*]), birds (mostly eggs), and marine invertebrates (Strang 1982). Bird remains and bird eggs were also frequently observed among the prey remains found in regurgitated pellets collected from glaucous gull colonies in the Beaufort Sea (Barry and Barry 1990). The remains of juvenile birds were found among the stomach contents of five glaucous gulls collected during summer from the Frans Josef Land Archipelago in the Russian Arctic (Weslawski et al. 1994). The juvenile bird prey accounted for more than 91% of the total prey weight and included thick-billed murres, kittiwakes, and dovekies (Weslawski et al. 1994). The large proportion of bird prey in the diet of glaucous gulls may overestimate the proportion of bird prey in the diet of glaucous gulls found in the pelagic environment, as most of the existing diet studies were either shore-based or conducted within the vicinity of seabird colonies where bird prey would be in greater abundance (Weiser and Gilchrist 2012). There is very limited information available describing the diet of glaucous gulls while at sea (Weiser and Gilchrist 2012) but fish appear to be a principal part of their diet throughout their range. The diet of glaucous gulls is regularly reported to include bird remains, including eggs, chicks, juveniles, and adults (e.g., Swartz 1966); though predation on uninjured adults is an uncommon occurrence and are most likely scavenged (Mallory et al. 2009, Weiser and Gilchrist 2012). More frequently glaucous gulls are consuming eggs, chicks, injured birds, or birds already dead from rockfalls or other circumstances. Eggs are not modeled as separate functional groups and represent losses from seabirds to respiration, or in other words a loss to detritus. Dead birds or injured and soon-to-be dead birds also represent a flow to detritus. Glaucous gulls preying on these sources are effectively feeding off of the detrital pool as opposed to depredating other seabird functional groups directly. In the eastern Chukchi Sea, murres were the principle seabird prey of glaucous gulls at seabird colonies (Swartz 1966). Lacking detailed information on the glaucous gull diet we attribute 5% to direct predation on murres (Alcids piscivorous) and 20% on detritus according to the detrital fate of seabirds (6% pelagic detritus, 14% benthic detritus). In lieu of a quantitative description of the pelagic diet of glaucous gulls, we divide the remaining 75% of the diet evenly (25% each) amongst Arctic cod, saffron cod, and pelagic forage fish (sand lance).

The diet of mew gulls varies with location and season (Moskoff and Bevier 2002) and is not described in the eastern Chukchi Sea. In other parts of their range they consume a variety of prey including fish, crabs, mollusks, polychaetes, and zooplankton, also terrestrial foods including birds (swallows and sparrows), mammals, insects, garbage, and sewage (Moskoff and Bevier 2002, Kubetzki and Garthe 2003). We use a general diet for mew gulls adapted from the diet reported by Sanger (1986) for mew gulls collected in the Gulf of Alaska and adjacent regions. Amphipods (58.1%), shrimp (23%), pelagic forage fish (16.5%), bivalves (1%), Arctic cod (1%), polychaetes (0.3%), and snails (0.1%) comprise the final diet.

Arctic terns are opportunistic foragers that primarily feed on fish, particularly pelagic forage fish and gadids, but also prey on invertebrates including amphipods, decapods, euphausiids, and polychaetes (Hatch 2002). The diet of Arctic terns collected offshore in the Beaufort Sea were dominated by weight by Arctic cod (64%), followed by euphausiids (35%) and amphipods (1%) (Divoky 1984). Near shore they fed upon (by % weight) euphausiids (23%), amphipods (31%), Arctic cod (20%), mysids (13%), and Pacific sand lance (12%). The diet of Arctic terns collected from Frans Josef Land Archipelago were dominated by amphipods (74.9% by weight), followed by unidentified fish remains (20.9%), and polychaetes (4.2%). Lacking a diet specific to the eastern Chukchi Sea, we use the diet of Arctic terns collected from offshore waters in the Beaufort Sea (Divoky 1984) as a proxy for their diet in the eastern Chukchi Sea. The final diet is 64% Arctic cod, 35% other zooplankton, and 1% amphipods.

The primary prey items of Aleutian terns are fish, including Pacific sand lance, capelin, and gadids, they also prey on invertebrates, including decapods, euphausiids, isopods, polychaetes, and insects (North 1997). During spring and summer in the southeastern Bering Sea, Aleutian terns primarily preyed upon fish (75-98% by weight) and euphausiids (25%) (Troy and Johnson 1989). Near Kodiak Island in the Gulf of Alaska, the diet of adult Aleutian terns contained (% by weight) euphausiids (54.7%), isopods (11.4%), arthropods (1.8%), insects (1.4%), Pacific sand lance (12.2%), capelin (7.3%), Gadidae (5.5%), and unidentified fish (5.6%) (Sanger 1986). We are unaware of any Aleutian tern diet records from the eastern Chukchi Sea and in their place we use a general diet adapted from the diet reported by Sanger (1986). The final diet consists of other zooplankton (58%), pelagic forage fish (21%), miscellaneous crustaceans (14%), Arctic cod (6%), and polychaetes (0.1%).

The Larid group diet is an average diet weighted by the estimated biomass of the constituent species within the model area. The primary prey items for Larids are Arctic cod (50.1%) and pelagic forage fish (33.3%). Prey groups of lesser importance include benthic amphipods (3.5%), other zooplankton (2.6%), polychaetes (2.4%), saffron cod (2.3%), detritus (1.9%), and shrimps (1.1%). Prey groups that individually represent less than 1% of the final Larid diet include snails, other crabs, Alcids piscivorous, miscellaneous shallow fish, snailfish, variegated snailfish, large-mouth sculpins, other sculpins, and miscellaneous crustaceans.

(u) Alcids-piscivorous

Six species from the family Alcidae, whose diets are dominated (>50%) by fish prey, comprise the alcids-piscivorous group. The group contains two species of murre (*Uria* spp.), two species of puffin (*Fratercula* spp.), and two species of guillemot (*Cepphus* spp.).

(i) Updated parameters

Biomass (B): Abundance estimates for all six species are derived from colony counts contained in the North Pacific Seabird Colony Database (Seabird Information Network 2011). The two species of murre, the common murre (*Uria aalge*) and thick-billed murre (*U. lomvia*), are the numerically dominant members of this group and also make the greatest contribution to group biomass. Additionally, murres are augmented by colony counts of unidentified murres. The total count for all colonies, for each species is multiplied by a species-specific mean body mass (Hunt et al. 2000) to arrive at a biomass estimate.

This estimate is then divided by the model area to calculate a biomass density estimate (t km^{-2}). This is reduced further by multiplying by one-third to account for the seasonal occupation (~4 months) of the model area. Alcids piscivorous have a B of 0.0012 t km^{-2}.

Production (P/B): The Alcids piscivorous P/B is calculated from species-specific annual survival rates (Schreiber and Burger 2001). When survival rate is given as a range the midpoint is used. Species-specific estimates were not available for the tufted puffin or horned puffin. So, in their place we use an annual survival rate for the Atlantic puffin (*Fratercula arctica*). For unidentified murres we used the average of the thick-billed murre and common murre survival rates, weighted by their estimated biomass. The functional group P/B of 0.1041 is a weighted average P/B (by biomass).

Consumption (Q/B): The Alcids piscivorous Q/B of 178.383 is an average of the constituent species Q/B's, weighted by biomass.

Food habits (DC): Common and thick-billed murres forage in the pelagic environment by diving for prey. Swartz (1966) examined stomachs from both species at nesting colonies in the Cape Thompson region and found fish to be the dominant component of the diet for both species. Arctic cod (*Boreogadus saida*) was the most frequently occurring prey, followed by Pacific sand lance (*Ammodytes hexapterus*). Other frequently encountered prey included sculpins, Stichaeids, hermit crabs (thick-billed murres only), snails (thick-billed murres only), polychaetes, and shrimps. Springer et al. (1984) examined the diet of common and thick-billed murres at two breeding colonies in the eastern Chukchi Sea at Cape Lisburne and Cape Thompson, between 1976 and 1980. For both species at both locations, the dominant prey items by weight were cods (Arctic cod and saffron cod [*Eleginus gracilis*]) followed by pelagic forage fish (sand lance and capelin [*Mallotus villosus*]). In all years of the study, Arctic cod represented the majority of the gadids taken by murres in mid to early summer, while saffron cod were the dominant gadid prey in late summer (Springer et al. 1984). Other fish prey of lesser importance included sculpins and flatfish. Invertebrate prey were also consumed by both species but figured more prominently in the diet of thick-billed murres. Invertebrate prey items included shrimps, amphipods, euphausiids, polychaetes, hermit crabs, and snails. The diet of common and thick-billed murres nesting at Cape Thompson were examined again in the summer of 1988 by Fadely et al. (1989). Fish were again the dominant prey items, with Arctic cod accounting for 94% of the prey by weight for both species. Of lesser importance were saffron cod, sand lance, and sculpins. Invertebrate prey were only found in the stomachs of thick-billed murres and collectively accounted for less than 1% of stomach contents by weight. The invertebrate prey included shrimps, amphipods, and gastropods. Hunt et al. (1981) summarized the prey of common and thick-billed murres breeding on the Pribilof Islands in the eastern Bering Sea and also found fish to be the most important part of the murre diet. Both species fed heavily on the dominant gadid of the region, walleye pollock (*Gadus chalcogrammus*).

The murre diet used here is derived from the values reported in Springer et al. (1984). The percent composition of the diet by weight reported for each study location in tables 2 &3 of Springer et al. (1984) were averaged for each species, weighted by the sample size at each location (total stomachs examined). The taxonomic categories of prey items reported by Springer et al. (1984) did not always taxonomically match the functional groups used in our model. Some prey groups needed to be divided to match more taxonomically narrow groups within our model, while others needed to be combined to fit more general groupings (Table 3). The prey categories of cods, sculpins, and other invertebrates had to be divided amongst existing functional groups in our Ecopath model. The portion of the diet Springer et al. (1984) allocated to "cods" was divided up evenly amongst Arctic cod and saffron cod; the only two gadids reported to occur in the murre diet in their study region (Springer et al. 1984, Fadely et al. 1989). Similarly, the "sculpin" portion of the diet was also divided evenly among our two sculpin functional groups, large-mouth sculpins and other sculpins. The "other invertebrate" category included snails and hermit crabs and was divided evenly between the snail and other crabs functional groups. Prey categories reported by Springer et al. (1984) that needed to be combined included two forage fish species, Pacific sand lance and capelin. The percent compositions for these two species were combined to fit within the pelagic forage fish functional group. The euphausiids and mysids portion of the diets were also combined to fit within the "other zooplankton" functional group. The dominant prey items in the final diets for both species are Arctic cod, saffron cod, pelagic forage fish, large-mouth sculpins, and other sculpins.

Two species of puffin are found in the eastern Chukchi Sea, the horned puffin (*Fratercula corniculata*) and tufted puffin (*F. cirrhata*). Horned puffins are the more prevalent of the two species, accounting for more than 97% of the total puffins in colony counts of the eastern Chukchi Sea region (Seabird Information Network 2011). Both species of puffin can be found in the pelagic environment, where they forage for their prey by diving. Hunt et al. (2000) attributed ~80% of the diet of horned and tufted puffins, found in the vicinity of the Pribilof Islands, to fish prey. The major prey item for the horned puffin was whitespotted greenling (*Hexagrammos stelleri*), and for the tufted puffin the major prey was walleye pollock. Both species of puffin also preyed on pelagic forage fish (Pacific sand lance and capelin), and the horned puffin additionally preyed upon the Pacific sandfish (*Trichodon trichodon*). Both species of puffins also consumed invertebrate prey including pelagic amphipods (*Parathemisto libellula*) , polychaete worms (Nereidae), and cephalopods (Hunt et al. 1981). The stomachs of horned puffins collected at Cape Thompson in the eastern Chukchi Sea were found to contain Arctic cod, capelin, Pacific sand lance, sculpins (*Triglops* sp.), polychaetes, sponge (Porifera) and unidentified crustaceans (Swartz 1966). Because horned puffins are the numerically dominant species of puffin in the eastern Chukchi Sea, their diet as described by Hunt et al. (1981) and Hunt et al. (2000) is used here to describe the feeding habits of both species of puffin. The prey categories of Hunt et al. (2000) are broader than the functional groups used in this model and not all prey taxa are listed in Hunt et al. (1981). To accommodate this difference, the 80% of the diet attributed to fish by Hunt et al. (2000) is divided evenly (40% each) amongst the primary fish prey categories of pelagic forage fish and Arctic cod. Pelagic amphipods (other zooplankton) account for 11% of the diet and polychaetes 4%. The remaining 5% percent of prey are listed as "unknown" in Hunt et al. (2000). Because we are unable to attribute this small amount to any one prey group, we exclude it and renormalize the diet to one. The final puffin diet is pelagic forage fish (42.1%), Arctic cod (42.1%), polychaetes (11.6%), and other zooplankton (4.2%).

Black guillemots forage for their prey by diving into the water and using their wings to swim under water (Butler and Buckley 2002). They primarily prey upon fish and may also consume benthic and sympagic invertebrates (Butler and Buckley 2002). Black guillemot stomachs collected from ice-covered waters near Svalbard contained fish, gammarid amphipods, and mysids (Lønne and Gabrielsen 1992). Of the fish prey, 72% of the otoliths found in the stomachs were identified as Arctic cod (Lønne and Gabrielsen 1992). Similarly, black guillemot stomachs collected from the Franz Josef Land Archipelago were dominated by Arctic cod, accounting for 88.1% of total stomach contents by weight (Weslawski et al. 1994). Other prey of lesser importance (by % weight) included shrimp (4.7%), *Myoxocephalus scorpius* (2.9%), unidentified fish (2.9%), and amphipods (1.3%). In pelagic ice-covered areas near Svalbard, the diet of black guillemots was dominated by Arctic cod which occurred in 71.4% of stomachs examined (Mehlum and Gabrielsen 1993). In coastal waters their diet was more diverse and included polychaetes, decapods, amphipods, gastropods, copepods, and euphausiids. In the Canadian High Arctic the diet of black guillemots collected near breeding colonies on Devon Island included crustaceans (amphipods and mysids), fish (Arctic cod, *Liparis tunicatus*, and sculpins [Cottidae]), polychaetes, gastropods, and cephalopods (Byers et al. 2010). A single black guillemot stomach collected in the eastern Chukchi Sea contained Arctic cod and polychaetes (Swartz 1966). The diet of black guillemots consistently features fish as prominent part of the diet, especially Arctic cod. Lacking more region-specific information we use the diet presented in Weslawski et al. (1994) for black guillemots. The final diet includes Arctic cod (90%), large-mouth sculpins (3%), shrimp (4.7%), and amphipods (2.3%).

Pigeon guillemots forage for prey by diving and using their wings to swim under water (Ewins 1993). They primarily feed on benthic and demersal fish and invertebrate prey but may also catch schooling fish in the water column or near the surface (Ewins 1993, Litzow et al. 2000). Reported fish prey of the pigeon guillemot in Alaska include pelagic forage fish (Pacific sand lance, capelin), salmonids, cods (Gadidae), sculpins (Cottidae, *Myoxocephalus* sp.), Pacific sandfish (*Trichodon trichodon*), pricklebacks (Stichaeidae), gunnels (Pholidae), ronquils (Bathymasteridae), and flatfish (Pleuronectidae) (Sanger 1986, Litzow et al. 2000). Identified invertebrate prey of pigeon guillemots in Alaska include shrimps (Hippolytidae, Pandalidae, Crangonidae), crabs (Anomura [Paguridae, Hapalogastridae], Brachyuran [Oregoniidae, Cheiragonidae, Cancridae]), gammarid amphipods, mysids, polychaetes, bivalves, and snails (Sanger 1986, Litzow et al. 2000). Lacking a diet description specific to the Chukchi Sea, we use a general diet adapted from the diet reported (by % volume) by Sanger (1986).

The final functional group diet for Alcids piscivorous is an average diet weighted by the estimated biomass of the constituent groups. The group diet composition is dominated by fish groups including pelagic forage fish (27.3%), Arctic cod (26%), saffron cod (23.7%), large-mouth sculpins (7.1%), other sculpins (7.1%), small-mouth flatfish (1.9%), miscellaneous shallow fish (0.3%), snailfish (0.3%), and the variegated snailfish (0.3%). The most prominent invertebrate prey groups are benthic amphipods (2.3%), other zooplankton (1.1%), and shrimp (1%). The remainder of the diet consists of polychaetes, other crabs, snails, and bivalves.

(v) Alcids Planktivorous

The Alcids planktivorous functional group consists of 4 species from the family Alcidae, whose diets are dominated by zooplankton (> 50%). The four species representing this group are the parakeet auklet (*Aethia psittacula*), least auklet (*A. pusilla*), crested auklet (*A. cristatella*), and the dovekie (*Alle alle*).

(i) Updated parameters

Biomass (B): Abundance estimates for all four species are derived from colony counts contained in the North Pacific Seabird Colony Database (Seabird Information Network 2011). Numerically, the group is dominated by crested auklets (219,000) and least auklets (207,000). Species of lower abundance in colony counts are the parakeet auklet (20,000) and dovekie (50). The abundance estimates were used in combination with estimates of average individual body mass from Hunt et al. (2000) to arrive at a group biomass of 0.00014 t km^{-2} (Table 5).

Production (P/B): The Alcids planktivorous P/B of 0.1404 was calculated from both species-specific estimates of annual survival and from an Order level estimate of adult survival (Schreiber and Burger 2001). An annual survival rate of 0.89 was used for the crested auklet and 0.808 for the Least auklet. An order level (Charadriiformes) adult survival rate of 0.85 was used for parakeet auklet and dovekie. The functional group P/B is an average P/B, weighted by biomass.

Consumption (Q/B): Alcids planktivorous have a weighted (by biomass) average Q/B of 247.507.

Food habits (DC): The least auklet feeds primarily by diving and using their wings for propulsion under water (Ainley and Sanger 1979, Bond et al. 2013). During summer they prey almost exclusively on crustacean zooplankton, with limited reports of larval fish or fish otoliths among prey items (Bond et al. 2013). Calanoid copepods are the principal prey of least auklets throughout their range in the north Pacific Ocean and Bering Sea during summer (Bedard 1969, Hunt et al. 1981, Springer and Roseneau 1985, Gall et al. 2006, Sheffield Guy et al. 2009, Bond et al. 2013). Other prey items include euphausiids, gammarid amphipods, hyperiid amphipods, and decapod larvae (Bedard 1969, Hunt et al. 1981, Springer and Roseneau 1985, Harrison 1990, Gall et al. 2006, Sheffield Guy et al. 2009). In lieu of diet data specific to the eastern Chukchi Sea, we use a general diet adapted from data presented (% biomass) in Gall et al. (2006) and Sheffield Guy et al. (2009) for least auklets sampled in the northern Bering Sea. The least auklet diet used here consists of 75% copepods and 25% other zooplankton (including decapod larvae, hyperiids, euphausiids, pteropods, and larval fish).

The crested auklet feeds by diving and pursuing their prey under water using their wings for propulsion (Ainley and Sanger 1979, Jones 1993). During summer the diet of crested auklets primarily consists of crustacean zooplankton, in particular euphausiids (Bedard 1969, Hunt et al. 1981, Jones 1993, Gall et al. 2006, Sheffield Guy et al. 2009). Other prey items taken during summer in the Bering Sea and Aleutian Islands include copepods, amphipods, shrimp, fish, jellyfish, pteropods, and cephalopods (Harrison 1990, Hunt et al. 1998, Gall et al. 2006, Sheffield Guy et al. 2009). Lacking diet data specific to the eastern Chukchi Sea, we use a general diet adapted from data presented (by % biomass) in Gall et al. (2006) and Sheffield Guy et al. (2009) for crested auklets sampled in the northern Bering Sea. The final diet used here is 25% copepods and 75% other zooplankton (including decapod larvae, hyperiids, euphausiids, pteropods, and larval fish).

The parakeet auklet feeds by diving and using their wings for propulsion under water (Ainley and Sanger 1979). The summer diet of the parakeet auklet is more general than the diet of least and crested auklets and includes pteropods, euphausiids, larval fish, gelatinous zooplankton (Ctenophora and

Scyphomedusae), polychaetes, amphipods, and copepods (Bedard 1969, Hunt et al. 1981, Harrison 1990, Hunt et al. 1998). In the Chirikov Basin, north of St. Lawrence Island and south of Bering Strait, gelatinous zooplankton were an important part of the diet and may be a preferred prey item (Harrison 1990). Similarly, gelatinous zooplankton was the predominant part of the diet of parakeet auklets collected during summer in the western Aleutian Islands (Hunt et al. 1998). In the absence of diet data specific to the eastern Chukchi Sea, we adapt a general diet from the values reported by % weight in Hunt et al. (1981) and by frequency of occurrence in Harrison (1990) and Hunt et al. (1998). Other zooplankton (60%), jellyfish (30%), and copepods (10%) comprise the final diet.

In coastal waters and in the pelagic marginal ice zone (MIZ) near Svalbard, the diet of dovekies was dominated by copepods in both frequency of occurrence and total numbers (Mehlum and Gabrielsen 1993). Copepods accounted for 85% of the diet by percent weight during summer in the coastal zone. The second and third most prominent prey items in the coastal area by percent weight were decapod larvae and hyperiid amphipods. Other prey items taken near Svalbard include gastropods, gammarid amphipods, chaetognaths, and larval fish. Similarly, the diet of dovekies at Bear Island (Bjørnøya, Norway) in the Barents Sea was dominated by copepods, accounting for more than 69% of food biomass, followed by decapod larvae (22%), and amphipods (5%) (Weslawski et al. 1999). In the Frans Josef Land Archipelago of the Russian Arctic, dovekie diet was also dominated by copepods, accounting for 72% of the diet by weight and 84% by number (Weslawski et al. 1994). Other important prey groups (by % weight) are euphausiids (12.6%), gammarid amphipods (13%), mysids (0.7%), and larval fish (0.3%). Lacking diet data specific to the eastern Chukchi Sea, we use a general diet for dovekies adapted from the data presented in Weslawski et al. (1994) and Mehlum and Gabrielsen (1993), with 75% of the diet consisting of copepods and 25% other zooplankton (includes mysids, hyperiids, decapod larvae, gastropods [pteropods], chaetognaths, and larval fish).

The functional group diet is an average diet weighted by the biomass estimated for each of the constituent species. Other zooplankton (63.2%), copepods (34.9%), and jellyfish (1.9%) comprise the final diet for the Alcids planktivorous group.

4.5 Fish

(w) All fish functional groups

(i) Biomass (B)

Survey derived estimates of biomass for most of the fish groups were insufficient to meet predator demands and balance the model (i.e., EE > 1). As a result we top-down balanced biomass for 11 of the 16 fish groups, assuming EE=0.8 (Table 1). Alaska skate, walleye pollock, Pacific cod, salmon outgoing, and salmon returning were not top-down balanced.

(ii) Production (P/B) and consumption (Q/B)

Estimates of P/B and Q/B were updated for all four gadid species (Arctic cod, saffron cod, Pacific cod, and walleye pollock), and for both large-mouth and small-mouth flatfish. P/B and Q/B are unchanged from the preliminary model for all other fish functional groups.

(iii) Food habits (DC)

The diet compositions of most fish functional groups were updated with food habits data gathered during Arctic Eis trawl surveys (Table 4).

(x) Large-mouth flatfish

Three species from the family Pleuronectidae, Bering flounder (*Hippoglossoides robustus*), Greenland turbot (*Reinhardtius hippoglossoides*), and Pacific halibut (*Hippoglossus stenolepis*) comprise the large-mouth flatfish group. All three of these species have large mouths relative to other Arctic flatfish (e.g., yellowfin sole, longhead dab, others) and fish are a featured part of their diet.

(i) Updated parameters

Biomass (B): Adding Bering flounder to the large-mouth flatfish group substantially increased the estimated biomass for this group as neither Greenland turbot nor Pacific halibut are abundant in the eastern Chukchi Sea. Small numbers of Greenland turbot and Pacific halibut were previously observed during trawl surveys of the eastern Chukchi Sea in 1976 (Wolotira et al. 1977) and 1990 (Barber et al. 1997). During the 2012 Arctic Eis bottom trawl survey, only a single Greenland turbot was caught (weight 0.01 kg, length 10 cm) and no Pacific halibut were encountered (Goddard et al. 2014). Bering flounder were substantially more abundant with more than 2.5 individuals per hectare (Goddard et al. 2014). Bering flounder compose more than 99.9% of the initial biomass input of 0.0095 t km^{-2} for this group. The addition of Bering flounder to this group also increased the pressure from predators as Bering flounder are present in the diets of seals, seabirds, and other fishes. As a result, the trawl survey derived biomass estimate was insufficient to meet predator demands and biomass was therefore top-down balanced (EE=0.8), which produced a biomass estimate of 0.1114 t km^{-2}.

Production (P/B): Region-specific information required to calculate P/B and Q/B for this functional group are only available for Bering Flounder. P/B is calculated with a regression of estimator of mortality (Hewitt and Hoenig 2005) under the assumption that under steady-state conditions P/B is equal to mortality, Z (Allen 1971). This method requires an estimate of maximum age (11) which we acquired from Smith et al. (1997). P/B is estimated to equal 0.401.

Consumption (Q/B): Q/B was calculated following the methods of Aydin (2004) which requires an estimate of mortality (Z) and the parameter *k* from the von Bertalanffy growth function (vBGF). Mortality was taken from the aforementioned P/B calculation (0.401) and *k* was taken from Smith et al. (1997) resulting in Q/B=1.78.

Food habits (DC): Region-specific diet information is extremely limited for Greenland turbot and is unavailable for Pacific halibut. A single Greenland turbot stomach was collected during the 2012 Arctic Eis bottom trawl survey. The turbot was 10 cm long and the stomach contained two cumaceans and one euphausiid. Sampling of Bering flounder stomachs was more fruitful, with 94 (non-empty) stomachs collected during the 2012 survey. Due to the lack of adequate sample size for Greenland turbot and Pacific halibut, the diet composition used for large-mouth flatfish is that of Bering flounder. Coyle et al. (1997) found the diet of Bering flounder captured near Pt. Hope to be dominated by fish. The most important identified fish prey was *Lumpenus* sp. (Stichaeidae, miscellaneous shallow fish), other prey fish families included eelpouts, poachers (misc. shallow fish), sculpins, and cods. Similarly from our stomach collections in the eastern Chukchi Sea, the Bering flounder diet composition consists of 33% miscellaneous shallow fish (Stichaeids), 24% Arctic cod, 20% shrimp, 14.5% other zooplankton, 5% polychaetes, 2.5% benthic amphipods, <1% bivalves, and <1% copepods.

The prey items contributing to the Arctic cod portion of the diet were identified as Gadidae when the stomach contents were analyzed in the lab. In the adjacent eastern Bering Sea, about 52% of the Bering flounder diet (n=830 non-empty stomachs) is walleye pollock, the dominant semi-pelagic gadid of that region. Walleye pollock are present in extremely low numbers in the Chukchi Sea. In the absence of information to guide how to divide the Gadidae portion of the Bering flounder diet up amongst our four gadid groups in the eastern Chukchi Sea; we have assigned all the prey identified as Gadidae to the dominant gadid (most abundant and highest biomass) of the region, Arctic cod.

(y) Small-mouth flatfish

The small-mouth flatfish group is represented by six species from the family Pleuronectidae, yellowfin sole (*Limanda aspera*), longhead dab (*L. proboscidea*), Sakhalin sole (*L. sakhalinensis*), Arctic flounder (*Liopsetta glacialis*), starry flounder (*Platichthys stellatus*), and Alaska plaice (*Pleuronectes quadrituberculatus*). All of these species are found in the benthic environment and their primary prey items are benthic invertebrates.

(i) Updated parameters

Biomass (B): Removing Bering flounder from this group reduced their trawl survey based biomass estimate to 0.0694 t km^{-2}, from 0.0799 t km^{-2}. The predation pressure from higher trophic levels was also reduced, however, a top-down balance of biomass was still required to meet predator demands. This resulted in a biomass estimate of 0.0902 t km^{-2} (EE=0.8).

Production (P/B): Under equilibrium conditions, P/B is assumed to be equal to mortality (Z) (Allen 1971). Following this relationship, P/B was calculated with the regression estimator of mortality from Hewitt and Hoenig (2005). This method requires only a single input, an estimate of maximum age. Estimates of maximum age for yellowfin sole, starry flounder, and Alaska plaice were taken from Wolotira et al. (1977). Estimates of P/B for longhead dab and Sakhalin sole were taken from the Ecopath model of the eastern Bering Sea (Aydin et al. 2007). An estimate of P/B or the data required to calculate it, were not available for Arctic flounder, so the other species in this group are taken as representative of this species. The functional group P/B of 0.308 is an average P/B, weighted by the estimated biomass of the constituent species from the 2012 survey.

Consumption (Q/B): Q/B was calculated following the methods of Aydin (2004) which requires an estimate of mortality (Z) and the growth parameter *k* from the von Bertalanffy growth function (vBGF). Estimates of mortality were taken from the aforementioned P/B calculations. The vBGF parameter *k* was taken from Wolotira et al. (1977) for yellowfin sole, starry flounder, and Alaska plaice. Estimates of longhead dab and Sakhalin sole Q/B are taken from the eastern Bering Sea Ecopath model (Aydin et al. 2007). The required information was not available to calculate Q/B for Arctic flounder, so the other members of this group are taken as representative for this species. The final group Q/B of 1.535 is an average Q/B, weighted by biomass estimates derived from the 2012 survey.

Food habits (DC): The diet composition is derived from stomach collections made during the 2012 trawl surveys (Table 4). The final diet is an average diet weighted by biomass. The diet composition for small-mouth flatfish is 37% bivalves, 35% polychaetes, 12% benthic amphipods, 5% urchins, dollars, cucumbers, 4% miscellaneous crustaceans, 3% brittle stars, 3% snow crab, and 1% worms, etc. The diet also includes traces (<1%) of snails, other crabs, and copepods.

(z) Large-mouth sculpin

This group of sculpins is represented by six species from two genera of the family Cottidae; *Hemilepidotus papilio* (butterfly sculpin), *Myoxocephalus scorpius* (shorthorn [warty] sculpin), *M. jaok* (plain sculpin), *M. polyacanthocephalus* (great sculpin), *M. quadricornis* (fourhorn sculpin), and M. scorpioides (Arctic sculpin). Although marine fishes of the Chukchi Sea are generally small in size (Norcross et al. 2010, Goddard et al. 2013, Goddard et al. 2014), these two genera are grouped together in part because they commonly grow to large sizes in other parts of their range in Alaska (e.g., the eastern Bering Sea).

(i) Updated parameters

Biomass (B): The initial biomass input for this group (0.0169 t km^{-2}) was calculated from 2012 bottom trawl survey. This estimate was insufficient to match predator demands, therefore biomass was top-down balanced (EE=0.8) producing a biomass estimate of 0.5997 t km^{-2}.

Food habits (DC): The diet composition of large-mouth sculpins was determined from stomach samples collected during the 2012 bottom trawl survey (Table 4). The functional group diet is an average diet weighted by biomass. Their diet (by weight) consists of 24% miscellaneous shallow fish, 21% other sculpins, 14% other crabs, 13% shrimps, 9% eelpouts, 8% snow crab, 7% benthic amphipods, 1% variegated snailfish and 1% polychaetes. Other prey groups of lesser importance (<1%) are other snailfish, miscellaneous crustaceans, other zooplankton, and brittle stars.

(ii) Parameters from W13

The **P/B** of 0.4 used here is unchanged from the preliminary model. In the absence of large-mouth sculpin life history data, this P/B is a general default that approximates other groundfish species (Aydin et al. 2007). The **Q/B** used here is unchanged from the preliminary model. The Q/B of 2 is a general default value that approximates other groundfish species (Aydin et al. 2007).

(aa) Other sculpins

The other sculpins functional group includes all Cottids not included in the large-mouth sculpin group, including the threaded sculpin (*Gymnocanthus pistilliger*), Arctic staghorn sculpin (*G. tricuspis*), hamecon (*Artediellus scaber*), ribbed sculpin (*Triglops pingeli*), belligerent sculpin (*Megalocottus platycephalus*), leister sculpin (*Enophrys lucasi*), antlered sculpin (*E. diceraus*), and spatulate sculpin (*Icelus spatula*). Additionally, this group includes at least two species from the family Hemitripteridae (sailfin sculpins), the eyeshade sculpin (*Nautichthys pribilovius*) and the crested sculpin (*Blepsias bilobus*).

(i) Updated parameters

Biomass (B): The trawl survey derived biomass input of 0.0123 t km^{-2} was insufficient to meet predator demands. We therefore used a top-down balance approach (EE=0.8) which resulted in a biomass estimate of 0.8553 t km^{-2}.

Production (P/B): The estimate of P/B for other sculpins has changed slightly from the preliminary model. The functional group P/B is an average P/B, weighted by biomass. P/B was re-calculated following the same methods as in the preliminary model, except the biomass weights form the 2012 survey are now used. The P/B has changed from 0.4611 to 0.4593.

Consumption (Q/B): Q/B is also weighted by biomass and it too has been recalculated, also following the same methods as in the preliminary model. Q/B has also modestly decreased from 2.4281 to 2.4152.

Food habits (DC): The diet of other sculpins was derived from the contents of stomachs collected during the 2012 bottom trawl survey (Table 4). The final functional group diet is an average diet weighted by biomass. The primary prey items (by % weight) are benthic amphipods (48%), polychaetes (24%), anemones (6%), worms etc. (6%), other crabs (6%), pelagic forage fish (4%), and other zooplankton (3%). Other prey groups accounting for `1% or less of the diet composition include, shrimps, miscellaneous crustaceans, brittle stars, snails, bivalves, and snow crabs.

(bb) Eelpouts

The eelpouts functional group represents at least 6 species from the family Zoarcidae; marbled eelpout (*Lycodes raridens*), wattled eelpout (*L. palearis*), saddled eelpout (*L. mucosus*), Canadian eelpout (*L. polaris*), polar eelpout (*L. turneri*), and halfbarred eelpout (*Gymnelus hemifasciatus*).

(i) Updated parameters

Biomass (B): The initial biomass input of 0.0168 t km^{-2} for eelpouts was determined from the catch of the 2012 bottom trawl survey. However, this estimate was not adequate to support predator demand and instead a top-down balance was performed (EE=0.8) producing a biomass estimate of 0.3822 t km^{-2}.

Food habits (DC): Eelpout diet composition was determined through the analysis of eelpout stomachs collected during the 2012 bottom trawl survey. The functional group diet is the average of the individual species diets, weighted by biomass. The primary prey items (by % weight) are polychaetes (54%), benthic amphipods (28%), miscellaneous shallow fish (8%), large-mouth sculpins (5%), other zooplankton (3%), and shrimps (1.5%). Other prey present in trace amounts include, other crabs, miscellaneous crustaceans, other sculpins, variegated snailfish, other snailfish, bivalves, and copepods.

(ii) Parameters from W13

The **P/B** of eelpouts is unchanged from the preliminary model. In the absence of sufficient eelpout life history data, a P/B estimate of 0.4 was used in the preliminary model, which closely approximated the P/B values of other demersal groundfish (Aydin et al. 2007). The eelpout **Q/B** of 2.0 is also unchanged from the preliminary model. The data required to calculate Q/B for species in this group are not available, and this estimate of Q/B is a general value that approximates the Q/B's of other groundfish (Aydin et al. 2007).

(cc) Pelagic forage fish

The pelagic forage fish group includes four species from three families, Pacific herring (*Clupea pallasi*) from Clupeidae, capelin (*Mallotus villosus*) and rainbow smelt (*Osmerus mordax*) from Osmeridae, and the Pacific sand lance (*Ammodytes hexapterus*) from Ammodytidae.

(i) Updated parameters

Biomass (B): The initial biomass input was calculated from the catch data of the 2012 bottom trawl survey (0.0976 t km^{-2}). This initial estimate was not adequate to match the trophic demands from predators and instead a top-down balance was performed (EE=0.8). This produced a biomass estimate of 1.1906 t km^{-2}.

Production (P/B): Our estimate of P/B for pelagic forage fish is an average P/B, weighted by biomass. In the preliminary -model, P/B was weighted by biomass estimates from the 1990 bottom trawl survey. We have re-calculated P/B here following the same methods, however we use biomass estimates from the 2012 survey as weights. P/B has decreased from 0.551 to 0.543.

Consumption (Q/B): Q/B is also weighted by biomass, and similarly, Q/B in the preliminary model was weighted by biomass from the 1990 trawl survey. We have recalculated here following the same procedure, but instead use the biomass estimates from the 2012 survey instead, resulting in a Q/B of 2.92.

Food habits (DC): The pelagic forage fish diet composition was determined through analysis of stomachs collected during the 2012 trawl surveys (Table 4). The diet composition for the functional group is an average of the individual species diet compositions, weighted by biomass. The dominant prey items are other zooplankton (46%), copepods (31%), and miscellaneous shallow fish (19%). Prey types of lesser importance include benthic amphipods, shrimps, large-mouth sculpin, other sculpins, polychaetes, miscellaneous crustaceans, and other crabs.

(dd) Miscellaneous shallow fish

Miscellaneous shallow fish is a composite group of demersal fishes from several families, including poachers (Agonidae), wolfish (Anarhichadidae), lumpsuckers (Cyclopteridae), greenlings (Hexagrammidae), and pricklebacks (Stichaeidae).

(i) Updated parameters

Biomass (B): Our initial biomass estimate of 0.0042 t km^{-2} was calculated from the catch data of the 2012 bottom trawl survey. This estimate was too low to meet predator demands during initial model balancing (i.e., EE>1). Instead we top-down balanced biomass and calculated a biomass estimate of 6.4984 t km^{-2}. This estimate is more than 3 orders of magnitude greater than the trawl survey derived estimate and gives this functional group the highest biomass of all the fish groups. Many species in this group are not efficiently caught with trawl survey gear and the disparity between the top-down forced biomass estimate and the survey derived estimate in part reflects this. Additionally, miscellaneous shallow fish are a very common prey group (especially Stichaeids) for other fishes of the Chukchi Sea and the top-down estimate reflects this demand from predator groups.

Food habits (DC): The diet composition of the miscellaneous shallow fishes was determined from analysis of stomachs collected during the 2012 bottom trawl survey of the eastern Chukchi Sea (Table 4). The final diet for the functional group is an average of the individual species diets, for those species for which we have diet information, weighted by biomass. The functional group diet composition (by % weight) consists of benthic amphipods (52%), polychaetes (13%), other zooplankton (10%), miscellaneous crustaceans (8%), shrimps (8%), bivalves (5%), and copepods (2%). Prey of lesser importance (1% or less) include worms etc., other crabs, and snails.

(ii) Parameters from W13

The estimated **P/B** of 0.4 is the same as in the preliminary model. The data required to calculate P/B are not available for species in this group, and this estimate is a general value that closely approximates other demersal groundfish (Aydin et al. 2007). The **Q/B** of miscellaneous shallow fish is unchanged from the preliminary model and remains at 2.0. The is a general value that closely approximates the Q/B of other demersal groundfish (Aydin et al. 2007)

(ee) Other snailfish

This functional group is primarily represented by two species from the family Liparidae, the kelp snailfish (*Liparis tunicatus*) and the festive snailfish (*L. marmaratus*). Also present in the catch of the 2012 Arctic Eis survey was the gelatinous seasnail (*L. fabricii*) and several other snailfish identified only as *Liparis* sp. The variegated snailfish (*Liparis gibbus*) is not included in this group and instead makes up its own single-species functional group, primarily due to its distinct diet composition (see below).

(i) Updated parameters

Biomass (B): The initial input for biomass of other snailfish was 0.00225 t km^{-2}. This density estimate was calculated from the catch data of the 2012 Arctic Eis bottom-trawl survey. This initial input for biomass was insufficient to balance the model and a top-down balance was performed with EE=0.8. This resulted in a density estimate of 0.1351 t km^{-2}.

Production (P/B): There is little to no information regarding life history or vital rates for the species in this functional group. In the absence of species- or region-specific information we assume a P/B of 0.4. This is equivalent to the P/B and Q/B of the miscellaneous shallow fish and variegated snailfish functional groups, and additionally is roughly equivalent to values for taxonomically similar functional groups in previously published models of the Gulf of Alaska, Aleutian Islands, eastern Bering Sea (Trites et al. 1999, Aydin et al. 2007), and northern California Current (Field et al. 2006).

Consumption (Q/B): Species-specific information, adequate to support calculation of Q/B for this functional group is presently unavailable. In lieu species-specific information we assume a Q/B of 2.0. This is equal to the Q/B for the miscellaneous shallow fish and variegated snailfish groups, and is also equivalent to generic values used for taxonomically similar functional groups in published Ecopath models of other northeastern Pacific large marine ecosystems (Trites et al. 1999, Field et al. 2006, Aydin et al. 2007)

Food habits (DC): Other snailfish diet composition was determined from kelp snailfish and festive snailfish stomachs collected during the 2012 bottom trawl survey (Table 4). The functional group diet is an average of these two diets, weighted by biomass. The primary prey items (by % weight) in the other snailfish diet are benthic amphipods (50%), polychaetes (15%), shrimps (10%), pelagic forage fish (7%), variegated snailfish (6%), other crabs (3%), small-mouth flatfish (3%), large-mouth sculpin (2%), other sculpins (1%), snow crabs (1%), and other zooplankton (1%). Prey items of lesser importance (<1%) include miscellaneous crustaceans, bivalves, and copepods.

(ff) Variegated snailfish

Variegated snailfish (*Liparis gibbus*) were included in the miscellaneous shallow fish functional group in W13. Information on the diet of variegated snailfish within the Chukchi Sea was previously unavailable and the assumed miscellaneous shallow fish diet was dominated by amphipods, shrimps, crabs, and polychaetes. During the 2012 Arctic Eis bottom trawl survey, 54 variegated snailfish stomachs were collected and their contents analyzed in the lab. From those stomachs, 58% of their diet was found to consist of fish, and about 33% were fishes from their same functional group, miscellaneous shallow fish. Keeping variegated snailfish and their new diet in the miscellaneous shallow fish group introduced a cannibalistic loop which created computational problems when attempting to balance the model. Therefore, we removed variegated snailfish from miscellaneous shallow fish and now treat them as a single species functional group.

(i) Updated parameters

Biomass (B): A biomass density estimate of 0.0073 t km^{-2} was calculated for variegated snailfish from the catch data of the 2012 Arctic Eis bottom-trawl survey, but was insufficient to balance the model (EE>1). Instead, a top-down balance was performed with EE of 0.8, producing a density estimate of 0.0987 t km^{-2}.

Production (P/B): Because there is little to no life history information for this species, we assume the same P/B as the miscellaneous shallow fish group, which formerly included the variegated snailfish. In lieu of a species-specific estimate, the P/B is assumed to be 0.4. This value is a default assumption used for taxonomically similar functional groups in previous Ecopath models of large marine ecosystems in Alaska. Trites et al. (1999) used a P/B of 0.4 for several demersal fish groups of the eastern Bering Sea and Aydin et al. (2007) used a P/B of 0.4 for their miscellaneous shallow fish group (including snailfish) in models of the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska.

Consumption (Q/B): There is no information available to support the calculation of Q/B for this species and therefore we assume the same Q/B as the miscellaneous shallow fish group, which formerly included variegated snailfish. The Q/B is assumed be to 2.0. This value is a default assumption used for taxonomically similar functional groups in previous Ecopath models of large marine ecosystems in Alaska. Aydin et al. (2007) used a Q/B of 2.0 for their miscellaneous shallow fish group (including snailfish) in models of the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska.

Food habits (DC): The diet composition for this group was determined through the analysis of variegated snailfish stomachs collected in the eastern Chukchi Sea during the 2012 bottom trawl survey (Table 4). The diet consists of shrimps (29%), miscellaneous shallow fish (18%), other snailfish (14%), other sculpins (11%), large-mouth sculpin (8%), benthic amphipods (7%), pelagic forage fish (3%), polychaetes (3%), large-mouth flatfish (1%), other zooplankton (1%), Arctic cod (1%), snow crab (1%), and eelpouts (1%). Other prey groups accounting for less than 1% of the diet include other crabs, bivalves, miscellaneous crustaceans, worms etc., and copepods.

(gg) Alaska skate

A single adult (95 cm total length) Alaska skate (*Bathyraja parmifera*) was caught in the southern Chukchi Sea during the 2012 Arctic Eis bottom trawl survey (Goddard et al. 2014). Beach cast specimens have previously been found in 2010 near Pt. Hope and Kivalina in the southern Chukchi Sea (Mecklenburg et al. 2011). Additionally, several Alaska skates were caught throughout the northern Bering Sea during 2010 NOAA summer bottom trawl survey (Lauth 2011). In consideration of these recent observations of Alaska skate we have decided to add them to our Ecopath model as a single species functional group.

(i) Updated parameters

Biomass (B): The biomass density of 0.00537 t km^{-2} for Alaska skates was calculated from the catch data of the 2012 Arctic Eis bottom trawl survey. There are no known predators of Alaska skate in the Chukchi Sea and their EE is 0.0.

Production (P/B): Frisk et al. (2001) compiled life-history parameters for elasmobranch fishes over a wide geographic range and estimated the potential rate of population increase for medium sized elasmobranchs (100-200cm) as 0.21. Aydin et al. (2007) used the medium-sized elasmobranch estimate of Frisk et al. (2001) as a proxy for the P/B ratio of Alaska skates in the eastern Bering Sea and assigned them a P/B of 0.20. Matta and Gunderson (2007) used three different published methods to indirectly estimate the natural mortality (M) of Alaska skate in the eastern Bering Sea and found M to range from 0.14 to 0.28. Here we use the midpoint (M=0.21) of the natural mortality rate range provided by Matta and Gunderson (2007) as a proxy for Z, the instantaneous mortality rate of Alaska skate in the eastern Chukchi Sea. Under steady-state conditions P/B is approximated by Z (Allen 1971) and we use P/B=0.21 for Alaska skate.

Consumption (Q/B): Sufficient information to estimate Q/B is not presently available for Alaska skates. In previous models of other Alaska ecosystems (eastern Bering Sea, Aleutian Islands, and Gulf of Alaska), Aydin et al. (2007) estimated Q/B by assuming a growth efficiency (GE) that was intermediate between sharks and large predatory fishes (e.g., Pacific halibut). They assumed a growth efficiency of 0.1 which produced a Q/B of 2.0. In lieu of adequate information, we make the same assumption here with a GE of 0.1 which resulted in a Q/B of 2.1.

Food habits (DC): The diet composition of skates in the eastern Chukchi Sea is unknown at this time. In the absence of region-specific data, the diet of Alaska skates was derived from stomach data collected in the eastern Bering Sea by scientists from the Resource Ecology and Ecosystem Modeling (REEM) program at the NOAA Alaska Fisheries Science Center in Seattle. The diet compositions were acquired by querying the REEM food habits database (a detailed description of the database can be found at, http://www.afsc.noaa.gov/REFM/REEM/Data/Default.htm) with their Diet Analysis Tool (Lang 2004). We limited our diet queries to survey strata in the northern half of the surveyed area and inshore of the continental slope (NMFS survey strata 20, 41, 42, and 43, station depth generally less than 100 m, see Figure 2 in Lauth (2011)). These strata experience seasonal ice coverage and are regularly encompassed by the eastern Bering Sea "cold pool" (see Figure 6 in Lauth (2011)) which creates cool summer demersal conditions (Wyllie-Echeverria and Wooster 1998, Mueter and Litzow 2008, Stabeno et al. 2012, Stevenson and Lauth 2012). Though the precise conditions and extent of the cold pool vary from year to year and are not equal to the Chukchi Sea, we assumed Alaska skate diet information collected from here was a better approximation of their diet in the Chukchi Sea than to import diet information from more distant ecosystems or from different species.

Alaska skate diet composition is described from stomachs collected in the eastern Bering Sea (n=1,773 non-empty stomachs). The primary prey items (by % weight) of Alaska skate are Arctic cod (27%), snow crab (26%), shrimps (11%), small-mouth flatfish (6%), other crabs (6%), pelagic forage fish (5%), eelpouts (4%), benthic amphipods (3%), large-mouth flatfish (3%), large-mouth sculpins (2%), salmon returning (2%), miscellaneous shallow fish (2%), polychaetes (1%), and other zooplankton (1%). Other prey items of lesser importance (<1%) include variegated snailfish, other snailfish, Pacific cod, other sculpins, benthic urochordate, miscellaneous crustaceans, urchins-dollars-cucumbers, cephalopods, snails, bivalves, anemones, brittle stars, and copepods.

(hh) Walleye pollock

Walleye pollock (*Gadus chalcogrammus*) are a dominant component of the ecosystem in the adjacent eastern Bering Sea, and there they support one of the world's largest single-species fisheries (Ianelli et al. 2013, Zador 2013). Due to their commercial importance and ecological significance in the eastern Bering Sea they are treated as a single-species in this Ecopath model.

(i) Updated parameters

Biomass (B): Walleye pollock biomass is estimated to be 0.00054 t km^{-2} from the catch data of the 2012 Arctic Eis bottom trawl survey. They experience little predation mortality in the Chukchi Sea and a top-down balance was not necessary.

Production (P/B): The data required to estimate P/B for walleye pollock in the Chukchi Sea is not presently available. Sufficient data does exist for walleye pollock in the eastern Bering Sea where this species is intensively studied, however, walleye pollock in the eastern Chukchi Sea experience considerably different growing conditions (e.g., temperature) and have only been observed at much smaller sizes (16 cm or less in the present study, Goddard et al. (2014)). In lieu of region-specific data, we apply the region-specific estimates of P/B for another gadid, Arctic cod (*Boreogadus saida*), to walleye pollock. Arctic cod are found at similar sizes to walleye pollock in the eastern Chukchi Sea, both species can be found in demersal and pelagic environments, and both are known to feed on zooplankton. Given the taxonomic relationship between Arctic cod and walleye pollock, and in consideration of ecological similarities between these two species, we felt the Arctic cod P/B was our best approximation of walleye pollock P/B in the eastern Chukchi Sea. We use the Arctic cod P/B of 0.8690 for walleye pollock.

Consumption (Q/B): The data required to calculate Q/B for walleye pollock in the eastern Chukchi Sea is not presently available. Instead we apply the region-specific Q/B of 3.008 calculated for Arctic cod to walleye pollock.

Food habits (DC): The diet composition of walleye pollock was determined from stomach specimens collected during the 2012 Arctic Eis bottom trawl survey (Table 4). The primary prey items were fish, in particular 6.5% Arctic cod and 47.2% Teleostei. In the absence of information to guide how to best attribute the teleost portion of the diet to our functional groups, we have attributed it to the only identified fish prey, Arctic cod. This increases the Arctic cod portion of the walleye pollock diet to 53.7%, but this is likely an overestimate. Because walleye pollock have such a small presence in the Chukchi Sea, they only account for less than 0.1% of Arctic cod predation mortality, despite Arctic cod accounting for more than half of their diet. The rest of the diet consists of copepods (15%), shrimps (14%), other zooplankton (10%), benthic amphipods (4%), and miscellaneous crustaceans (3%).

(ii) Pacific cod

Pacific cod (*Gadus macrocephalus*) is a predatory groundfish present in low abundance in the Chukchi Sea, but is far more abundant and is commercially important in other more southerly parts of their range in Alaska, such as the Bering Sea.

(i) Updated parameters

Biomass (B): Pacific cod are present in very low abundance in the eastern Chukchi Sea, only four were caught during the 2012 bottom trawl survey (Goddard et al. 2014). From that catch data, their biomass is estimated to be 3.79*10-5 t km^{-2}. Pacific cod are subject to very little predation mortality in the Chukchi Sea and have an EE of 0.744.

Production (P/B): The information required to calculate P/B for Pacific cod in the Chukchi Sea is not presently available. Based on taxonomic relation and presumed similarities in diet and habitat requirements, we apply the region-specific estimate of P/B=0.5477 calculated for saffron cod to Pacific cod.

Consumption (Q/B): Sufficient information is not presently available to support region-specific calculations of Q/B for Pacific cod. In lieu of this information, we use the region-specific estimate of Q/B for saffron cod instead. Pacific cod are assigned a Q/B of 2.8028.

(ii) Parameters from W13

Only one Pacific cod stomach was collected during the 2012 Arctic Eis bottom trawl survey and that was not an adequate sample size to define a new diet for this species. The one stomach contained two prey types, shrimp (81% by weight) and polychaetes (19%). Diet composition **(DC)** is unchanged from the preliminary model. The major prey groups are shrimps (29%), Arctic cod (16%), snow crab (15%), benthic amphipods (14%), polychaetes (7%), miscellaneous shallow fish (6%), other zooplankton (5%), and other crabs (5%).

(jj) Saffron cod

Saffron cod (*Eleginus gracilis*) is a demersal gadid typically found in shallow, near shore waters of Alaska (Wolotira 1985).

(i) Updated parameters

Biomass (B): Our initial biomass input for saffron cod of 0.1080 t km^{-2}, was derived from the catch data of the 2012 Arctic Eis bottom trawl survey. This estimate was insufficient to meet predator demands (EE>1) during initial attempts to balance the model and a top-down balance was performed instead. This produced a biomass estimate of 0.9791 t km^{-2}.

Production (P/B): Under the assumption of equilibrium conditions, P/B is equal to Z, the instantaneous natural mortality rate (Allen 1971). Following this assumption, we use the regression estimator of mortality of Hewitt and Hoenig (2005) to approximate P/B. This method only requires an estimate of maximum age. We acquired a preliminary maximum age estimate of 8 (Helser et al. *Accepted*) derived from specimens collected during the Arctic Eis trawl surveys. This produced an estimated P/B of 0.5477.

Consumption (Q/B): We calculated Q/B following the methods of Aydin (2004) which requires only an estimate of mortality (Z) and an estimate of the growth parameter *k* from the von Bertalanffy growth function (vBGF). We used our estimate of Z from the aforementioned P/B calculation and used a preliminary estimate of the vBGF *k* parameter for saffron cod from Helser et al. (*Accepted*) . This resulted in a Q/B estimate of 2.8028.

Food habits (DC): The diet composition of saffron cod was determined from stomachs collected during the 2012 Arctic Eis bottom trawl survey (Table 4). The primary prey items (by % weight) of saffron cod are shrimps (48%), miscellaneous shallow fish (35%), worms etc. (6%), benthic amphipods (4%), other zooplankton (4%), and polychaetes (3%). Prey items present in trace amounts (<1%) include miscellaneous crustaceans, snails, other crabs, and copepods.

(kk) Arctic cod

Arctic cod (*Boreogadus saida*) is one of the more ubiquitous groundfish species in the eastern Chukchi Sea and can be found in demersal and pelagic environments as well as in association with sea ice during ice-covered periods (Bradstreet et al. 1986, Gradinger and Bluhm 2004, Geoffroy et al. 2011, Parker-Stetter et al. 2011, Renaud et al. 2012).

(i) Updated parameters

Biomass (B): The initial input for Arctic cod biomass (0.1460 t km^{-2}) was calculated from the 2012 Arctic Eis bottom trawl survey. This estimate was insufficient to match demands from predators and a top-down balance (EE=0.8) was performed instead. This resulted in a biomass estimate of 1.0449 t km^{-2}.

Production (P/B): Under the assumption of equilibrium conditions, P/B is equal to Z, the instantaneous natural mortality rate (Allen 1971). Following this assumption, we use the regression estimator of mortality of Hewitt and Hoenig (2005) to approximate P/B. This method only requires an estimate of maximum age. We acquired a preliminary maximum age estimate of 5 (Helser et al. *Accepted*) derived from specimens collected during the Arctic Eis trawl surveys. This produced an estimated P/B of 0.8690.

Consumption (Q/B): We calculated Q/B following the methods of Aydin (2004) which requires only an estimate of mortality (Z) and an estimate of the growth parameter *k* from the von Bertalanffy growth function (vBGF). We used our estimate of Z from the aforementioned P/B calculation and used a preliminary estimate of the vBGF *k* parameter for Arctic cod from Helser et al. (*Accepted*). This resulted in a Q/B estimate of 3.008.

Food habits (DC): We determined the diet composition of Arctic cod from stomachs collected during the 2012 Arctic Eis trawl surveys. The primary prey items (by % weight) of Arctic cod include copepods (37%), other zooplankton (28%), shrimps (16%), benthic amphipods (10%), pelagic forage fish (5%), and miscellaneous crustaceans (1%). Other prey groups of lesser importance (<1%) include Arctic cod, polychaetes, large-mouth sculpin, large-mouth flatfish, eelpouts, snailfish, miscellaneous shallow fish, other crabs, and bivalves.

(ll) Salmon outgoing

The salmon outgoing functional group includes at least five species of anadromous Pacific salmon: pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), sockeye salmon (*O.*

nerka), and Chinook salmon (*O. tshawytscha*) (Alverson and Wilimovsky 1966, Smith et al. 1966). Salmon are present in the ecosystem in two distinct pulses, the outgoing smolts leaving streams for the ocean, and the adults returning to spawn in the streams. The salmon outgoing group represents the out-migrating smolts leaving streams for the ocean.

(i) Updated parameters

None

(ii) Parameters from W13

The biomass and abundance of outgoing salmon smolts in the Chukchi Sea are not known with precision. The biomass estimate **(B)** used here is unchanged from the preliminary model. In the absence of suitable data to calculate abundance or biomass estimates, the biomass of outgoing salmon was assumed to be 1/10 of the returning salmon biomass, for a density estimate of $5.21 * 10^{-4}$ t km^{-2}. In lieu of a region-specific estimate of **P/B**, the P/B of 1.28 for salmon outgoing is taken from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). A **Q/B** of 13.56 is used for outgoing salmon and is unchanged from the preliminary model. Lacking a region-specific estimate of Q/B, this estimate is taken from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The diet composition **(DC)** we use for outgoing salmon is unchanged from the preliminary model. The diet compositions of juvenile pink and chum salmon in the northern Bering and eastern Chukchi seas is dominated by zooplankton, including copepods (Moss et al. 2009), and the diet used here is divided evenly between these two groups.

(mm) Salmon returning

The salmon returning functional group includes at least five species of anadromous Pacific salmon: pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), coho salmon (*O. kisutch*), sockeye salmon (*O. nerka*), and Chinook salmon (*O. tshawytscha*) (Alverson and Wilimovsky 1966, Smith et al. 1966). Salmon are present in the ecosystem in two distinct pulses, the outgoing smolts leaving streams for the ocean, and the adults returning to spawn in the streams. The salmon returning group represents the adult salmon returning from the ocean to spawn in streams.

(i) Updated parameters

None

(ii) Parameters from W13

The salmon returning biomass estimate **(B)** of 0.00521 t km^{-2} is unchanged from the preliminary model. There are few estimates of abundance for returning salmon in the eastern Chukchi Sea (e.g., Smith et al. 1966). In their place, catch records (Booth and Zeller 2008, Eggers et al. 2010) were used as a best, conservative indication of abundance and were used to derive the density estimate. The salmon returning **P/B** of 1.65 is taken from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The **Q/B** of 11.6 for salmon returning is also unchanged from

W13, and similarly, is taken from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). Diet **(DC)** descriptions for juvenile pink and chum salmon in the northern Bering and eastern Chukchi seas indicate their diet is dominated by zooplankton, including copepods (Moss et al. 2009). The diet of salmon in the Bering Sea is also dominated by zooplankton (Davis et al. 2009). The diet composition used here is divided evenly between copepods and other zooplankton.

4.6 Benthic Invertebrates

(nn) Cephalopods

The cephalopods group is assumed to consist of only octopods. Recently, two unidentified squid (Order Teuthoidea) were caught within the Chukchi Sea and weighed a combined 12g (Weems 2014). However, at this time observations of squid in the Chukchi Sea are very limited and therefore, they are not formally included in this functional group. Historically, octopods have been recorded throughout the eastern Chukchi Sea (Sparks and Pereyra 1966, Feder and Jewett 1978). Recent records of octopods in the Chukchi Sea have primarily been for *Benthoctopus sibiricus* (Blanchard et al. 2013b, Goddard et al. 2014). Previous records from the northeastern Chukchi Sea have also included *Benthoctopus leioderma* (Feder et al. 1994a).

(i) Updated parameters

Biomass (B): Octopods were not present in the 2012 beam trawl catch data and were scarcely represented in the catch from the 2012 bottom trawl survey (Goddard et al. 2014). Octopods are not well sampled with bottom trawling gear and producing reliable biomass estimates from survey data in the nearby eastern Bering Sea has proven problematic (Conners and Conrath 2010). We calculated an estimated biomass of 6.5 * 10-4 t km^{-2} from the Arctic Eis bottom trawl data and used that as an initial biomass input. However, this estimate was insufficient to meet predator demands and a top-down balance was performed (EE=0.8) resulting in a biomass estimate of 0.011 t km^{-2}.

(ii) Parameters from W13

The cephalopod **P/B** of 1.77 is unchanged from the preliminary model and is a molluscan mean P/B from Cusson and Bourget (2005). Cephalopod **Q/B** of 8.85 was estimated by assuming a growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. 1999). The cephalopod diet composition **(DC)** is the same as the diet used in the preliminary model. Octopods in Alaska are known to consume crabs, bivalves, and snails (Vincent et al. 1998). Lacking region-specific and species-specific information the cephalopod diet composition is divided evenly between bivalves, snails, snow crabs, and other crabs.

(oo) Bivalves

The bivalves group is represented by numerous species from at least 13 families of the Class Bivalvia, including, clams, mussels, cockles, scallops, and scaphopods. Bivalves are a dominant part of the eastern Chukchi Sea benthic community in abundance and biomass (Feder et al. 2007, Schonberg et al. 2014).

(i) Updated parameters

Biomass (B): Many bivalves burrow into the sediment and are not well sampled by trawling gear. To calculate biomass we instead use data from quantitative benthic grab samples collected with van Veen grabs (0.1 m^{-2}) at sampling stations across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007). We calculated a biomass estimate of 90.288 t km^{-2}.

Production (P/B): The bivalve P/B (1.3) from the preliminary model was taken from taxonomically equivalent groups in Ecopath models of other Alaska ecosystems (data pedigree=6, Aydin et al. 2007). This estimate was derived from a from a single study conducted on the coast of Sweden (Evans 1984). Expanding our literature search we identified 8 P/B estimates for 5 bivalve species known to occur in the Chukchi Sea, taken from 6 different studies (Table 8). None of these studies used specimens collected within the Chukchi Sea, but the calculated P/B estimates were for species known to occur in the Chukchi Sea. These species-specific estimates were seen as an improvement over the previous P/B estimate and are used here in place of the P/B used in the previous model. The P/B's are averaged producing a functional group P/B of 0.756. The data pedigree for this new P/B is 5 (species-specific estimates).

Table 8. Bivalve P/B values used in the calculation of the bivalve group P/B. *Genus now changed to *Astarte*.

Reference	Taxa	P/B	Region
Asmus (1987)	*Mya arenaria*	0.41	North Sea
Burke and Mann (1974)	*Mya arenaria*	2.54	Nova Scotia
Gagayev (1990)	**Nicania montagui*	1.74	East Siberian Sea
Gagayev (1990)	**Tridonta borealis*	0.55	East Siberian Sea
Petersen (1978)	*Serripes groenlandicus*	0.13	Greenland
Petersen (1978)	*Serripes groenlandicus*	0.1	Greenland
Sejr et al. (2002)	*Hiatella arctica*	0.095	Greenland
Warwick and Price (1975)	*Mya arenaria*	0.48	England

Consumption (Q/B): Q/B is solved for by Ecopath with an assumed GE of 0.2. The updated estimate of P/B in combination with GE=0.2 results in a Q/B of 3.78.

(ii) Parameters from W13

Bivalves are assumed to primarily be benthic detritivores and may also feed on suspended particles and small phytoplankton (Ruppert and Barnes 1994). Their diet **(DC)** is divided between benthic microbes (25%) and benthic detritus (75%).

(pp) Snails

The snail functional group includes all gastropods (including nudibranchs) found in the eastern Chukchi Sea, except for pteropods which are included in other zooplankton. Numerous gastropod species are present in the eastern Chukchi Sea, representing at least 17 families (Blanchard et al. 2013a).

(i) Updated parameters

Biomass (B): The snail functional group is dominated by Buccinids in terms of biomass, which account for more than 70% of the snail biomass caught with beam trawl gear during the 2012 Arctic Eis survey. Of secondary importance are the Naticids, who represent more than 19% of the snail biomass caught in beam trawls. We calculated a biomass density estimate of 1.384 t km^{-2} from the Arctic Eis beam trawl catch data, and used this as our biomass input.

Production (P/B): The snail P/B (1.81) used by W13 was derived from a single study conducted in the intertidal zone of the North Sea (Asmus 1987). That P/B was neither region-specific nor species-specific. Lacking region-specific or species-specific estimates of P/B we instead use a molluscan mean P/B of 1.77 (±0.14, n=230) (Cusson and Bourget 2005).

Consumption (Q/B): Ecopath solves for Q/B with an assumed GE of 0.2. The updated P/B estimate of 1.77 in combination with the assumed GE results in a Q/B of 8.85.

Food habits (DC): The snail diet used in the preliminary model was based on general diet descriptions presented in Feder and Jewett (1981). Lacking more specific diet data, the estimated snail diet in W13 was spread evenly amongst possible prey groups. We improve upon this diet here by incorporating information from snail diet studies conducted in Alaska (Shimek 1984), Russia (Kosyan 2007), and the north Atlantic (Taylor 1978). The Buccinid diet at high latitudes is generally dominated by bivalves and polychaetes (Taylor 1978, Shimek 1984). Other prey items of lesser importance include barnacles, amphipods, sipunculans, priapulans, and carrion (detritus) (Taylor 1978, Shimek 1984, Kosyan 2007). Naticids specialize in feeding on bivalves by boring holes through their shells (Kabat 1990). Based on dietary descriptions from a variety of sources the snail diet used here consists of bivalves (50%), polychaetes (30%), amphipods (5%), worms etc. (5%), miscellaneous crustaceans (5%), and benthic detritus (5%).

(qq) Snow crab

Snow crab (*Chionoecetes opilio*) are a commercially important species of crab in the nearby eastern Bering Sea (NPFMC 2011) and are considered a species of potential commercial importance within the Arctic management area (NPFMC 2009, Wilson and Ormseth 2009). Tanner crabs (*C. bairdi*) are also sometimes referred to as snow crab, but they are not included here as their range does not extend north into the Chukchi Sea. Snow crabs in the eastern Chukchi Sea are generally smaller than those found in the eastern Bering Sea, and rarely grow to commercially legal size (carapace width ≥ 78 mm). During the 2012 Arctic Eis bottom trawl survey, only 29 of the ~28,000 snow crab caught were legal sized males (Goddard et al. 2014).

(i) Updated parameters

Biomass (B): We calculated a snow crab biomass estimate of 3.170 t km^{-2} from the Arctic Eis beam trawl catch data.

(ii) Parameters from W13

Snow crab **P/B** of 1.0 was derived from stock assessment data-specific to the eastern Bering Sea stock by Trites et al. (1999), Aydin et al. (2002), and Aydin et al. (2007). The **Q/B** estimate of 2.75 is also unchanged from the preliminary model, and was previously derived by Trites et al. (1999), Aydin et al. (2002), and Aydin et al. (2007).

The diet composition **(DC)** of snow crabs in Alaska is not well known. Previous food web models of large marine ecosystems in Alaska (Aydin et al. 2002, Aydin et al. 2007, W13) have based the diet composition of snow crabs (*Chionoecetes opilio* and *C. bairdi*) on the work of Tarverdieva (1981) who reported on the diet of *C. opilio* and *C. bairdi* in the eastern Bering Sea. Identification of snow crab stomach contents is hampered by the grinding of prey in the gastric mill, which reduces prey to a mushy pulp and limits the quantification of snow crab diet composition. The mastication of prey precludes the use of other common methods for quantifying stomach contents (Hyslop 1980), such as percent number (%N) or percent weight (%W). Divine et al. (In press) have been working toward addressing this data gap by examining the stomach contents of snow crabs (*C. opilio*) collected in the Chukchi and Beaufort seas. They have compiled a list of prey taxa they found in the stomachs of snow crabs and reported the frequency that these items occurred in stomachs (% frequency of occurrence [FO]). Some of the most frequently occurring prey categories across their study region were the polychaete Cistenides hyperborea(59.5%), bivalves (57.1%), and other polychaetes (42.9%). Other prey groups that were less frequently observed included amphipods (27.2%), decapods (25.7%), brittle stars (22.2%), and fishes (7.4%). Among the decapod prey, Divine et al. (In press) frequently observed brachyuran crabs which they note could possibly have been snow crabs. Detritus, sediment, and various bits of otherwise taxonomically unidentifiable prey (e.g., bits of shells, crustacean exoskeleton, fleshes) were also commonly observed among stomach contents. Similarly, Feder and Jewett (1978) examined the stomach contents of snow crabs collected in Norton Sound and also found sediment (56% FO), detritus (22.5% FO), and unidentified material (18.0%) to be among the most frequently occurring prey categories.

Our Ecopath modeling framework requires predator diet compositions to be expressed in terms of percent weight (or volume). It is not possible to accurately translate diet data described in terms of %FO to %W or volumetric composition. %FO can provide a qualitative view of observed prey items, but gives no indication of volumetric or numerical importance (Hyslop 1980). %FO may also be positively biased for prey with hard, indigestible parts (e.g., shells, exoskeletons) that linger in the digestive track for longer periods of time, and be negatively biased for softer prey items (e.g., worms, mollusk flesh) that are digested and evacuated quickly. In consideration of the limitations of %FO diet data, we do not use the %FO values provided in Divine et al. (In press) and continue to use the snow crab diet composition previously described by Tarverdieva (1981) and summarized by Aydin et al. (2007). The major prey groups are polychaetes (27%), benthic detritus (27%), bivalves (21%), brittle stars (6%), and benthic amphipods (6%). Other prey of lesser importance include other crabs, snails, worms etc., miscellaneous crustaceans, the urchins-dollars-cucumbers group, other zooplankton, phytoplankton, sponge, sea stars, and anemones.

(rr) Other crabs

The other crabs group includes all anomuran and brachyuran crabs with the exception of snow crab (*C. opilio*). Other brachyurans caught during the 2012 Arctic Eis trawl surveys included the circumboreal toad crab (*Hyas coarctatus*) and helmet crab (*Telmessus cheiragonus*). Anomurans caught during the Arctic Eis surveys included several species of hermit crabs (Paguridae) and two species of king crab; red king crab (*Paralithodes camtschaticus*) and blue king crab (*P. platypus*).

(i) Updated parameters

Biomass (B): We calculated a biomass estimate of 3.067 t km^{-2} from the 2012 Arctic Eis beam trawl catch data.

(ii) Parameters from W13

The other crabs **P/B** of 0.82 was taken from Ecopath models of the western and eastern Bering Sea (Aydin et al. 2002, Aydin et al. 2007). The **Q/B** of 4.10 was calculated with an assumed growth efficiency of 0.2 (an average growth efficiency for benthic invertebrates from Trites et al. 1999). The other crabs diet composition **(DC)** is based on the diets of taxonomically similar functional groups in the eastern Bering Sea Ecopath model (Aydin et al. 2007), and is divided equally among bivalves, polychaetes, worms etc., and benthic detritus.

(ss) Shrimps

The shrimp functional group includes all decapod shrimps occurring in the eastern Chukchi Sea. Shrimps are represented in the trawl survey data by multiple species from the families Crangonidae, Hippolytidae, and Pandalidae (Goddard et al. 2014).

(i) Updated parameters

Biomass (B): Shrimp are not well sampled with the trawling gear, and biomass estimates calculated from the catch data are assumed to underestimate the actual biomass. Initial attempts to balance the model with a biomass estimate of 1.655 t km^{-2}, calculated from the Arctic Eis beam trawl data, proved to be insufficient to meet predator demands (EE > 1). A top-down balance was performed instead resulting in a biomass estimate of 7.4922 t km^{-2}.

(ii) Parameters from W13

The shrimp **P/B** of 0.58 and **Q/B** of 2.41 are unchanged from W13 and are from taxonomically similar functional groups in Ecopath models of other large marine ecosystems in Alaska (Aydin et al. 2007). The diet composition **(DC)** of shrimps is the same as that used in the preliminary model. Lacking region-specific information, the diet composition in the preliminary model was based on diet descriptions found in multiple studies (Rice et al. 1980, Feder and Jewett 1981, Feder et al. 1981, Rice 1981). The estimated diet consists of benthic detritus (40%), bivalves (15%), benthic amphipods (15%), polychaetes (15%), and miscellaneous crustaceans (15%).

(tt) Sea stars

The sea star functional group is represented by several species from the families, Solasteridae, Goniopectinidae, Echinasteridae, Asteriidae, and Pterasteridae, all belonging to the Class Asteroidea.

(i) Updated parameters

Biomass (B): We calculated a sea star biomass estimate of 2.180 t km^{-2} from the 2012 Arctic Eis beam-trawl catch data.

Production (P/B): The P/B used for sea stars in the preliminary model (P/B=1.21) was borrowed from Ecopath models of other Alaska ecosystems and was derived from a minimum amount of information (Aydin et al. 2007). That P/B estimate was neither region-specific nor species-specific. Lacking P/B estimates of taxonomic and geographic relevance to our study region, we instead use an Echinoderm mean P/B of 0.34 (±0.06, n=28) calculated by Cusson and Bourget (2005).

Consumption (Q/B): Q/B is calculated by Ecopath with an assumed GE of 0.2. The updated P/B estimate in combination with the assumed GE results in a Q/B of 1.70.

(ii) Parameters from W13

The diet composition (DC) of sea stars is unchanged from the preliminary model. The diet was derived from information from multiple studies (Feder and Jewett 1978, Feder and Jewett 1981) and consists of bivalves (52%), sand dollars (27%), polychaetes (13%), snails (5%), and benthic urochordates (3%).

(uu) Brittle stars

Species from the order Ophiurida comprise the brittle star functional group. They are represented in the 2012 Arctic Eis trawl survey catch data by species from four genera, *Amphiophiura*, *Ophiura*, *Ophiacantha*, and *Ophiopholis*.

(i) Updated parameters

Biomass (B): We calculated a biomass estimate of 5.644 t km^{-2} for brittle stars from quantitative benthic grab samples collected with van Veen grabs (0.1 m^{-2}) from sampling locations across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007).

Production (P/B): Previously, brittle stars were assigned a P/B of 1.21 in W13. This estimate was neither species-specific nor region-specific. It was taken from Ecopath models of other Alaska ecosystems and was derived from a minimum of information (Aydin et al. 2007). P/B estimates for species known to occur in the Chukchi Sea are unavailable at the time of this writing. We have identified 5 P/B estimates for brittle star species belonging to genera that are known to occur in the Chukchi Sea, *Ophiocten* and

Ophiura (Table 9). A P/B range of 0.43 to 0.54 was calculated by Gage (2003) for *Ophiocten gracilis* along the Scottish continental slope in the NE Atlantic Ocean. Dahm (1993) estimated P/B ratios of 0.32 for *Ophiura albida* and 0.43 for *Ophiura ophiura* at locations on the German Bight in the southeastern North Sea. A P/B of 0.69 was calculated by Warwick et al. (1978) for *O. ophiura* in Carmarthen Bay, Wales. Similarly, a P/B of 0.5 was estimated for *O. ophiura* in Bristol Channel, Wales, by Warwick and George (1980) (cited by Dahm 1993). In lieu of P/B estimates specific to our study region and taxa, we calculate a mean P/B from the aforementioned sources. We use the midpoint of the range (0.485) reported by Gage (2003) and the 4 other point estimates to calculate a mean P/B of 0.485.

Table 9. Brittle star P/B values used to calculate the brittle star group P/B. †Midpoint of range reported by Gage (2003). *Cited by Dahm (1993).

Reference	Species	P/B	Region
Gage (2003)	*Ophiocten gracilis*	†0.485	NE Atlantic Ocean
Dahm (1993)	*Ophiura albida*	0.32	North Sea
Dahm (1993)	*Ophiura ophiura*	0.43	North Sea
Warwick et al. (1978)	*Ophiura ophiura*	0.69	Wales
Warwick and George (1980)*	*Ophiura ophiura*	0.5	Wales

Consumption (Q/B): Q/B is calculated by Ecopath with GE set at 0.2. The updated estimate of P/B in combination with GE results in Q/B=2.43.

(ii) Parameters from W13

The brittle star diet composition **(DC)** is unchanged from the preliminary model. In the absence of region-specific information, the diet composition was based on information from multiple sources (Warner 1982, Harris et al. 2009). The diet consists of 50% benthic detritus, with the remaining 50% divided evenly among bivalves, benthic amphipods, polychaetes, and miscellaneous crustaceans.

(vv) Basket stars

Basket stars of the eastern Chukchi Sea are represented by a single species, *Gorgonocephalus eucnemis* of the family Gorgonocephalidae. They are among the most abundant trawl caught invertebrates in the eastern Chukchi Sea by weight (Goddard et al. 2014).

(i) Updated parameters

Biomass (B): Basket star biomass was estimated from the 2012 Arctic Eis beam trawl catch data as 0.5099 t km^{-2}.

Production (P/B): In the preliminary food web model, basket stars were assigned a P/B of 1.21 which was borrowed from Ecopath models of other Alaska ecosystems (Aydin et al. 2007). This P/B estimate was a general proxy and was neither species-specific nor region-specific. Lacking a P/B estimate specific to our study region or taxa, we use an Echinoderm mean P/B of 0.34 (±0.06, n=28) calculated by Cusson and Bourget (2005).

Consumption (Q/B): The Q/B of 1.70 is calculated by Ecopath with an assumed GE of 0.2.

(ii) Parameters from W13

The basket star diet composition **(DC)** is unchanged from the preliminary model. In lieu of region-specific diet data, the basket star diet was derived from information from multiple sources (Patent 1970, Warner 1982, Emson et al. 1991, Rosenberg et al. 2005). The diet consists of equal parts benthic amphipods, miscellaneous crustaceans, copepods, and other zooplankton.

(ww) Urchins, dollars, cucumbers

The urchins, dollars, cucumbers functional group combines echinoderms from three orders; Clypeasteroida (sand dollars), Dendrochirotida (sea cucumbers), and Echinoida (sea urchins). It is primarily represented in the eastern Chukchi Sea by the green sea urchin (*Strongylocentrotus droebachiensis*), the common sand dollar (*Echinarachnius parma*), sea cucumbers of the genera Psolus and Cucumaria.

(i) Updated parameters

Biomass (B): We estimated the biomass of urchins, dollars, cucumbers to be 36.2897 t km^{-2} from quantitative benthic grab samples collected with van Veen grabs (0.1 m^{-2}) at sampling locations across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007). Larger organisms, such as the green sea urchin and common sand dollar, may not have been well sampled with the benthic grabs.

Production (P/B): The group consisting of sea urchins, sand dollars, and sea cucumbers was assigned a P/B of 0.61in W13. This P/B was borrowed from Ecopath models of other Alaska ecosystems (Aydin et al. 2007) and was not specific the Chukchi Sea. We have expanded our literature search and identified 5 species-specific P/B estimates (Table 10), including 3 estimates from high latitude regions surrounding Greenland (Blicher et al. 2007, Blicher et al. 2009). 4 of the P/B estimates are for the sea urchin *Strongylocentrotus droebachiensis*, and one for the sand dollar, *Echinarachnius parma*. We have averaged these 5 P/B estimates together to arrive at a group P/B of 0.695.

Table 10. P/B estimates from the literature used to calculate P/B for the urchins, dollars, cucumbers functional group.

Reference	Taxa	P/B	Location
Miller and Mann (1973)	*Strongylocentrotus droebachiensis*	0.8	NW Atlantic, Canada
Blicher et al. (2007)	*S. droebachiensis*	0.29	NE Greenland
Blicher et al. (2009)	*S. droebachiensis*	0.31	SW Greenland
Blicher et al. (2009)	*S. droebachiensis*	0.37	SW Greenland
Steimle (1990)	*Echinarachnius parma*	1.705	NW Atlantic, USA

Consumption (Q/B): The Q/B of 3.48 is calculated by Ecopath with the updated P/B estimate and an assumed GE of 0.2.

(ii) Parameters from W13

The diet composition **(DC)** of urchins, dollars, cucumbers is not changed from the preliminary model. Quantitative diet descriptions were not available for this group and the diet was based on generalized diet descriptions (DeRiddler and Lawrence 1982, Massin 1982, Ables 2000). The diet consists of benthic detritus (75%) and phytoplankton (25%).

(xx) Sponge

The sponge functional group contains all taxa from the Phylum Porifera. Sponge are frequently damaged when caught with trawling gear and are often only identified as Porifera in survey catch data (Wolotira et al. 1977, Barber et al. 1994). Recently, the black papilate sponge (*Halichondria sitiens*) was found to be one of the dominant benthic invertebrates (by weight) caught during the 2012 Arctic Eis bottom trawl survey of the eastern Chukchi Sea (Goddard et al. 2014).

(i) Updated parameters

Biomass (B): We calculated a sponge biomass estimate of 0.527 t km^{-2} from the 2012 Arctic Eis beam trawl catch.

(ii) Parameters from W13

Sponge **P/B** is unchanged from the preliminary model and remains at 1.0 (Aydin et al. 2007). The sponge **Q/B** is also unchanged and remains at 5.0, which was calculated be assuming a growth efficiency of 0.2. The diet composition **(DC)** of sponges is not changed from the preliminary model, and consists of benthic microbes (25%) and benthic detritus (75%).

(yy) Benthic Urochordate

Tunicates from the Class Ascidiacea comprise the benthic urochordate group. In the eastern Chukchi Sea, they are represented by species from at least four families; Pyuridae, Corellidae, Styelidae, and Didemnidae (Blanchard et al. 2013b). During the 2012 Arctic Eis bottom trawl survey of the eastern Chukchi Sea, Ascidians were found to be among the dominant benthic invertebrates (by weight), including *Boltenia ovifera*, the sea potato (*Styela rustica*), and the sea peach (*Halocynthia aurantium*) (Goddard et al. 2014).

(i) Updated parameters

Biomass (B): We estimated the biomass of benthic urochordates from the 2012 Arctic Eis beam trawl catch data as 1.160 t km^{-2}.

(ii) Parameters from W13

We did not change benthic urochordate **P/B** from W13 and it remains at 3.58 (Asmus 1987). The **Q/B** of 17.9 is also unchanged from the preliminary model, and was calculated assuming a growth efficiency of 0.2. The diet composition **(DC)** of this group has not changed from the preliminary model. They are filter feeders (Abbott 1966, Ruppert and Barnes 1994)and their diet consists of benthic bacteria (25%) and benthic detritus (75%).

(zz) Anemones

The Anemones functional group consists of Cnidarians from the Order Actinaria. In the eastern Chukchi Sea they are primarily represented by the mottled anemone (*Urticina crassicornis*) and species from the genus *Stomphia* (Blanchard et al. 2013b, Goddard et al. 2014).

(i) Updated parameters

Biomass (B): We estimated anemone biomass from the 2012 Arctic Eis beam trawl catch as 0.384 t km^{-2}.

(ii) Parameters from W13

P/B is unchanged from W13 and remains at 1.0. This P/B is from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The **Q/B** has also not changed and remains at 5.0, which was calculated with an assumed growth efficiency of 0.2. The food habits of anemones in Alaska are not well known and the diet composition **(DC)** is based on anemone diet descriptions from other regions (Frank and Bleakney 1978, Dalby 1992, Kruger and Griffiths 1998). The diet composition is divided evenly between benthic amphipods, miscellaneous crustaceans, bivalves, benthic microbes, and benthic detritus.

(aaa) Corals

Cnidarians from the Order Alcyonacea (soft corals) comprise the corals functional group. In the eastern Chukchi Sea they are primarily represented by species of the genus *Gersemia* (Blanchard et al. 2013b, Goddard et al. 2014, Schonberg et al. 2014).

(i) Updated parameters

Biomass (B): We estimated coral biomass to be 0.026 t km^{-2} from the 2012 Arctic Eis beam trawl catch.

(ii) Parameters from W13

P/B has not been changed from the preliminary model and remains at 0.05. This P/B is from a taxonomically similar functional group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). The corals **Q/B** of 0.23 was calculated with an assumed growth efficiency of 0.2. The diet composition **(DC)** of corals has not changed from the preliminary model, and consists of benthic microbes (25%) and benthic detritus (75%).

(bbb) Benthic Amphipods

The benthic amphipods functional group includes species from the crustacean suborders Gammaridea and Caprellidea. Amphipods are found throughout the eastern Chukchi Sea and are an important prey item for gray whales who migrate to the Chukchi Sea to feed during summer (Highsmith and Coyle 1992).

(i) Updated parameters

Biomass (B): Our initial biomass estimate of 8.074 t km^{-2} was calculated from the benthic grab data collected with van Veen grabs (0.1 m^{-2}) (Feder et al. 1994b, Feder et al. 2007), but was insufficient to balance the model (EE > 1). Instead we performed a top-down balance which resulted in an estimated biomass of 20.526 t km^{-2}.

(ii) Parameters from W13

The **P/B** of benthic amphipods has not changed from the preliminary model and remains at 1.0 (Highsmith and Coyle 1992). **Q/B** has also not changed from W13 and stays at 5.0, which was calculated with an assumed growth efficiency of 0.2. Benthic amphipod diet composition **(DC)** is the same as in W13. They are assumed to primarily be detritivores (Thomson 1986) and their diet is divided evenly between benthic microbes and benthic detritus.

(ccc) Polychaetes

Polychaete worms are a dominant component of the eastern Chukchi Sea benthic community in terms of abundance and biomass (Feder et al. 2007, Blanchard et al. 2013a, Schonberg et al. 2014). The polychaete assemblage in the eastern Chukchi Sea is diverse as well, with over 100 species known to occur there (Blanchard et al. 2013a, Schonberg et al. 2014).

(i) Updated parameters

Biomass (B): The biomass of polychaetes was estimated at 27.808 t km^{-2} from the benthic grab data collected with van Veen grabs (0.1 m^{-2}) at sampling stations spread across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007).

Production (P/B): The P/B used for polychaetes (P/B=1.645) in W13 was an average based on multiple polychaete P/B values presented in McLusky and McIntyre (1988). There are several published estimates of P/B for polychaetes (e.g., Cusson and Bourget 2005), none of which are specific to our study region. Estimates of polychaete P/B are also available from other Ecopath models. Trites et al. (1999) use a P/B of 1.37 for a composite functional group including polychaetes in their model of the eastern Bering Sea. In a similar composite benthic group, Field (2004) used a P/B of 2.5 in a model of the northern California Current. Harvey et al. (2010) use a P/B of 4.4 for polychaetes in their model of Puget Sound, Washington, USA. Pedersen et al. (2008) used P/B's of 0.5 and 0.75 for composite functional groups which included polychaetes in their model of a Norwegian fjord. A P/B of 2.97 was used for polychaetes in models of the eastern Bering Sea, Gulf of Alaska, and Aleutian Islands by Aydin et al. (2007) and in the western Bering Sea by Aydin et al. (2002). Cusson and Bourget (2005) calculated a mean P/B for all Annelida as 3.37 (±0.38, n=120). In our search of the literature we identified 15 P/B estimates for polychaete species known to occur in the eastern Chukchi Sea (Table 11), however none of the estimates are specific to our study region. We have averaged these 15 P/B estimates to arrive at a functional group P/B of 2.916.

Consumption (Q/B): Q/B is calculated by Ecopath with an assumed GE of 0.2. In combination with the updated P/B estimate this results in Q/B=14.58.

(ii) Parameters from W13

The diet composition (DC) of polychaetes is unchanged from the preliminary model. They are assumed to primarily be detritivores and their diet is divided evenly between benthic microbes and benthic detritus.

Table 11. Polychaete P/B values used in the calculation of the Polychaete group P/B. †Reported as Harmothoe sarsi by Asmus (1987). *Reported as Tharyx marioni by Asmus (1987) and Warwick et al. (1978).

Reference	Species	P/B	Region
Asmus (1987)	*Ampharete acutifrons*	2.23	Wadden Sea, intertidal (North Sea)
Asmus (1987)	*Capitella caitata*	3.78	Wadden Sea, intertidal (North Sea)
Asmus (1987)	*Eteone longa*	4.67	Wadden Sea, intertidal (North Sea)
Asmus (1987)	*†Bylgides sarsi*	1.14	Wadden Sea, intertidal (North Sea)
Asmus (1987)	*Heteromastus filiformis*	2.75	Wadden Sea, intertidal (North Sea)
Asmus (1987)	*Scoloplos armiger*	2.99	Wadden Sea, intertidal (North Sea)
Asmus (1987)	**Aphelochaeta marioni*	5.99	Wadden Sea, intertidal (North Sea)
McLusky and McIntyre (1988)	*Ampharete acutifrons*	4.58	Long Is., subtidal
McLusky and McIntyre (1988)	*Chaetozone setosa*	1.28	England, offshore 80m
McLusky and McIntyre (1988)	*Heteromastus filiformis*	1.01	England, offshore 80m
McLusky and McIntyre (1988)	*Lumbrineris fragilis*	1.34	England, offshore 80m
Valderhaug (1985)	*Lumbrineris fragilis*	0.826	Oslofjord, Norway
Warwick and Price (1975)	*Ampharete acutifrons*	5.5	England (intertidal estuary)
Warwick et al. (1978)	*Spiophanes bombyx*	4.86	Carmarthen Bay, S. Wales
Warwick et al. (1978)	**Aphelochaeta marioni*	0.79	Carmarthen Bay, S. Wales

(ddd) Worms, etc.

Worms etc. is a composite group that consists of several invertebrate taxa including the phyla, Sipuncula, Echiura, Priapula, Nemertea, Brachiopoda, and Bryozoa; and additionally the annelid Subclass Hirudinea (leeches) and the cnidarian Class Hydrozoa (hydroids).

(i) Updated parameters

Biomass (B): We estimate the biomass of worms etc. to be 17.039 t km^{-2} from the benthic grab data collected with van Veen grabs (0.1 m^{-2}) at sampling stations spread across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007).

(ii) Parameters from W13

The worms etc. **P/B** of 2.23 was taken from taxonomically equivalent groups in Ecopath models of the Bering Sea (Aydin et al. 2002). The **Q/B** of 11.15 was solved with an assumed growth efficiency of 0.2. The worms etc. diet composition **(DC)** has not changed from the preliminary model. They are assumed to primarily be detritivores and their diet is evenly divided between benthic microbes and benthic detritus.

(eee) Miscellaneous crustaceans

The miscellaneous crustaceans group combines all the remaining benthic oriented crustaceans that are not already included in a functional group. This group includes isopods, cumaceans, barnacles, pycnogonids, and ostracods.

(i) Updated parameters

Biomass (B): We calculated the miscellaneous crustaceans biomass to be 5.581 t km^{-2} from the benthic grab data collected with van Veen grabs (0.1 m^{-2}) at sampling stations spread across the eastern Chukchi Sea (Feder et al. 1994b, Feder et al. 2007).

Production (P/B): In the preliminary model, the miscellaneous crustaceans group had a P/B of 3.83. That estimate was derived from multiple P/B estimates that were not specific to the Chukchi Sea and included P/B estimates for several species not known to occur within our study region. We have improved upon that estimate here and calculate a mean P/B from published P/B estimates for species known to occur within the eastern Chukchi Sea (Table 12). Asmus (1987) calculated a P/B of 1.11 for the barnacle, *Balanus crenatus*, in the North Sea. Persson (1989) studied the life cycle and productivity of the cumacean, *Diastylis rathkei*, in the southern Baltic Sea and calculated a mean P/B of 2.03. Rachor et al. (1982) also studied the productivity of *D. rathkei* in the southern Baltic in Kiel Bay, and in the German Bight of the North Sea, where they calculated P/B ratios of 2.7 and 3.2, respectively. Ansell et al. (1978) reported a P/B estimate of 1.0 for *D. rathkei*. Lacking P/B estimates specific to our study region, we use a mean P/B of 2.008 calculated from the aforementioned P/B estimates.

Table 12. P/B values used in the calculation of the functional group P/B for Miscellaneous crustaceans.

Reference	Taxa	P/B	Region
Asmus (1987)	*Balanus crenatus*	1.11	North Sea
Persson (1989)	*Diastylis rathkei*	2.03	Southern Baltic Sea
Rachor et al. (1982)	*D. rathkei*	3.2	North Sea
Rachor et al. (1982)	*D. rathkei*	2.7	Southern Baltic Sea
Ansell et al. (1978)	*D. rathkei*	1	Temporate/northern boreal

Consumption (Q/B): Q/B is calculated by Ecopath with an assumed GE of 0.2. In combination with the estimated P/B of 2.008, this results in an estimated Q/B of 10.04.

(ii) Parameters from W13

The diet composition (DC) of miscellaneous crustaceans has not been changed from the preliminary model. They are assumed to primarily be detritivores and their diet is divided evenly between benthic microbes and benthic detritus.

4.7 Pelagic Invertebrates and Microbes

(fff)Jellyfish

The jellyfish group includes all Scyphozoan jellies found in the eastern Chukchi Sea and is primarily represented by the sunrise jellyfish (*Chrysaora melanaster*) (Goddard et al. 2014).

(i) Updated parameters

Biomass (B): We calculated a biomass estimate of 0.372 t km^{-2} from the 2012 Arctic Eis bottom trawl survey.

(ii) Parameters from W13

We did not change the jellyfish **P/B** from the preliminary model, and it remains 0.88. This P/B was taken from a taxonomically equivalent functional group in a Bering Sea Ecopath model (Aydin et al. 2007). The jellyfish **Q/B** of 3.0 was estimated by Aydin et al. (2007) from summer ration information reported by Brodeur et al. (2002) for an equivalent jellyfish group in a Bering Sea Ecopath model. The jellyfish diet composition **(DC)** is unchanged from W13 and they are assumed to feed on pelagic prey. Their assumed diet consists of copepods (67.5%), other zooplankton (22.5%), pelagic microbes (5%), and phytoplankton (5%).

(ggg) Copepods

Copepods are a dominant component of the pelagic ecosystem in the Chukchi Sea in terms of biomass and abundance (Ashjian et al. 2003, Hopcroft et al. 2010, Matsuno et al. 2011, Eisner et al. 2013, Questel et al. 2013). They are an important node in the Chukchi Sea food web, connecting pelagic and sympagic primary production to higher trophic level predators, including larger zooplankton (Båmstedt and Karlson 1998, Brodeur and Terazaki 1999, Dalpadado et al. 2008), fish (Gray et al. 2015, Whitehouse et al. *Accepted*), seabirds (Springer and Roseneau 1985), and marine mammals (Moore et al. 2010). Many of the copepod species found in the Chukchi Sea are of Pacific origin and have been advected into the Chukchi Sea through the Bering Strait (Springer et al. 1989), though the species composition and geographic distribution is known to vary annually (Pinchuk and Eisner *Accepted*).

(i) Updated parameters

Biomass (B): Biomass is not input to the model and instead we used a top-down balance, assuming EE=0.8, to estimate copepod biomass as 2.04 t km^{-2}. Copepod biomass was also top-down balanced in the preliminary model, also with EE=0.8.

(ii) Parameters from W13

We did not change copepod **P/B** from W13 and continue to use the P/B of 6.0, which was taken from a taxonomically equivalent group in an Ecopath model of the eastern Bering Sea (Aydin et al. 2007). We also continue to use the **Q/B** of 27.74 for copepods from W13, which was taken from a taxonomically equivalent group in the eastern Bering Sea Ecopath model (Aydin et al. 2007). We did not change the diet composition **(DC)** of copepods from the diet used in the preliminary model. Arctic copepods are generally omnivorous, consuming both phytoplankton and microzooplankton (Conover et al. 1986, Runge and Ingram 1988, 1991, Levinsen et al. 2000, Campbell et al. 2009). The specific composition of copepod diets within the Chukchi Sea is not well known, and the assumed diet used here is evenly split between pelagic microbes (microzooplankton) and phytoplankton.

(hhh) Other zooplankton

The other zooplankton group consists of all other meso- and macro-zooplankton species excluding copepods. This group includes euphausiids, mysids, hyperiids, larvaceans, pteropods, chaetognaths, meroplankton, and ctenophores. Similar to copepods, many of the species in the other zooplankton group are of Pacific origin and have been advected into the Chukchi Sea through the Bering Strait (Springer et al. 1989, Hopcroft et al. 2010).

(i) Updated parameters

Biomass (B): As in the preliminary model, we did not input biomass to the model and instead biomass is estimated by Ecopath, with EE set to 0.8. This produced a biomass estimate of 1.225 t km^{-2}.

(ii) Parameters from W13

P/B is not changed from the preliminary model and remains at 5.48. This P/B was originally calculated for euphausiids in the southeastern Bering Sea (Smith 1991), and is used for taxonomically similar functional groups in the eastern Bering Sea Ecopath model (Aydin et al. 2007). The **Q/B** of 15.64 is also unchanged from the preliminary model, and was solved for with an assumed growth efficiency of 0.35 (Aydin et al. 2007). We did not change the diet composition **(DC)** of other zooplankton from the diet used in the preliminary model. Diet studies of related taxa in other ecosystems indicates that species from this group may feed on phytoplankton, copepods, other zooplankton, and pelagic microbes (Båmstedt and Karlson 1998, Brodeur and Terazaki 1999, Acuña et al. 2002, Dalpadado et al. 2008). Lacking region-specific diet data, the diet for other zooplankton is based on the estimated diet of taxonomically similar functional groups from the eastern Bering Sea Ecopath model (Aydin et al. 2007), and consists of phytoplankton (60%), copepods (25%), and pelagic microbes (15%).

(iii) Pelagic microbes

The pelagic microbes (microzooplankton) group is a composite group that primarily consists of bacteria and protozoans, and is intended to represent processes in the pelagic microbial loop.

(i) Updated parameters

Biomass (B): Biomass estimates of pelagic microbes in the eastern Chukchi Sea are not available. A top-down balance, with EE=0.8, was used in the preliminary model and we use the same approach here. The top-down biomass estimate of pelagic microbes is 1.49 t km^{-2}.

(ii) Parameters from W13

We did not change the pelagic microbe **P/B** and continue to use the P/B of 26.25 from W13. This P/B was derived from information in Kirchman et al. (2007) on growth rates for bacteria and the total prokaryotic community in shelf areas (<100 m) of the western Arctic Ocean. **Q/B** remains at 75.0, which was estimated with an assumed growth efficiency of 0.35 (Aydin et al. 2007). We did not change the diet composition **(DC)** of pelagic microbes from the diet in the preliminary model. Pelagic microbes are assumed to primarily consume phytoplankton and pelagic detritus (Sherr et al. 2009). Their assumed diet consists of 70% phytoplankton and 30% pelagic detritus.

(jjj) Benthic microbes

The benthic microbes group is a composite group that primarily consists of bacteria and protozoans, and is intended to represent processes in the benthic microbial loop.

(i) Updated parameters

Biomass (B): The biomass of benthic microbes on the eastern Chukchi Sea shelf is not well known, so a top-down balance with EE=0.8 was used in the preliminary model and we use the same approach here. This resulted in a density estimate of 22.31 t km^{-2}.

(ii) Parameters from W13

The **P/B** for benthic microbes is assumed to be similar to pelagic microbes so they are given the same P/B of 26.25. **Q/B** is assumed to be the same for benthic microbes as for pelagic microbes, and is solved for with an assumed growth efficiency of 0.35 (Aydin et al. 2007). The diet **(DC)** of benthic microbes is not changed from the preliminary model. Their diet is assumed to consist of 100% benthic detritus.

4.8 Phytoplankton

Phytoplankton is a composite group combining all primary producers in the eastern Chukchi Sea. The dominant component of the autotrophic phytoplankton biomass in the Chukchi Sea is diatoms and they also rank second in terms of abundance (Sukhanova et al. 2009).

Primary production in the Chukchi Sea is seasonally limited by light (e.g., day length, low sunlight angle) and sea ice cover. During winter the low levels of light in combination with the presence of sea ice prevent phytoplankton blooms from initiating. As day length increases during spring, the snow cover begins to melt and primary production begins with an ice algae bloom within the sea ice (Cota et al. 1991, Horner et al. 1992). As the sea ice continues to melt and break-up under increasing amounts of sunlight, the water column becomes stratified with low-density melt-water at the surface helping create conditions favorable for development of an ice-edge bloom (Alexander and Niebauer 1981, Sakshaug and Skjoldal 1989, Perrette et al. 2011). The ice edge bloom then follows the receding ice edge northward.

During the open water season in the Chukchi Sea, primary production is highest near the ice edge and in the open water of the southern Chukchi Sea where primary production is fueled by the input of nutrient-rich water from the Bering Sea (Hansell et al. 1993, Wang et al. 2005). In general, ice algae is thought to only account for a small portion of total primary production on seasonally ice-covered Arctic shelves and most of the primary production is thought to come from phytoplankton production in open waters and near the ice edge (Subba Rao and Platt 1984, Gosselin et al. 1997, Hill and Cota 2005, Pabi et al. 2008). Recent field studies in the Chukchi Sea have recorded the presence of prolific phytoplankton blooms in the water column beneath fully consolidated sea ice (Arrigo et al. 2014). Under ice production is not detected by satellite-based methods used for estimating primary production and if such under ice blooms occur regularly, satellite-based estimates may underestimate total production on Arctic shelves (Arrigo et al. 2012). Lowry et al. (2014) re-analyzed the satellite record back to 1998, attempting to identify evidence of under ice phytoplankton blooms, and found evidence suggesting that such under-ice blooms may be widespread in the Chukchi Sea .It is not yet know whether under ice blooms in the Chukchi Sea are something that has only recently begun to occur or whether they have been a regular feature for many years but have gone undetected (Arrigo et al. 2014).

Primary production is spatially variable in the eastern Chukchi Sea and generally ranges from about 20 to >400 g C m^{-2}yr^{-1} (Sakshaug 2004). Parrish (1987) estimated primary production to range from ~50 g C m^{-2}yr^{-1} in the northeastern Chukchi Sea to ~150 g C m^{-2}yr^{-1} over the southern Chukchi Sea. Similarly, Hill and Cota (2005) estimated primary production to be 70.5 g C m^{-2}yr^{-1} over the northeastern Chukchi Sea continental shelf. Portions of the southern Chukchi Sea that are supplied with nutrient-rich water flowing in from the Bering Sea may experience much higher levels of productivity. Springer and McRoy (1993) described such a location in the south-central Chukchi Sea which had an estimated annual production of 470 g C m^{-2}yr^{-1}, and may range as high as 720 g C m^{-2}yr^{-1}.

(iii) Updated parameters

Biomass (B): Phytoplankton biomass was initially top-down balanced with EE set to 0.8 which resulted in a low biomass estimate of ~2.4 t km^{-2}. If we assume that C weight is 45% of dry weight and that dry weight is 15% of wet weight (Valiela 1995), that's approximately 0.16 g C m^{-2}. Assuming a 150 day growing season and our P/B of 75, this is equivalent to ~12 g C m^{-2}yr^{-1} which is lower than most estimates of primary production in the eastern Chukchi Sea. This low top-down estimate is primarily due to the relatively low grazing pressure from zooplankton (Campbell et al. 2009, Sherr et al. 2009). A side effect of this low phytoplankton biomass estimate is that benthic detritus was out of balance (EE>1). This is the result of heavy trophic pressure on benthic detritus by abundant benthic invertebrates (See Detritus section below). In this model phytoplankton is the largest contributor to benthic detritus. This same situation with benthic detritus being out of balance, occurred during efforts to balance the preliminary model. To bring benthic detritus back into balance, W13 increased the biomass of phytoplankton in increments of 1 t km^{-2} until benthic detritus became balanced (EE ≤ 1). The resulting combination of B and P/B was equivalent to ~170 g C m^{-2}yr^{-1} (Whitehouse et al. 2014). We elected to use the same approach here and increased phytoplankton biomass in increments of 0.1 t km^{-2} until benthic detritus came back into balance. This resulted in a biomass estimate of 27.8 t km^{-2}. In combination with P/B=75 and assuming a 150 day growing season, this is equivalent to an annual production of ~141 g C m^{-2}.

(iv) Parameters from W13

Phytoplankton **P/B** is unchanged from the preliminary model and remains 75. This P/B was derived from an average maximum daily growth rate of 0.5 d^{-1} for Arctic diatoms in the Barents Sea (Gilstad and Sakshaug 1990), scaled up to an annual rate.

4.9 Detritus

During our initial attempts to balance the model, benthic detritus was out-of-balance (EE > 1). This was the result of high trophic demand for detritus in combination with insufficient supply to the benthic detrital pool. Within the model, the primary source to the benthic detrital pool is phytoplankton. In the eastern Chukchi Sea much of the phytoplankton bloom and ice algae experience low grazing pressure by zooplankton and ultimately sink out of the water column and are incorporated into the benthic detrital pool. Additionally, phytoplankton and detritus may be advected into the Chukchi Sea from the northern Bering Sea through Bering Strait (Stoker 1981, Hansell et al. 1989, Springer and McRoy 1993, Feder et al. 1994b, Dunton et al. 2005, Carmack and Wassmann 2006). Such outside production may represent a significant portion of the total annual phytoplankton production in the Chukchi Sea. Using a nitrogen budget, Hansell and Goering (1990) estimated that approximately 60% of the annual primary productivity in the highly productive northern Bering Sea (just south of the Bering Strait) is advected into the southern Chukchi Sea where it eventually settles to the benthos. Additionally, other detrital matter, such as phytodetritus, detritus of terrestrial origin, marine snow, and zooplankton fecal pellets, may be advected into the southern Chukchi Sea from the northern Bering Sea (Walsh et al. 1997). The downward flux and horizontal distance that detrital matter may travel before deposition to the benthos is affected by the sinking rate, the horizontal velocity, water column depth, and grazing by zooplankton (Turner 2002). The sinking rate of such detrital matter is influenced by particle size, particle aggregation potential, particle fragmentation, the presence or colonization by microbes, and for fecal pellets, the predator diet (Turner 2002). In the area of the Bering Strait there is reduced deposition of organic matter to the benthos, as reflected by lower sediment oxygen uptake rates (Grebmeier and McRoy 1989), which may be due to increased current velocities while transiting the narrow Bering Strait (Coachman et al. 1975, Clement et al. 2005, Woodgate et al. 2005). The suspended organic content passing through the Bering Strait eventually settles to the benthos in the south-central Chukchi Sea where the current slows at recognized areas of increased sedimentation (Dunton et al. 2005, Grebmeier et al. 2006). The delivery of organic matter to the Chukchi Sea is also affected by inter-annual and seasonal variation in the flow velocity through Bering Strait. The flow regime through Bering Strait and the subsequent residence time of water parcels within the Chirikov Basin are related to the local wind regime (Coachman et al. 1975, Coachman and Shigaev 1992). During periods when wind conditions reduce flow through the Bering Strait, water parcels and their entrained organic matter may spend increasing amounts of time transiting the Chirikov Basin, increasing the deposition of organic matter south of Bering Strait and reducing the amount of organic matter available for deposition north of Bering Strait (Coachman and Shigaev 1992). Increased velocity and turbulence as water masses pass through Bering Strait mixes the water column, resupplying surface layers with nutrients, setting the stage for another production cycle to begin in the southern Chukchi Sea (Coachman and Shigaev 1992).

The biomass of the benthic community is positively correlated with primary production in the overlying water masses throughout the Chukchi Sea (Grebmeier et al. 1988, Grebmeier 1993, Dunton et al. 2005). Primary production rates are lower in the northeastern Chukchi Sea (Parrish 1987, Springer and McRoy 1993, Hill and Cota 2005) but high benthic biomass is thought to be sustained there by the advection of carbon rich waters from the northern Bering and southern Chukchi seas into the northeastern Chukchi Sea (Feder et al. 1994b). Organic contributions from the Bering Sea to food webs of the Chukchi Sea have been supported by stable isotope analyses (Dunton et al. 1989).

The advection of primary production and other organic matter northward through Bering Strait is an important part of the carbon budget (Walsh et al. 1989, Walsh et al. 1997) and food web of the Chukchi Sea (Dunton et al. 1989, Dunton et al. 2005, Grebmeier et al. 2006). The seasonal and inter-annual variation of physical, chemical, and biological properties of water masses transiting Bering Strait make it difficult, if not impossible, to know with accuracy the specific contribution of outside primary production and other organic matter make to the eastern Chukchi Sea food web. Lacking the required information to adequately portray these processes in our trophic model, we elect to use the same approach here to balance benthic detritus as that used in the preliminary model. Previously, W13 brought benthic detritus into balance by supplementing the benthic detrital pool with additional phytodetritus by increasing the phytoplankton biomass, and the same approach is used here in this model update (See Phytoplankton above). This approach resulted in a phytoplankton biomass of 27.8 t km^{-2}, which in combination with its P/B of 75, and assuming a 150 day growing season was equivalent to an annual primary production of ~141 g C m^{-2}.

4.10 Model Balancing

There were few adjustments to input parameters required to bring the updated model into balance. This was at least in part due to the present model update beginning with the preliminary model that was already balanced. Many of the updated input parameter values were only modestly different from the pre-existing model parameters, and therefore the new input parameters resulted in minimal change to model outputs (e.g., EE). However, a few significant adjustments were required to achieve a balanced model.

Perhaps the most conspicuous parameter adjustment was the increase in phytoplankton biomass. The initial top-down estimate of phytoplankton biomass was low, and when considered in combination with P/B (i.e., B*(P/B)) was equivalent to a total annual production estimate lower than most published estimates for this region (~12 g C m^{-2}yr^{-1}). Additionally, benthic detritus was out of balance (EE > 1). In both the preliminary model and the present model update, phytodetritus is the largest contributor to the benthic detrital pool. To satisfy the estimated detrital demand from consumers and bring benthic detritus back into balance, we supplemented the benthic detrital pool with phytodetritus by increasing phytoplankton biomass. This same tactic for balancing benthic detritus was used to balance the preliminary model (W13). This line of reasoning is consistent with previous studies documenting the strong pelagic-benthic coupling in this ecosystem (e.g., Dunton et al. 2005, Grebmeier 2012, Blanchard et al. 2013a, Blanchard and Feder 2014). The final phytoplankton biomass was equivalent to an annual production rate of ~141 g C m^{-2}, which falls within the range of annual primary production estimates reported in the literature (e.g., Sakshaug 2004).

Another significant adjustment was the reconfiguration of the miscellaneous shallow fish functional group. Previously, this functional group contained a number of lesser-known demersal fish taxa including, pricklebacks, snailfish, and poachers, and had a generalized diet based on stomachs collected for some of the same species in the eastern Bering Sea (W13), as opposed to the Chukchi Sea. In this model update we were able to improve the diet description for miscellaneous shallow fish with region-specific diet information (Whitehouse et al. *Accepted*). However, this new diet data brought to light the high level of predation between species within this functional group. Some of the species within the miscellaneous shallow fish group were important predators of each other, and that was not the case with the diets used in the preliminary model. Because this group was top-down balanced, cannibalism created a loop that resulted in unreasonably high biomass estimates for several fish functional groups. To eliminate the looping problem introduced by cannibalism, we removed from the miscellaneous shallow fish group those species that were feeding on other species within this functional group, primarily the variegated snailfish and other snailfish species (*Liparis* sp.). We split the miscellaneous shallow fish functional group from W13 into three functional groups: 1) miscellaneous shallow fish, 2) variegated snailfish, and 3) other snailfish. This eliminated the problems associated to within group cannibalism and reduced the top-down biomass estimates of fish groups to better reflect the true demand of these fish species within the ecosystem.

Biomass was top-down balanced for several of the functional groups for which survey data was available to calculate a biomass estimate. This included 11 of the 16 fish functional groups, cephalopods, and shrimp. The combinations of initial input parameters (e.g., B, P/B, etc.) for these functional groups were insufficient to balance the model (EE > 1). After reviewing all the input parameters for these functional groups and examining related input parameters for predators (e.g., B, Q/B, P/B, DC) of these functional groups, it was determined the most likely cause for imbalance was underestimation of biomass. For the fish functional groups, cephalopods, and shrimp, this is consistent with the findings of Whitehouse et al. (2014), who also top-down balanced these same groups. An underestimation of biomass for fish, cephalopods, and shrimp from the bottom trawl survey data, may reflect spatial limitations of survey coverage, patchy species distribution, and inter-annual variation in abundance, or low catchability of some species to the sampling gear (e.g., mesh size of the bottom-trawl net).

The biomass of benthic amphipods was not top-down balanced in the preliminary model but is top-down balanced in the present model. In this model we used a considerably lower region-specific density estimate (8.1 t km^{-2} vs. 33.9 t km^{-2}) as an initial model input which resulted in insufficient biomass to satisfy the trophic demand for benthic amphipods in the system (i.e., EE > 1). The higher biomass density estimate of 33.9 t km^{-2} used by W13 was taken from an area in the northern Bering Sea known to have high densities of amphipods (Stoker 1981), and may have overestimated the biomass of benthic amphipods in the eastern Chukchi Sea. After re-examining all the input parameters for benthic amphipods and their predators (e.g., B, Q/B, DC), it was determined that underestimation of biomass was the most likely cause for imbalance. Benthic invertebrate groups, including amphipods, have patchy distributions in the Chukchi Sea which may arise from variation in the properties of the overlying water masses (e.g., temperature, salinity), sediment characteristics, and food availability (e.g., delivery of organic nutrients) (Feder et al. 2007, Blanchard et al. 2013a, Blanchard and Feder 2014, Schonberg et al. 2014). Amphipod densities as high as 26 t km^{-2} have been observed at sampling stations in the northeastern Chukchi Sea (Schonberg et al. 2014). The Ecopath top down biomass estimate of 20.5 t km^{-2} for benthic amphipods is lower than the densities observed in the northern Bering Sea and lower than some of the higher amphipod densities recently observed in eastern Chukchi Sea (e.g., Schonberg et al. 2014).

4.11 Model comparisons

(kkk) Updated model vs. Preliminary model

(i) Biomass

The pattern of biomass distribution amongst the broader taxonomic categories is much the same in the updated model as it was in Whitehouse et al. (2014) (Table 13). Benthic-oriented invertebrates account for the majority (76.6%) of the total system biomass (excluding detritus), followed by phytoplankton (9.6%) and microbes (8.2%). All remaining aggregate groups account for 5.6% of total system biomass combined.

Despite the broad similarities between the preliminary model and this model update; there are some significant changes in the biomass estimates for the aggregated groups. In general, biomass estimates increased for the higher trophic level (TL) groups (TL>3.5); mammals (average TL=4.4), seabirds (average TL=4.1), and fishes (average TL=3.9), and biomass estimates generally decreased for lower trophic level groups; benthic invertebrates (average TL=2.8), jellyfish (TL=3.4), microbes (average TL=2), and phytoplankton (TL=1). The one exception to this pattern is zooplankton (average TL=2.5), whose aggregate biomass had a modest increase.

The aggregated biomass of marine mammal groups increased by 10% from the preliminary model to the updated model, due to an increase in the estimated biomass of bowhead whales. The bowhead whale biomass estimate in the preliminary model was based on an estimate of the population size in 1988 (6,928 whales) (George et al. 2004). Bowhead whale biomass in the updated model is based on a more recent abundance estimate for the population in 2004 of 12,631 whales (Koski et al. 2010), which is nearly double the estimate used in the preliminary model. The biomass estimates used for gray whales and Pacific walrus in the updated model are both also based on more recent abundance estimates; however, unlike bowhead whales these changes resulted in a decrease in their respective biomass estimates. The biomass estimates for all other marine mammals are unchanged. The net result is an increase in total marine mammal biomass of ~10%.

Table 13. Comparison of the distribution of biomass among aggregated groups and system metrics between the preliminary model of Whitehouse et al. (2014) and the present model update. The proportion of total system biomass (excluding detritus) represented by aggregated functional groups is shown as a percentage. The percent change in the aggregated biomass for each group is shown in the

column “% change in B”. Similarly, changes in the value of system metrics from the preliminary model to the present model updated are shown in the column “% change in metric”.

Aggregate group	This study	Whitehouse et al. (2014)	% change in B
Mammals	0.3%	0.2%	10%
Seabirds	0.0012%	0.0004%	144%
Fish	4.1%	1.1%	215%
Benthic invertebrates	76.6%	81.1%	-23%
Jellyfish	0.1%	0.2%	-43%
Zooplankton	1.1%	0.9%	3%
Microbes	8.2%	7.0%	-4%
Phytoplankton	9.6%	9.6%	-18%
System metric			**% change in metric**
Total system throughput (t km^{-2} yr^{-1})	8,452	10,000	-15%
Total production (P, t km^{-2} yr^{-1})	3,000	3,578	-16%
Total net primary production (t km^{-2} yr^{-1})	2,085	2,550	-18%
Total biomass (B, t km^{-2}, excluding detritus)	291.1	355.5	-18%
Total P/Total B (excluding detritus)	10.3	10.1	2%

There was a substantial increase in seabird biomass of 144%. This increase in seabird biomass is due to the addition of two new seabird functional groups (Procellarids and Scolopacids) representing four species, whose biomass was not included in the preliminary model. The biomass estimates of all other bird species did not change.

Total fish biomass made the largest leap, increasing by 215%. This increase is not due to the new trawl-survey data and new biomass estimates, but rather the new region-specific diet compositions we added showing higher levels of piscivory than previously modeled. As was the case with the preliminary model, survey derived estimates of fish biomasses were not sufficient to supply the estimated consumption, and top-down balance was required to estimate biomass. For several fishes, the new diet information indicated higher levels of piscivory than was estimated in the preliminary model with diet data for the same species from the nearby eastern Bering Sea. The higher levels of piscivory also necessitated breaking the miscellaneous shallow fish group into three functional groups to eliminate computational problems associated with cannibalism. The additional top-down pressure from other fishes due to the updated information on diet composition was sufficient to substantially increase the total fish biomass.

The aggregated biomass of benthic-oriented invertebrates decreased by 23% from the preliminary model to the updated model. This is primarily due to the inclusion of updated biomass estimates for several benthic invertebrate functional groups in the updated model. In the preliminary model, density estimates for eight of the benthic invertebrate groups were based on average densities reported in Stoker (1981) for the combined continental shelves of the eastern Chukchi and eastern Bering seas. Density estimates for those same eight groups (bivalves, snails, sea stars, brittle stars, urchins-dollars-cucumbers, benthic amphipods, polychaetes, and worms etc.) in the updated model are derived from benthic survey data (grab samples and beam trawls) gathered only in the eastern Chukchi Sea, and resulted in generally lower biomass estimates. The biomass estimates used in the updated model are region-specific and therefore have a higher data pedigree (2) than the biomass estimates used in the preliminary model (7).

The biomass of jellyfish (Schyphozoa) decreased by 43% from the preliminary model to the updated model. Both the biomass estimate in the preliminary model and the estimate we calculated here for the updated model are derived from bottom-trawl survey catch data and do not accurately estimate the total jellyfish biomass as jellies may be found throughout the water column, and are poorly sampled by bottom trawl gear. Though the two surveys used comparable trawling gear; the sampling design, total area surveyed, and total number of stations sampled, differ between the two surveys. Additionally, the difference between the two biomass estimates may reflect inter-annual variation in species abundance, species composition, and spatial distribution. The two density estimates are merely point estimates and are not suitable for establishing any trend in biomass or abundance.

There was a small increase in the estimated aggregate biomass of zooplankton (copepods and other zooplankton). As these groups are top-down balanced, this gain in biomass reflects an overall (slight) increase in demand from predators. There is an equally small increase in the proportion of total system biomass represented by zooplankton (+0.2%). This is the net result of an overall decrease in total system biomass (excluding detritus) in combination with the small increase in zooplankton biomass. The decrease in total system biomass is largely driven by the 23% decrease in benthic-oriented invertebrates, which are not important consumers of zooplankton. The consumptive demand for zooplankton from predators in the updated model is sufficient to maintain biomass levels roughly equivalent to their values in the preliminary model.

Similar to zooplankton, the aggregate biomass of microbes decreased 4% from the preliminary model to the updated model. As these groups are also top-down balanced, this reduction in biomass reflects a net decrease in demand from predators. However, the proportion of total system biomass represented by microbes increased by 1.2% from the preliminary model to the updated model. This is primarily the result of a decrease in total system biomass (down 18%) that is proportionally greater than the decrease in microbe biomass (down 4%).

The estimated biomass of phytoplankton decreased 18% from the preliminary model (34 t km^{-2}) to the updated model (27.8 t km^{-2}). This is directly related to our method for balancing benthic detritus by supplementing the benthic detrital pool with phytodetritus (i.e., increasing phytoplankton biomass). The amount of organic material required to balance the benthic pool is directly related to the trophic demand for benthic detritus from benthic detritivores. Because the estimated biomass of benthic detritivores decreased from the preliminary to the updated model, so did the trophic demand for benthic detritus. This resulted in a lower amount of phytodetritus required to balance the benthic detrital pool in the updated model, and ultimately a lower biomass estimate for phytoplankton.

(ii) Ecosystem metrics

The ecosystem level metrics highlight a few key differences between the preliminary model and our updated model. In general, the preliminary model had more biomass, production, and total flow than the updated model (Table 13). Changes to these ecosystem-scale metrics can largely be traced back to changes in input parameters that improved several data pedigrees. The 23% decrease in benthic-oriented invertebrate biomass had the most profound effect on these ecosystem metrics. The improved data used to estimate benthic-oriented invertebrate biomass improved the data pedigree for most of these groups from 7 to 2, but ultimately resulted in lower biomass estimates. Benthic invertebrates dominate this ecosystem in terms of biomass, and the total reduction in their biomass estimates (65.3 t km^{-2}) is approximately equal to the reduction in total system biomass from the preliminary model (355.5 t km^{-2}) to the updated model (291.1 t km^{-2}). Increases in biomass for mammals, seabirds, fish, and zooplankton (combined increase of 8.3 t km^{-2}) are similar in magnitude to biomass decreases for jellyfish, microbes, and phytoplankton (combined decrease of 7.4 t km^{-2}, Table 13).

The reduction in benthic invertebrate biomass also effects the reduction in total production (Table 13). Because many of these benthic invertebrates with lower biomass estimates are important consumers of benthic detritus, and benthic detritus is balanced by supplementing the benthic detrital pool with phytodetritus; the reduction in benthic invertebrate biomass ultimately resulted in lower phytoplankton biomass in the updated model than in the preliminary model. This resulted in lower total primary production and ultimately lower total ecosystem production. The reduction in net primary production from the preliminary model (2,550 t km^{-2} yr^{-1}) to the updated model (2,085 t km^{-2} yr^{-1}) accounts for ~80% of the reduction in total ecosystem production between these two models. Additionally, the lower biomass estimates of benthic invertebrates in combination with changes to several of their P/B rates resulted in a net loss in production of these groups, accounting for ~16% of the loss in total system production in the updated model. Overall, the total production in the updated model is about 16% lower than in the preliminary model.

Total system throughput measures the total mass flow in an ecosystem and reflects the overall size of the ecosystem (Christensen et al. 2005). Total system throughput in the updated model is about 15% lower than the preliminary model and is a reflection of the combined decreases in biomass and production. Not coincidentally, the size of reduction in total system throughput is similar in magnitude to the reductions seen in total biomass (-18%), production (-16%), and net primary production (-18%). The decreases in biomass and production reduce the mass flow rates for consumption, respiration, and flow to detritus, ultimately lowering the total system throughput.

Overall, the fundamental structure and function of the preliminary model is maintained in the updated model (Figures 3 and 4). The majority of biomass is found in benthic invertebrate groups and mass flows are dominated by flows from benthic sources (blue boxes in Figures 3 and 4). The combined changes in total ecosystem production and total biomass resulted in a modest ~2% increase in the ratio of total production to total biomass. The total ecosystem P/B is 10.3 in the updated model, up from 10.1 in the preliminary model. Despite the numerous, small changes to input parameter values that resulted in substantial decreases in total biomass, production and net primary production, the relatively unchanged state of the ecosystem P/B reflects the maintenance of key structural and functional properties from the preliminary model in the updated model.

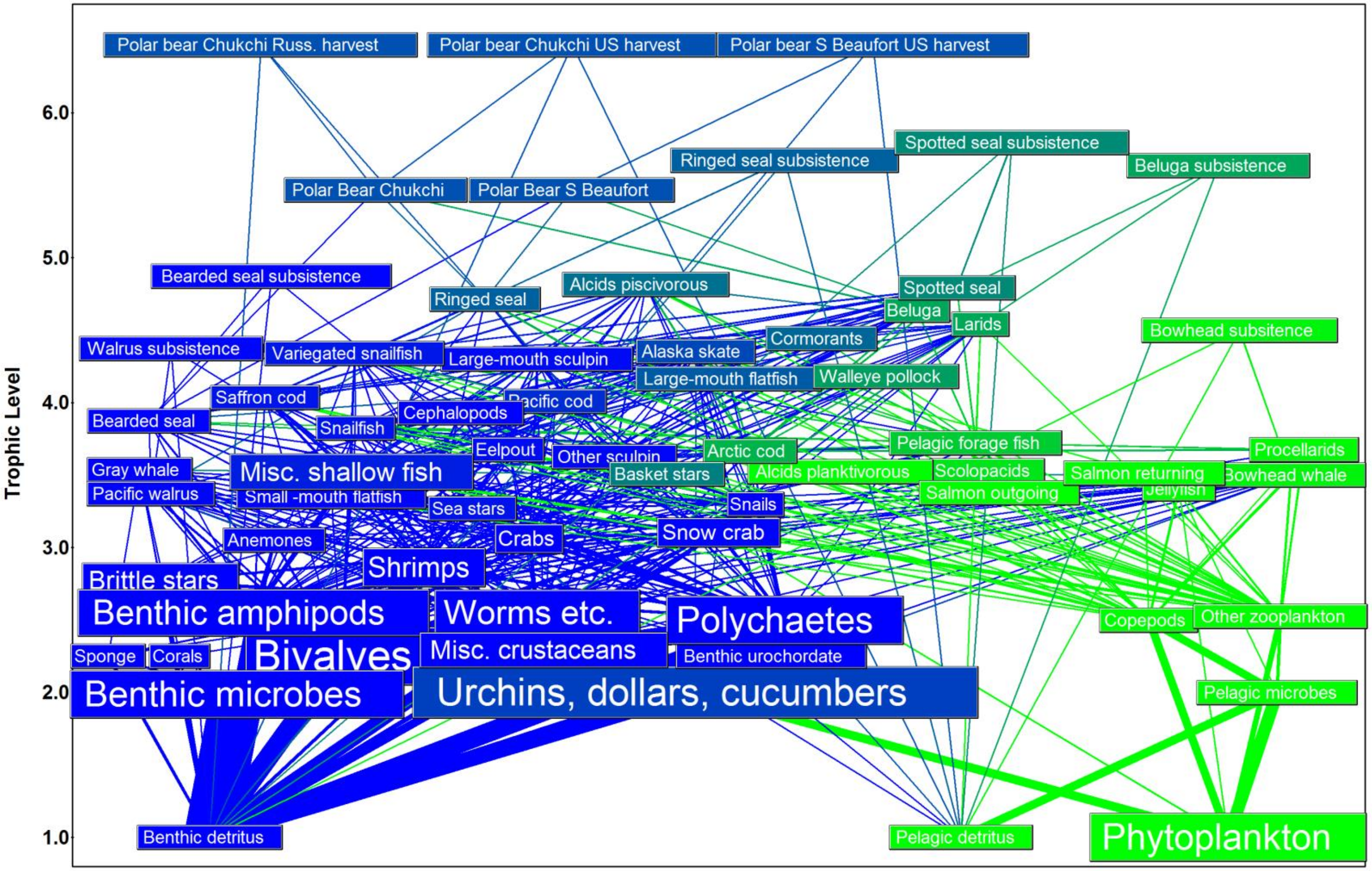

Figure 3. Food web diagram of the updated eastern Chukchi Sea food web (~2012). Functional groups (boxes) are arranged vertically by trophic level (a few groups moved up or down to improve readability). The height of the box is roughly proportional to the log biomass of the group. The width of the line between groups is proportional to the magnitude in mass flow. Blue boxes highlight benthic basal resource, and green boxes highlight pelagic sources, with varying shades in between.

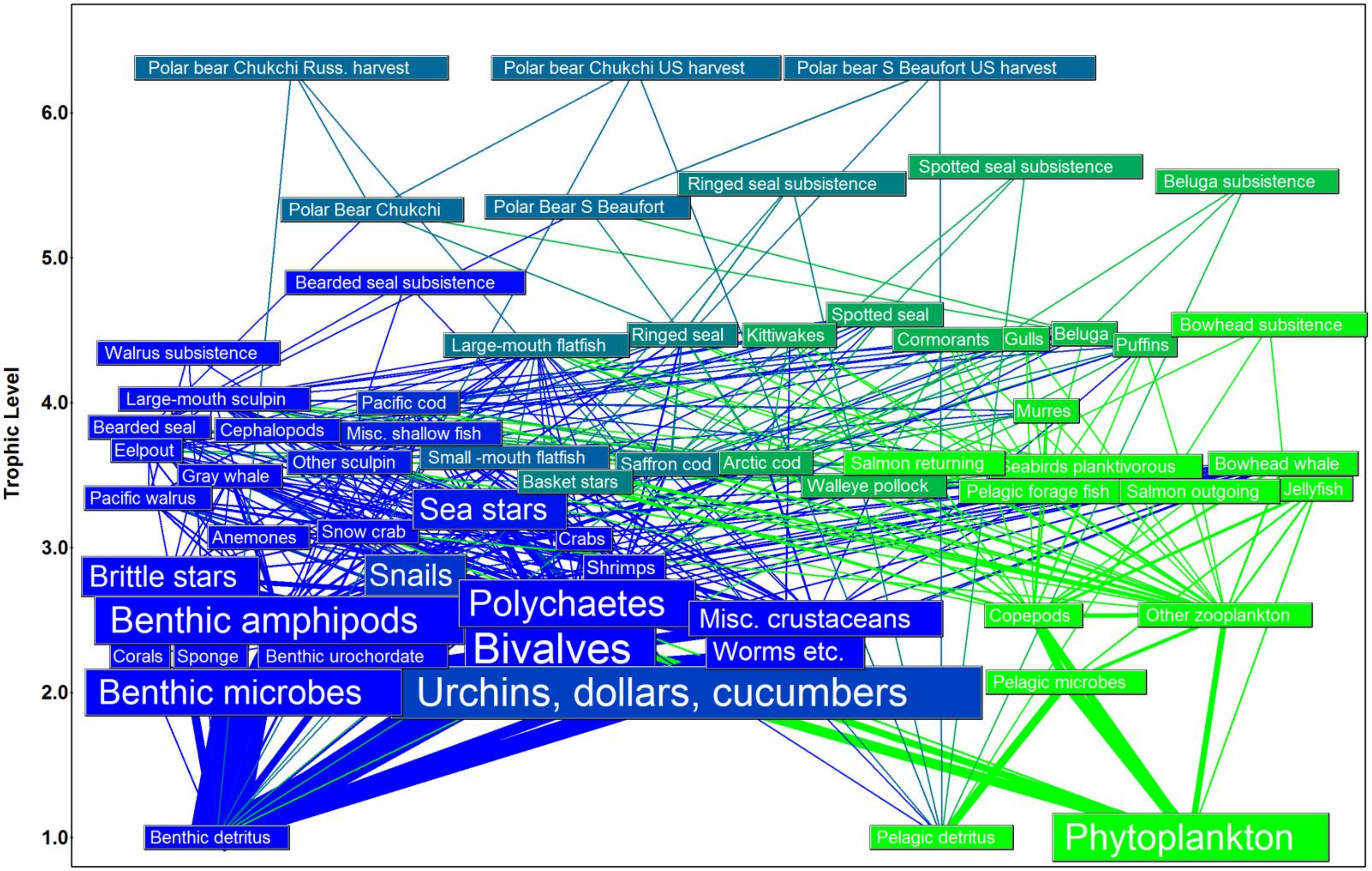

Figure 4. Food web diagram of the preliminary eastern Chukchi Sea food web (~1990). Functional groups (boxes) are arranged vertically by trophic level (a few groups moved up or down to improve readability). The height of the box is roughly proportional to the log biomass of the group. The width of the line between groups is proportional to the magnitude in mass flow. Blue boxes highlight benthic basal resource, and green boxes highlight pelagic sources, with varying shades in between.

5. Discussion

It is unclear whether any differences in Ecopath model properties and food web metrics between the preliminary model base time period (~1990) and the present model update (~2012) reflect any change in the true ecosystem conditions. Virtually, all differences in model metrics and outputs can be traced to changes to model inputs, reflecting new and improved data (i.e., higher data pedigree). To properly evaluate changes across time would require an adequate time series of data that connects the two model time periods (1990 to 2012). The two models are more appropriately viewed as two benchmarks, using many different data and parameter sources, and separated by about 20 years. Overall, the fundamental structure and function of the two models are the same; the system is dominated by benthic invertebrates and we observed little change in the ecosystem metrics and the proportions of total biomass represented by the aggregated groups.

A key limitation of both the preliminary model and the present model update is the seasonal nature of most of the data sets used to parameterize the models. The southward advance of sea ice during fall makes accessing the Alaska Arctic for fieldwork extremely difficult and costly, not to mention cold and dark. Offshore field studies during winter months are confined to a limited number of vessels with ice-breaking capacity. As a result, much of the offshore marine field research in the Alaska Arctic has been performed between spring and fall, and much of the data this trophic model is based upon reflects summer conditions. Until winter fieldwork becomes more feasible or the environmental conditions allow (sea ice reduction) more winter fieldwork, this is a limitation on the available data sets. For those model parameters that are derived from summer data sets we are making the assumption that conditions do not appreciably change during winter months, though this is certainly untrue in many cases (e.g., primary and secondary production). For example there is a strong seasonal signal with summer peaks in primary production (Springer and McRoy 1993) and secondary production of pelagic invertebrates (Matsuno et al. 2011, Questel et al. 2013). Future fieldwork emphasizing winter data collections would help to address this shortcoming for resident species, present in the Chukchi Sea year-round. However, cost and logistical challenges will likely persist and continue to limit winter collections.

The static Ecopath framework assumes a spatially homogenous model and does not address spatial differences in biomass or species composition. The community compositions of seabirds, fishes, and benthic invertebrates are all known to be spatially variable in the eastern Chukchi Sea and related to spatially varying oceanographic conditions (Norcross et al. 2010, Day et al. 2013, Gall et al. 2013, Norcross et al. 2013, Blanchard and Feder 2014). Patterns in the spatial distribution of zooplankton species have also been linked with distinct water masses and environmental variables (Springer et al. 1989, Hopcroft et al. 2010, Questel et al. 2013, Pinchuk and Eisner *Accepted*). Primary production is also spatially variable and associated with sea ice phenology and distinct water masses (Hansell et al. 1993, Springer and McRoy 1993). Spatial variation in community composition and biomass would likely to lead to spatial variation in food web structure. In the southern Chukchi Sea, Iken et al. (2010) found the structure of the benthic food web to vary depending upon the overlying water mass. Given the observed spatial differences in primary production and species distributions, future modeling efforts addressing these spatial patterns may find the food webs to have similar spatially variability. For example, in the south-central Chukchi Sea where primary production is high, there is strong pelagic-benthic coupling, and high benthic biomass (Grebmeier et al. 1988), we may hypothesize that in this area the food web structure and energy flow would be dominated by benthic organisms. In contrast, in coastal waters of the Chukchi Sea where primary production and benthic biomass is generally lower (Dunton et al. 2005), food web structure there may be more balanced between pelagic and benthic basal resources. Future food web modeling with a spatially explicit framework (e.g., Ecospace) could help to reveal such patterns in food web structure and could be informative for describing predator spatial distributions.

(lll) Fish

An important outcome of both the preliminary model and the present model update is that survey derived estimates of fish biomass were insufficient to balance either of the models and fish biomass needed to be increased substantially to meet the estimated demand by predators. This result implies that some portion of the fish biomass is unavailable to the fish sampling gear or the locations surveyed, or that the Ecopath model overestimates fish biomass. Though it is possible that some portion of the fish biomass is unavailable, there are several possible explanations that may help explain the apparent underestimation of fish biomass by the trawl survey. Low biomass in the trawl survey data may reflect low catchability of some groups to the bottom trawl gear, particularly pelagic fish. Large mesh size may have permitted smaller fishes to escape capture. Additionally, fish may be patchily distributed and not encountered by the trawl. The survey-derived estimates reflect just a single year, and inter-annual variation in fish abundance may have contributed to an underestimation of fish biomass. Further, any imprecision in the predator diets included in the model, or overestimation of predator biomass and consumptive rates would have additionally contributed to the mismatch in biomass estimates between the trawl-derived estimates (EBT and beam-trawl) and the top-down forced Ecopath estimate.

At 40 of the sampling stations during the 2012 Arctic Eis survey both bottom trawling gears were used. The catch data from these gear comparison tows indicated differences in the catch data between the two gear types were present and may reflect differences in gear design and performance (Britt et al. 2013). A greater abundance of smaller fish and smaller benthic invertebrates, including infauna typically found just below the surface, were observed in the beam trawl catch and is thought to reflect the finer mesh size in the beam trawl and a tendency to scour the bottom harder than the EBT (Britt et al. 2013). The size composition of fishes and snow crabs caught with the EBT were generally larger than those caught with the beam trawl. The EBT was more efficient at catching larger and more mobile organisms, including those found just above the seafloor, due to its greater net width, higher vertical opening, and higher towing speed (Britt et al. 2013).

When we compare biomass estimates calculated for our Ecopath fish functional groups from the two gear types a few differences in the data become apparent (Figure 5). The EBT gear produced higher biomass estimates for gadids, pelagic forage fish, and Alaska skate. The beam trawl produced higher density estimates for miscellaneous shallow fish, snailfish, sculpins, and small-mouth flatfish. The most pronounced difference was for the miscellaneous shallow fish group, where the beam trawl estimate was 0.333 t km^{-2} and the EBT was 0.004 t km^{-2}. This may reflect actual differences in the density of miscellaneous shallow fishes encountered by the two gears, but may also reflect differences in gear design (e.g., mesh size) and performance (e.g., harder contact with the bottom). The miscellaneous shallow fish group is dominated by stichaeids (e.g., pricklebacks, eelblennys) which are generally small and slender fish that could escape through net meshes or pass under a foot rope. Though the two gears may have in fact encountered different densities of miscellaneous shallow fish, it is also possible that differences in mesh size and bottom contact, may have contributed to the disparity in biomass estimates for this functional group.

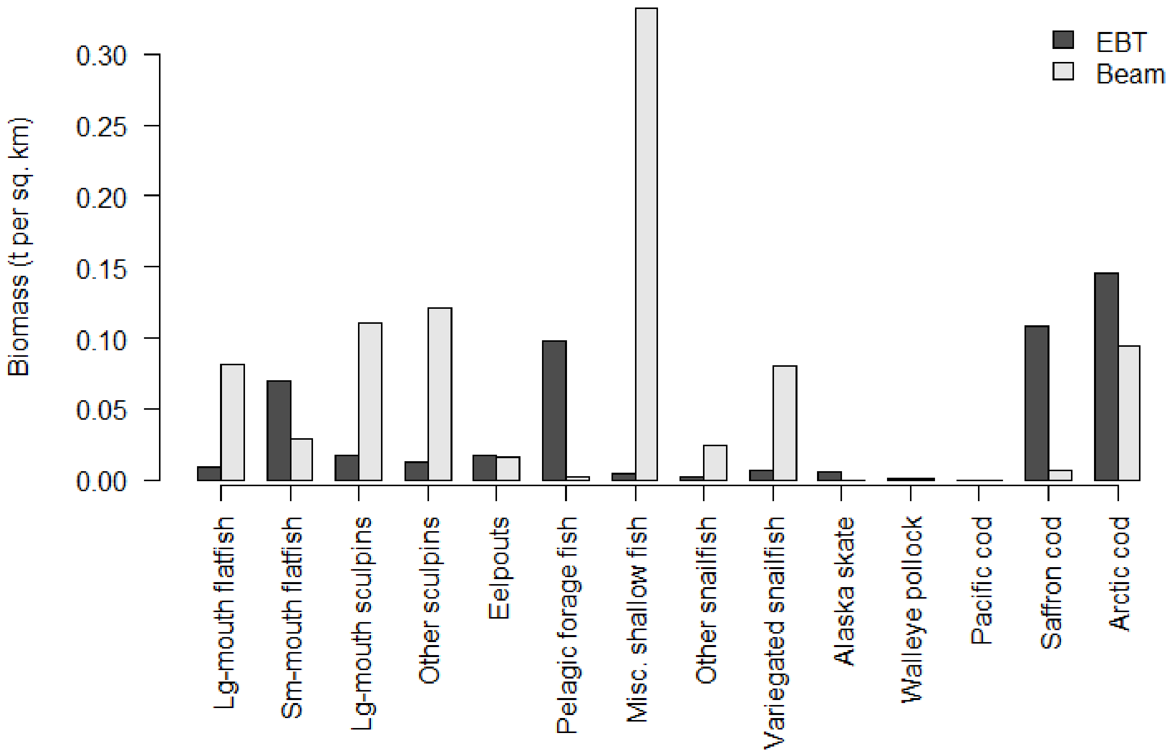

Figure 5. Biomass estimates (t km^{-2}) for fish functional groups (excluding salmonids) derived from the catch data of the 83-112 Eastern bottom trawl (EBT) and the beam trawl.

The top-down forced estimates of biomass for the fish functional groups calculated by Ecopath are in general, significantly larger than the estimates derived from the trawl survey catch data. The disparity between these different estimates makes it difficult to visually compare them side-by-side (Figure 6). Alternatively, we can look at the proportions of the fish groups relative to total fish biomass to gain a sense for any differences in the distribution of biomass amongst the fish functional groups. We can accomplish this by summing up the fish biomass estimates and dividing each group by this total to determine a group's contribution to total fish biomass. Figure 7 shows the relative fish proportions for the EBT, beam trawl, and Ecopath estimates side-by-side. The most conspicuous result is that both the Ecopath output and the beam trawl data indicate the relative prominence of miscellaneous shallow fish amongst all fish groups. This observation supports the notion that the EBT may have under sampled the miscellaneous shallow fish group and that the beam trawl correctly indicated the prominence of this functional group. Or rather, the beam trawl data are consistent with the Ecopath results suggesting the prominence of this functional group amongst fish groups. Miscellaneous shallow fish, in particular stichaeids, were a prominent prey item commonly observed in the diets of piscivorous fishes in the eastern Chukchi Sea (Whitehouse et al. *Accepted*). Because the biomass estimate of miscellaneous shallow fishes is forced with top-down pressure, the high proportion of miscellaneous shallow fish amongst all other fish groups in the Ecopath model is in large part a reflection of their dietary importance as prey to other piscivorous fishes.

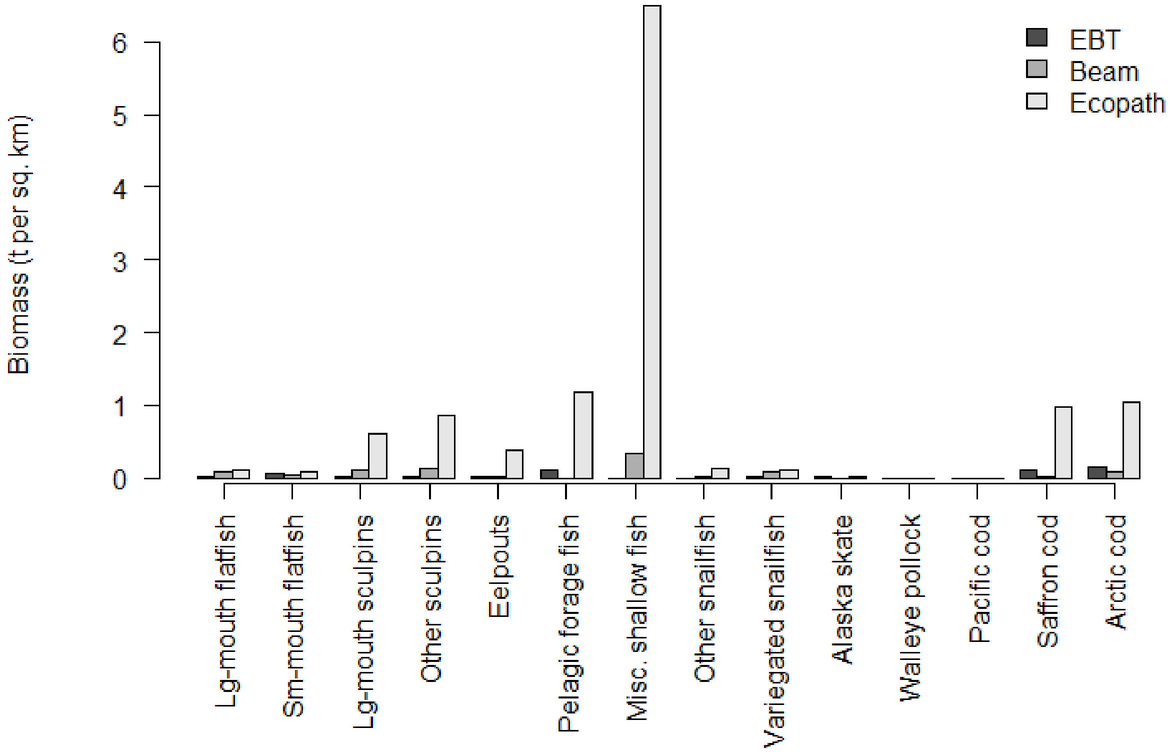

Figure 6. Biomass estimates (t km^{-2}) for fish functional groups (excluding salmonids) derived from the catch data of the 83-112 Eastern bottom trawl (EBT), the catch data from the beam trawl, and the biomass estimates produced by Ecopath, assuming EE=0.8.

Another noteworthy contrast is the difference in the proportion of pelagic forage fishes (Figure 7). The bottom trawl catch data indicates this group to be among the more prominent groups while they are barely represented in the beam trawl catch. The proportion of pelagic fish from the top-down estimate of Ecopath is intermediate between these two estimated proportions. The disparity in the proportions from the two sets of trawl data may reflect the low catchability of this group to bottom trawling gear in general. The higher density estimate from the EBT data may be a result of the higher vertical opening of the net and higher trawling speed.

Some conspicuous contrasts in Figure 7 are the different proportions for Arctic cod and saffron cod. The relative proportions of Arctic cod and saffron cod are greatest in the bottom trawl data. They are the two most prominent portions (functional groups) of the fish community in the EBT data. The proportion of Arctic cod in the beam trawl data is less than half that of the bottom trawl, but roughly equivalent to the proportion estimated with the Ecopath model. The relative proportion of Arctic cod ranks fifth amongst the fish groups from the beam trawl data. For saffron cod, they are scarcely represented in the beam trawl data, while the Ecopath proportion of saffron cod is intermediate between the EBT and beam trawl estimates. Differences in the relative proportions of gadids between the two trawling gears may reflect actual differences in the densities of gadids encountered, patchy fish distribution (trawling locations), and likely reflect different efficiencies between the two gears to catch Arctic cod and saffron cod (Britt et al. 2013). Recent studies employing the same EBT gear in eastern Bering Sea have shown the effective fishing height of the EBT for another species of Gadidae, the walleye pollock, to be greater than the measured vertical opening of the net (Kotwicki et al. 2013).

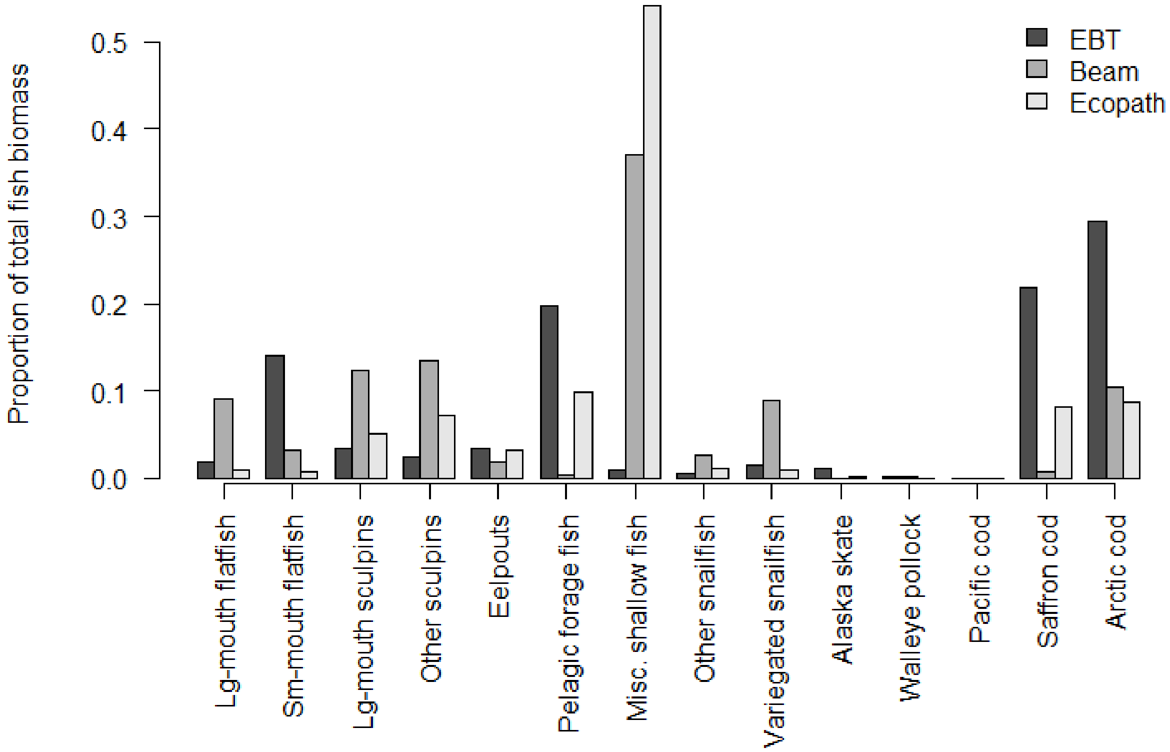

Figure 7. The proportional contribution of fish functional groups to the combined biomass of all fish groups (excluding salmonids) using three different estimates of biomass; the catch data from the 83-112 Eastern bottom trawl (EBT), the beam trawl, and the biomass estimates produced by Ecopath (assuming EE=0.8).

In general, the overall pattern of biomass dominance by the miscellaneous shallow fish group in the Ecopath model results is supported by a similar pattern observed in the beam trawl data (Figure 7). Though the biomass estimate produced by Ecopath for miscellaneous shallow fish is considerably higher than the biomass estimates calculated by either gear types (EBT and beam), the pattern of biomass dominance by this group is consistent with the pattern we observe in the beam trawl catch. Given the slender shape and small size of many of the miscellaneous shallow fishes (e.g., stichaeids), and taking differences in the design and performance of the two gear types into consideration, this functional group of fishes may have been more efficiently caught with the beam trawl and could be under represented in the EBT catch. The vast differences between the dimensions, performance, and catches of the two gear types make statistical comparisons impracticable at this time (Britt et al. 2013). The top-down forced biomass estimate of miscellaneous shallow fish generated by the Ecopath model is largely driven up by top-down pressure from other fishes. The diets of those predator fishes included in the present model update are derived from fish stomachs that were collected in the eastern Chukchi Sea, during the 2012 Arctic Eis trawl surveys.

6. Conclusions

We were able to update, or otherwise improve (data pedigree) input parameter estimates for numerous functional groups. Despite all of the changed input parameters, the fundamental structure and function of this trophic mass balance model of the eastern Chukchi Sea remains the same as that of the original preliminary model. The eastern Chukchi Sea is an ecosystem characterized strong pelagic-benthic coupling, where a large portion of the primary production within the pelagic realm is unutilized in the pelagic food web and most of it eventually settles to the seafloor where it supports an abundant benthic community. A large majority of the living biomass in this ecosystem resides in the benthic community. Similar to the preliminary model, survey derived estimates of fish biomass were insufficient to balance the model, and top-down estimates indicate fish biomass may be much higher than the survey derived estimates. Small demersal fishes, especially pricklebacks, may represent a significant portion of total fish biomass and may be underestimated by trawl survey derived estimates.

In general, changes to key model parameters, such as biomass, or changes to system level metrics, were the reflection of the new and improved data or parameters used as model inputs, and do not necessarily reflect any change in ecosystem (or functional group) state from the preliminary model (~1990) to our updated model (~2012). The two models are analogous to two data points in time and are not equivalent to a time series. A more rigorous analysis of available time series data for individual functional groups will be required to evaluate changes over time.

We updated 93 of the 227 basic model input parameters (B, P/B, Q/B, EE, GE, DC, C), which resulted in improved data pedigrees for 34 of the input parameters. Given the improvements to input parameter quality and the more current base time period of this model update(~2012 vs. ~1990), we recommend the use of this updated model over the preliminary model for future food web modeling studies, including simulation and sensitivity analyses with Ecosim, or spatially explicit studies with Ecospace (Pauly et al. 2000).

Our food web model represents just one of many possible mass-balanced states (Essington 2004). The table of data quality grades for the basic model input parameters (Appendix B) highlighted the many parameters in need of improved estimates and may help to direct future research and field collections. Regular updates to food web models (every ~3-5 years), such as ours, can support the calculation of informative ecosystem indicators, help to identify ecologically important species still in need of further research, and aid in the identification of trends and changes to the trophic structure and functioning of an ecosystem (Aydin et al. 2007).

7. Acknowledgements

This study was funded [in part] by the U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM) through Cooperative Agreement M12PG00018 between BOEM , Alaska Outer Continental Shelf Region and the NOAA Alaska Fisheries Science Center. Ivonne Ortiz (UW/JISAO) provided invaluable assistance with model balancing. Thank you to Robb Kaler (USFWS) for help with the North Pacific Seabird Colony Database. Thanks to Bob Lauth (NOAA/AFSC) for providing catch data from the BOEM sponsored Arctic Eis trawl survey of 2012. We are grateful to Richard Hibpshman, Caroline Robinson, Sean Rohan, and Kim Sawyer from the University of Washington (UW/SAFS) for analysis of fish stomach contents and their incredible attention to detail. Thank you to Geoff Lang (NOAA/AFSC) for data editing and providing access to the REEM food habits database. We would like to thank Arny Blanchard (University of Alaska Fairbanks) for sharing benthic grab data. Troy Buckley (NOAA/AFSC) and Stephani Zador (NOAA/AFSC) provided valuable criticism during model development. Thank you to all Arctic Eis survey participants who helped with stomach sample collection. We would also like to thank the Captain and crew of the FV Alaska Knight and the Captain and crew of the FV Bristol Explorer for their efforts. Special thanks to Troy Buckley and Ivonne Ortiz for critical reviews of an earlier version of this report. The findings and conclusions in this report are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service. This publication is [partially] funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement No. NA10OAR4320148, Contribution No. 2607.

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9. Appendix A

Diet Matrix

Table A1. The diet matrix of the updated eastern Chukchi Sea Ecopath model. Rows represent prey groups and the columns are predators. The predator column numbers correspond to the prey group numbers and names. Each column represents a single predator's diet and the values sum to 1 (some columns may not sum to 1 due to rounding). Values of 0.0000 are prey items present in trace amounts.

Table A1. Diet matrix

	Functional Group	1	2	3	4	5	6	7	8
1	Beluga				0.1000	0.1000			
2	Gray whale								
3	Bowhead whale								
4	Polar Bear Chukchi								
5	Polar Bear S Beaufort								
6	Pacific walrus								
7	Bearded seal				0.2500	0.2500	0.0003		
8	Ringed seal				0.6500	0.6500	0.0007		
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish							0.0215	
17	Small -mouth flatfish							0.0215	
18	Large-mouth sculpin	0.0100						0.0586	0.0331
19	Other sculpin	0.0100							0.0069
20	Eelpout	0.0100							
21	Pelagic forage fish	0.5544						0.0023	0.0300
22	Misc. shallow fish								
23	Other snailfish								
24	Variegated snailfish								
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod	0.0359						0.0180	0.3300
29	Arctic cod	0.2797						0.0085	0.4500
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods	0.0001					0.0100		
33	Bivalves		0.0434	0.0192			0.6990	0.3286	
34	Snails		0.0043	0.0019			0.0600	0.0170	
35	Snow crab		0.0003	0.0001			0.0230	0.1948	
36	Other crabs		0.0001	0.0000			0.0070	0.0601	
37	Shrimps	0.0999	0.0000	0.0000			0.0200	0.2464	0.1000
38	Sea stars		0.0040	0.0018					
39	Brittle stars		0.0037	0.0016					
40	Basket stars		0.0001	0.0001					
41	Urchins, dollars, cucumbers		0.0229	0.0102			0.0802		
42	Sponge		0.0002	0.0001					
43	Benthic urochordate		0.0026	0.0012			0.0092		
44	Anemones		0.0026	0.0012					
45	Corals		0.0000	0.0000					
46	Benthic amphipods		0.9000	0.0057			0.0448	0.0113	0.0400
47	Polychaetes		0.0109	0.0048			0.0380	0.0113	
48	Worms etc.		0.0022	0.0010			0.0078		
49	Misc. crustaceans		0.0026	0.0011					
50	Jellyfish								
51	Copepods			0.7125					
52	Other zooplankton			0.2375					0.0100
53	Pelagic microbes								
54	Benthic microbes								
55	Phytoplankton								
56	Pelagic detritus								
57	Benthic detritus								

Table A1 (continued). Diet matrix

	Functional Group	9	10	11	12	13	14	15	16
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar Bear Chukchi								
5	Polar Bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous					0.0047			
15	Alcids planktivorous								
16	Large-mouth flatfish	0.0085					0.0096		
17	Small -mouth flatfish	0.0085					0.0096		
18	Large-mouth sculpin	0.1197				0.0017	0.0714		
19	Other sculpin	0.0247				0.0017	0.0713		
20	Eelpout								
21	Pelagic forage fish	0.4574	0.0587	0.2500		0.3325	0.2732		
22	Misc. shallow fish	0.0108		0.2500		0.0035	0.0033		0.3332
23	Other snailfish	0.0108				0.0035	0.0033		
24	Variegated snailfish	0.0108				0.0035	0.0033		
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod	0.0924				0.0233	0.2372		
29	Arctic cod	0.2163	0.0697	0.2500		0.5013	0.2595		0.2409
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods	0.0200							
33	Bivalves					0.0000	0.0000		0.0073
34	Snails					0.0053	0.0030		
35	Snow crab								
36	Other crabs					0.0053	0.0030		
37	Shrimps	0.0100		0.2500		0.0106	0.0100		0.1977
38	Sea stars								
39	Brittle stars								
40	Basket stars								
41	Urchins, dollars, cucumbers								
42	Sponge								
43	Benthic urochordate								
44	Anemones								
45	Corals								
46	Benthic amphipods	0.0100	0.0022		0.1000	0.0345	0.0233		0.0252
47	Polychaetes					0.0237	0.0082		0.0497
48	Worms etc.								
49	Misc. crustaceans					0.0001			
50	Jellyfish							0.0193	
51	Copepods		0.0044		0.4500			0.3486	0.0000
52	Other zooplankton		0.8650		0.4500	0.0263	0.0108	0.6321	0.1459
53	Pelagic microbes								
54	Benthic microbes								
55	Phytoplankton								
56	Pelagic detritus					0.0056			
57	Benthic detritus					0.0130			

Table A1 (continued). Diet matrix

	Functional Group	17	18	19	20	21	22	23	24
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar Bear Chukchi								
5	Polar Bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish								0.0126
17	Small -mouth flatfish							0.0286	
18	Large-mouth sculpin				0.0480	0.0058		0.0164	0.0819
19	Other sculpin		0.2068		0.0008	0.0042		0.0120	0.1074
20	Eelpout		0.0893						0.0091
21	Pelagic forage fish			0.0373				0.0661	0.0323
22	Misc. shallow fish		0.2435		0.0788	0.1874			0.1844
23	Other snailfish		0.0035		0.0001				0.1430
24	Variegated snailfish		0.0113		0.0003			0.0586	
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod								
29	Arctic cod								0.0120
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods								
33	Bivalves	0.3710		0.0014	0.0004		0.0539	0.0003	0.0037
34	Snails	0.0005		0.0068			0.0004		
35	Snow crab	0.0265	0.0753	0.0023				0.0131	0.0093
36	Other crabs	0.0002	0.1497	0.0573	0.0021	0.0003	0.0070	0.0350	0.0038
37	Shrimps		0.1319	0.0123	0.0155	0.0098	0.0773	0.1046	0.2867
38	Sea stars								
39	Brittle stars	0.0304	0.0000	0.0054					
40	Basket stars								
41	Urchins, dollars, cucumbers	0.0511							
42	Sponge								
43	Benthic urochordate								
44	Anemones			0.0638					
45	Corals								
46	Benthic amphipods	0.1203	0.0703	0.4825	0.2815	0.0134	0.5202	0.4949	0.0714
47	Polychaetes	0.3520	0.0105	0.2353	0.5377	0.0046	0.1270	0.1528	0.0288
48	Worms etc.	0.0083		0.0600			0.0149		0.0003
49	Misc. crustaceans	0.0368	0.0069	0.0075	0.0009	0.0006	0.0827	0.0053	0.0006
50	Jellyfish								
51	Copepods	0.0001			0.0000	0.3125	0.0179	0.0003	0.0000
52	Other zooplankton	0.0028	0.0008	0.0282	0.0340	0.4613	0.0987	0.0119	0.0126
53	Pelagic microbes								
54	Benthic microbes								
55	Phytoplankton								
56	Pelagic detritus								
57	Benthic detritus								

Table A1 (continued). Diet matrix

	Functional Group	25	26	27	28	29	30	31	32
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar Bear Chukchi								
5	Polar Bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish	0.0249		0.0015		0.0061			
17	Small -mouth flatfish	0.0643		0.0107					
18	Large-mouth sculpin	0.0236		0.0066		0.0063			
19	Other sculpin	0.0003		0.0049					
20	Eelpout	0.0413		0.0043		0.0036			
21	Pelagic forage fish	0.0528				0.0495			
22	Misc. shallow fish	0.0155		0.0635	0.3514	0.0021			
23	Other snailfish	0.0014		0.0007		0.0028			
24	Variegated snailfish	0.0040		0.0021					
25	Alaska skate								
26	Walleye pollock			0.0006					
27	Pacific cod	0.0014							
28	Saffron cod								
29	Arctic cod	0.2730	0.5367	0.1560		0.0082			
30	Salmon outgoing								
31	Salmon returning	0.0210							
32	Cephalopods	0.0001							
33	Bivalves	0.0000		0.0014	0.0000	0.0000			0.2500
34	Snails	0.0001		0.0015	0.0023				0.2500
35	Snow crab	0.2568		0.1453					0.2500
36	Other crabs	0.0608		0.0526	0.0006	0.0011			0.2500
37	Shrimps	0.1139	0.1424	0.2859	0.4781	0.1601			
38	Sea stars								
39	Brittle stars	0.0000							
40	Basket stars								
41	Urchins, dollars, cucumbers	0.0001							
42	Sponge								
43	Benthic urochordate	0.0002							
44	Anemones	0.0000							
45	Corals								
46	Benthic amphipods	0.0302	0.0430	0.1378	0.0380	0.0957			
47	Polychaetes	0.0074		0.0692	0.0336	0.0045			
48	Worms etc.				0.0597				
49	Misc. crustaceans	0.0001	0.0344	0.0015	0.0012	0.0120			
50	Jellyfish								
51	Copepods	0.0000	0.1473		0.0000	0.3725	0.5000	0.5000	
52	Other zooplankton	0.0066	0.0963	0.0539	0.0352	0.2756	0.5000	0.5000	
53	Pelagic microbes								
54	Benthic microbes								
55	Phytoplankton								
56	Pelagic detritus								
57	Benthic detritus								

Table A1 (continued). Diet matrix

	Functional Group	33	34	35	36	37	38	39	40
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar Bear Chukchi								
5	Polar Bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish								
17	Small -mouth flatfish								
18	Large-mouth sculpin								
19	Other sculpin								
20	Eelpout								
21	Pelagic forage fish								
22	Misc. shallow fish								
23	Other snailfish								
24	Variegated snailfish								
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod								
29	Arctic cod								
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods								
33	Bivalves		0.5000	0.2075	0.2500	0.1500	0.5155	0.1250	
34	Snails			0.0326			0.0516		
35	Snow crab								
36	Other crabs			0.0411					
37	Shrimps								
38	Sea stars			0.0015					
39	Brittle stars			0.0590					
40	Basket stars								
41	Urchins, dollars, cucumbers			0.0081			0.2723		
42	Sponge			0.0028					
43	Benthic urochordate						0.0314		
44	Anemones			0.0012					
45	Corals								
46	Benthic amphipods		0.0500	0.0553		0.1500		0.1250	0.2500
47	Polychaetes		0.3000	0.2720	0.2500	0.1500	0.1292	0.1250	
48	Worms etc.		0.0500	0.0313	0.2500				
49	Misc. crustaceans		0.0500	0.0143		0.1500		0.1250	0.2500
50	Jellyfish								
51	Copepods								0.2500
52	Other zooplankton			0.0041					0.2500
53	Pelagic microbes								
54	Benthic microbes	0.2500							
55	Phytoplankton			0.0039					
56	Pelagic detritus								
57	Benthic detritus	0.7500	0.0500	0.2657	0.2500	0.4000		0.5000	

Table A1 (continued). Diet matrix

	Functional Group	41	42	43	44	45	46	47	48
1	Beluga								
2	Gray whale								
3	Bowhead whale								
4	Polar Bear Chukchi								
5	Polar Bear S Beaufort								
6	Pacific walrus								
7	Bearded seal								
8	Ringed seal								
9	Spotted seal								
10	Procellarids								
11	Cormorants								
12	Scolopacids								
13	Larids								
14	Alcids piscivorous								
15	Alcids planktivorous								
16	Large-mouth flatfish								
17	Small -mouth flatfish								
18	Large-mouth sculpin								
19	Other sculpin								
20	Eelpout								
21	Pelagic forage fish								
22	Misc. shallow fish								
23	Other snailfish								
24	Variegated snailfish								
25	Alaska skate								
26	Walleye pollock								
27	Pacific cod								
28	Saffron cod								
29	Arctic cod								
30	Salmon outgoing								
31	Salmon returning								
32	Cephalopods								
33	Bivalves				0.2000				
34	Snails								
35	Snow crab								
36	Other crabs								
37	Shrimps								
38	Sea stars								
39	Brittle stars								
40	Basket stars								
41	Urchins, dollars, cucumbers								
42	Sponge								
43	Benthic urochordate								
44	Anemones								
45	Corals								
46	Benthic amphipods				0.2000				
47	Polychaetes								
48	Worms etc.								
49	Misc. crustaceans				0.2000				
50	Jellyfish								
51	Copepods								
52	Other zooplankton								
53	Pelagic microbes								
54	Benthic microbes		0.2500	0.2500	0.2000	0.2500	0.5000	0.5000	0.5000
55	Phytoplankton	0.2500							
56	Pelagic detritus								
57	Benthic detritus	0.7500	0.7500	0.7500	0.2000	0.7500	0.5000	0.5000	0.5000

Table A1 (continued). Diet matrix

	Functional Group	49	50	51	52	53	54
1	Beluga						
2	Gray whale						
3	Bowhead whale						
4	Polar Bear Chukchi						
5	Polar Bear S Beaufort						
6	Pacific walrus						
7	Bearded seal						
8	Ringed seal						
9	Spotted seal						
10	Procellarids						
11	Cormorants						
12	Scolopacids						
13	Larids						
14	Alcids piscivorous						
15	Alcids planktivorous						
16	Large-mouth flatfish						
17	Small -mouth flatfish						
18	Large-mouth sculpin						
19	Other sculpin						
20	Eelpout						
21	Pelagic forage fish						
22	Misc. shallow fish						
23	Other snailfish						
24	Variegated snailfish						
25	Alaska skate						
26	Walleye pollock						
27	Pacific cod						
28	Saffron cod						
29	Arctic cod						
30	Salmon outgoing						
31	Salmon returning						
32	Cephalopods						
33	Bivalves						
34	Snails						
35	Snow crab						
36	Other crabs						
37	Shrimps						
38	Sea stars						
39	Brittle stars						
40	Basket stars						
41	Urchins, dollars, cucumbers						
42	Sponge						
43	Benthic urochordate						
44	Anemones						
45	Corals						
46	Benthic amphipods						
47	Polychaetes						
48	Worms etc.						
49	Misc. crustaceans						
50	Jellyfish						
51	Copepods		0.6750		0.2500		
52	Other zooplankton		0.2250				
53	Pelagic microbes		0.0500	0.5000	0.1500		
54	Benthic microbes	0.5000					
55	Phytoplankton		0.0500	0.5000	0.6000	0.7000	
56	Pelagic detritus					0.3000	
57	Benthic detritus	0.5000					1.0000

10. Appendix B

(mmm) Data pedigree

Table B1. Data characteristics and data pedigree for the basic model input parameters. To aid the interpretation of parameter quality, the grades are color coded with light red as good (1-3), medium red as acceptable (4-6), and dark red (7-8). *The Chukchi Sea stock of polar bears has two separate subsistence harvests (U.S. and Russian) that were parameterized separately. The data grade for the U.S. harvest is 2 and 7 for the Russian harvest. B = biomass, P/B = production/biomass ratio, Q/B = consumption/biomass ratio, DC = diet composition, and C = fishery catch or subsistence harvest.

Model parameter	B		P/B		Q/B		DC		C	
Functional Group	**Grade**	**Data characters**	**Grade**	**Data characters**	**Grade**	**Data characters**	**Grade**	**Data characters**	**Grade**	**Data characters**
Beluga	5	Region-specific but required extrapolation based on migration patterns	6	General life history proxy	6	General life history proxy	5	Same species and same region	5	Estimate requires extrapolation and uncertain scaling factors
Gray whale	5		6		6		5			
Bowhead whale	5		6		6		5		2	Direct estimate with limited coverage
Polar bear Chukchi stock	7	Incomplete sources with wide range	5	Estimate based on same species	6		6	Same species in adjacent region	7* 2*	Single incomplete source Direct estimate with limited coverage
Polar bear S. Beaufort stock	5	Region-specific but required extrapolation based on migration patterns	4	Direct estimate	6		4	Direct estimate with limited coverage	2	Direct estimate with limited coverage
Pacific walrus	5		6	General life history proxy	6		5	Same species and same region	4	Direct estimate but with high variation/limited confidence
Bearded seal	7	Incomplete sources with wide range	6		6		4	Direct estimate with limited coverage	4	
Ringed seal	6	Single study with limited coverage	6		6		4		4	
Spotted seal	7	Incomplete sources with wide range	6		6		4		5	Estimate requires extrapolation and uncertain scaling factors
Procellarids	4	Direct estimate but with high variation/limited confidence	6		6		6	Same species in other regions		
Cormorants	4		6		6		6			
Scolopacids	4		6		6		6			
Larids	4		6		6		6			
Alcids piscivorous	4		6		6		6			
Alcids planktivorous	4		6		6		6			
Large-mouth flatfish	8	Estimated by Ecopath	5	Same species, different time period	5	Same species, different time period	2	Direct estimate with limited coverage		
Small-mouth flatfish	8		6	General life history proxy or other Ecopath model	6	General life history proxy or other Ecopath model	2			
Large-mouth sculpin	8		6		6		2			
Other sculpin	8		6		6		2			
Eelpout	8		6		6		2			
Pelagic forage fish	8		6		6		2			
Misc. shallow fish	8		6		6		2			
Other snailfish	8		6		6		2			
Variegated snailfish	8		6		6		2			

Model parameter	**B**		**P/B**		**Q/B**		**DC**		**C**	
Functional Group	**Grade**	**Data characters**	**Grade**	**Data characters**	**Grade**	**Data characters**	**Grade**	**Data characters**	**Grade**	**Data characteristics**
Alaska skate	2	Direct estimate with limited coverage	6	General life history proxy or other Ecopath model	7	General literature review from a range of species	6	Same species in adjacent region		
Walleye pollock	2		6		6	General life history proxy or other Ecopath model	2	Direct estimate with limited coverage		
Pacific cod	2		6		6		6	Same species in adjacent region		
Saffron cod	8	Estimated by Ecopath	2	Direct estimate with limited coverage	2	Direct estimate with limited coverage	2	Direct estimate with limited coverage		
Arctic cod	8		2		2		2			
Salmon outgoing	7	Incomplete sources with wide range	6	General life history proxy or other Ecopath model	6	General life history proxy or other Ecopath model	6	Same species in adjacent region		
Salmon returning	7		6		6		6			
Cephalopods	8	Estimated by Ecopath	6		7	General literature review from a range of species	7	General literature review from a range of species		
Bivalves	2	Direct estimate with limited coverage	5	Species specific	7		7			
Snails	2		6	General life history proxy or other Ecopath model	7		7			
Snow crab	2		6		6	General life history proxy or other Ecopath model	6	Same species in adjacent region		
Miscellaneous crabs	2		6		7	General literature review from a range of species	7	General literature review from a range of species		
Shrimps	8	Estimated by Ecopath	6		7		7			
Sea stars	2	Direct estimate with limited coverage	6		7		7			
Brittle stars	2		6		7		7			
Basket stars	2		6		7		7			
Urchins, dollars, cucumbers	2		5	Species specific	7		7			
Sponge	2		6	General life history proxy or other Ecopath model	7		7			
Benthic urochordate	2		6		7		7			
Anemones	2		6		7		7			
Corals	2		6		7		7			
Benthic amphipods	8	Estimated by Ecopath	6		7		7			
Polychaetes	2	Direct estimate with limited coverage	5	Species specific	7		7			
Worms etc.	2		6	General life history proxy or other Ecopath model	7		7			
Miscellaneous crustaceans	2		6		7		7			
Jellyfish	2		6		6	General life history proxy or other Ecopath model	7			
Copepods	8	Estimated by Ecopath	6		6		7			
Other zooplankton	8		6		7	General literature review	7			
Model parameter	**B**		**P/B**		**Q/B**		**DC**		**C**	

Functional Group	**Grade**	**Data characters**	**Grade**	**Data characters**	**Grade**	**Data characters**	**Grade**	**Data characters**	**Grade**	**Data characters**
Pelagic microbes	8	Estimated by Ecopath	7	General literature review from a range of species	7	General literature review from a range of species	6	Same species and same region		
Benthic microbes	8		7		7		7	General literature review from a range of species		
Phytoplankton	8		7							
Pelagic detritus	8									
Benthic detritus	8									

Appendix X.

Demersal and pelagic fish food habits in the eastern Chukchi and northern Bering seas

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March 2, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

List of Oral and Poster Presentations

Buckley, TW, GA Whitehouse, KA Sawyer, and CL Robinson. 2014. Latitudinal and ontogenetic shifts in the diet of Arctic cod (*Boreogadus saida*). Poster, American Fisheries Society Annual Meeting, August 2014, Quebec City, Quebec, Canada.

Whitehouse, GA, TW Buckley, R Hibpshman, CL Robinson, S Rohan, and KA Sawyer. 2015. Latitudinal and size-based variation in the diet of Arctic cod in the eastern Chukchi Sea. Poster, Alaska Marine Science Symposium, January 2015, Anchorage, Alaska, USA.

Whitehouse, GA, and TW Buckley. 2015. Diet compositions and trophic guild structure of the demersal fish community in the eastern Chukchi Sea. Poster, Alaska Marine Science Symposium, January 2015, Anchorage, Alaska, USA.

Whitehouse, GA, TW Buckley, RE Hibpshman, CL Robinson, Sean K Rohan, and KA Sawyer. Trophic guilds of the eastern Chukchi Sea demersal fish community. Poster, American Fisheries Society Annual Meeting, August 16-20, 2015, Portland, OR.

Proposed Objectives and Study Chronology

The objective of the demersal and pelagic fish food habits portion of the Arctic Eis project was to collect stomach content data and assess the food habits of common demersal and pelagic fish species in the eastern Chukchi Sea, quantifying consumption and variation in major prey items. Stomach specimens were collected during Arctic Eis summer trawl survey operations in the eastern Chukchi Sea and northern Bering Sea. The selected specimens were preserved in the field and prepared for shipping back to the AFSC in Seattle, where the stomach contents were analyzed in the laboratory. Stomach specimens were collected during the 2012 bottom trawl survey and the 2012 surface/midwater survey of the eastern Chukchi Sea and northern Bering Sea. Additional stomachs were collected during the 2013 surface/midwater trawl survey and prepared for shipping; however, those stomach specimens never arrived at the AFSC, and at this point will presumably not be found. Exhaustive attempts were made to locate the missing specimens, including searching possible storage locations and other programs in Dutch Harbor, AK, and in Seattle, WA. We searched for a paper-trail and shipping manifests, and also corresponded with personnel involved in vessel offload at the conclusion of the cruise. All of these efforts were fruitless. Thus, only stomach specimens collected in 2012 were available for analysis. Laboratory analysis of stomach specimens occurred between the fall of 2012 and fall of 2014. Analysis of diet data and manuscript preparation occurred between fall of 2014 and March 2016. Preliminary results of diet analysis were presented as posters at the American Fisheries Society Annual Meeting in August 2014, the Alaska Marine Science Symposium in January 2015, and the American Fisheries Society Annual Meeting in August 2015. A manuscript detailing the diet compositions of the demersal caught fishes was submitted in July of 2015 to the Arctic Eis Special Issue in the peer-reviewed journal Deep-Sea Research Part 2. The manuscript was accepted in December 2015, pending revisions, which will be complete in March 2016. This submitted manuscript constitutes chapter one of this report. Chapter two of this report documents the collection of stomach specimens from the 2012 Arctic Eis surface/midwater trawl survey and presents summarized diet compositions for the sampled species. This chapter was prepared in February-March 2016. The results of our stomach collections from the Arctic Eis have also contributed to our outreach efforts. The results from this project have been the focus of our exhibit, presented to the public, during Polar Science Weekend at the Pacific Science Center in Seattle, WA, in March 2015 and 2016. The data gathered for this project will be made available through the Alaska Ocean Observing System workspace (aoos.org/), following the terms of the Arctic Eis data sharing agreement

11. Chapter 1 - Diet compositions and trophic guild structure of the eastern Chukchi Sea demersal fish community

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1.1 Abstract

Fishes are an important link in Arctic marine food webs, connecting production of lower trophic levels to apex predators. We analyzed 1,773 stomach samples from 39 fish species collected during a trawl survey of the eastern Chukchi Sea in the summer of 2012. We used hierarchical cluster analysis of diet dissimilarities on 21 of the most well sampled species to identify four distinct trophic guilds: gammarid amphipod consumers, benthic invertebrate generalists, fish and shrimp consumers, and zooplankton consumers. The trophic guilds reflect dominant prey types in predator diets. We used constrained analysis of principal coordinates (CAP) to determine if variation within the composite guild diets could be explained by a suite of non-diet variables. All CAP models explained a significant proportion of the variance in the diet matrices, ranging from 7 to 25% of the total variation. Explanatory variables tested included latitude, longitude, predator length, depth, and water mass. These results indicate a trophic guild structure is present amongst the demersal fish community during summer in the eastern Chukchi Sea. Regular monitoring of the food habits of the demersal fish community will be required to improve our understanding of the spatial, temporal, and interannual variation in diet composition, and to improve our ability to identify and predict the impacts of climate change and commercial development on the structure and functioning of the Chukchi Sea ecosystem.

8. 1.2 Introduction

Evidence of contemporary climate change in the Arctic has been accumulating over recent decades (Wassmann et al., 2011); the most visible change has been the reduction in sea ice cover, with the nine lowest annual sea ice minima over the satellite record (1979-present) occurring in the last 9 years, 2007 to 2015 (Stroeve et al., 2012, http://nsidc.org). Reductions in sea ice coverage already allow greater access to the Arctic for increased commercial development including energy extraction (Shell Gulf of Mexico Inc., 2015), shipping (Smith and Stephenson, 2013), tourism (Williams, 2014), and possibly even fisheries (Zeller et al., 2011). The effects of climate change and reduced sea ice coverage may also affect the structure and function of Arctic marine food webs and alter trophic relationships. On shallow Arctic continental shelves characterized by strong pelagic-benthic coupling, much of the primary production is not utilized in the water column and ultimately settles to the seafloor to support an abundant benthic food web (Grebmeier et al., 2006a). With reduced sea ice coverage becoming common in the Arctic (Jeffries et al., 2013; Wood et al., 2015), it is hypothesized that more of the primary production will occur later in the growing season during open water blooms in relatively warmer water, rather than earlier and in relation to sea ice, allowing for more of the primary production to be consumed by grazers in the pelagic realm, leaving less of the primary production to be exported to the benthos (Carroll and Carroll, 2003; Piepenburg, 2005; Bluhm and Gradinger, 2008; Wassmann and Reigstad, 2011; Grebmeier et al., 2015; Moore and Stabeno, 2015). As a result these marine ecosystems may switch from having a benthic-dominated food web to a pelagic-dominated food web with changed species compositions and altered trophic relationships (Grebmeier et al., 2006b; Wassmann et al., 2011; Doney et al., 2012; Grebmeier, 2012). In consideration of the increasing commercial interests and the potential effects of climate change on the Arctic ecosystem, there is a growing need to provide stakeholders, resource managers, and decision makers with sufficient information to support an ecosystem-based approach to managing Arctic resources (Clement et al., 2013).

Information on trophic relationships is an essential part to incorporating ecosystem considerations into the management of living marine resources (Hilborn, 2011; Link and Browman, 2014; Travis et al., 2014). Fishes form an important link in Arctic marine food webs, connecting production on lower trophic levels to upper level predators (Welch et al., 1992; Whitehouse et al., 2014) including people. In the Alaskan Arctic, fishes prey on a variety of pelagic and benthic invertebrates and other fishes (Coyle et al., 1997; Cui et al., 2012), and are themselves an important prey for seasonally abundant and resident marine mammals (Lowry et al., 1980; Seaman et al., 1982; Dehn et al., 2007) and seabirds (Springer et al., 1984). Additionally, fishes, seabirds, and marine mammals are important subsistence resources for Arctic residents (Hovelsrud et al., 2008; Zeller et al., 2011). Because of the central role fishes play in Arctic marine food webs, the increasing commercial activity in the Alaska Arctic, the effects of climate change, and the subsistence needs and cultural traditions of Arctic communities (Hovelsrud et al., 2011), it has become increasingly important to improve our knowledge of the trophic relationships among fishes and their prey to better understand the potential impacts these stressors may have on the Arctic marine ecosystem.

There have been only a limited number of studies on the food habits of demersal fishes in the Alaska Arctic and most of these studies have been qualitative in nature or focused on a limited number of species. Frost and Lowry (1983) described the stomach contents of nine demersal fish species collected across the northeastern Chukchi Sea and western Beaufort Sea. Craig (1984) provided general diet descriptions for six fish species found in the coastal waters of the Alaskan Beaufort Sea. Coyle et al. (1997) described the relative importance of different prey groups to four common demersal fish species collected in the northeastern Chukchi Sea. Recently, Cui et al. (2012) has provided quantitative diet descriptions for six of the most abundant demersal fishes in the northern Bering Sea. The diets of demersal fishes in the Alaska Arctic are primarily composed of benthic-oriented prey, such as polychaetes, amphipods, decapods, and mollusk siphons. Gray et al. (this issue) examined regional and size-based variation in the diet of two abundant sculpin (Cottidae) species found in the western Beaufort Sea and northeastern Chukchi Sea. The diet of the semi-pelagic species, Arctic cod (*Boreogadus saida*), consists of calanoid copepods, euphausiids, and hyperiid amphipods, but they are flexible predators and have been found to consume fish and benthic invertebrates(Lowry and Frost, 1981; Craig et al., 1982; Coyle et al., 1997; Gallaway and Norcross, 2011; Cui et al., 2012; Rand et al., 2013; Gray et al., 2015). As an alternative to analysis of stomach contents, Marsh et al. (this issue) examined the trophic role of several demersal fish species in the eastern Chukchi Sea with stable isotope analyses and found trophic level and diet to vary with predator size and by water mass.

Quantifying diet composition and the sources of diet variation among a large number of species individually can be impractical. A convenient method for summarizing food habits data for a large group of species is through the use of guilds; i.e., non-taxonomic groups of species which exploit the same resource(s) (Root, 1967). Trophic guilds are aggregations of species with similar diet compositions And may provide valuable guidance in the development of functional groups for use in ecosystem and network models (Yodzis and Winemiller, 1999). Trophic aggregation has the advantage of simplifying an otherwise complex web of interactions between numerous species to a much more manageable food web of discrete trophic guilds, without incurring marked change to salient food web properties

(Sugihara et al., 1989; Sugihara et al., 1997; Gauzens et al., 2013). Trophic guild analysis has previously been applied to numerous marine ecosystems in a range of habitats to explore the trophic structure among fishes (e.g., Garrison and Link, 2000; Bulman et al., 2001; Luczkovich et al., 2002; Marancik and Hare, 2007; Reum and Essington, 2008; Abdurahiman et al., 2010; Kellnreitner et al., 2012; Varghese et al., 2014), including a deep-sea benthic fish community in Davis Strait in the Canadian Arctic (Chambers and Dick, 2005).

This study addresses a portion of the knowledge gap on fish food habits in the Alaska Arctic. The objectives of this study are to provide quantitative information on the trophic ecology of the demersal fish community in the eastern Chukchi Sea and to use this information to describe trophic guilds within the community and to determine potentially important non-diet drivers of guild structure. We analyzed the stomach contents from 39 demersal fish species encountered in the eastern Chukchi Sea during the summer of 2012. We used multivariate statistical techniques to identify distinct trophic guilds and to describe differences and similarities in the trophic guild diet compositions at the regional scale. Additionally, we use constrained ordination to determine whether any of the variation present in the diets of the trophic guilds can be explained by a collection of non-diet variables including, predator size, location, depth, and water mass. This study provides a current quantitative baseline for trophic interactions among the demersal fish community in advance of hypothesized climate-related changes to the structure and function of the Arctic marine food web.

9. 1.3 Methods

(i) 1.3.1 Study Area

Our study area was the US territorial waters of the eastern Chukchi Sea between the Bering Strait in the south and Pt. Barrow in the north (Figure 1.1). The Chukchi Sea is a marginal Arctic Sea with a broad and shallow continental shelf, with most depths less than 60 m (Jakobsson, 2002). The Chukchi shelf, being an inflow conduit from the Bering Sea, provides the only oceanic connection between the Pacific and Arctic Oceans (Coachman et al., 1975; Carmack and Wassmann, 2006). Waters of Pacific origin flow into the Chukchi Sea through the Bering Strait with an annual mean transport of 0.8 Sv (1 Sv=106 m3 s-1) (Woodgate et al., 2005) and on average maintain a net northward flow across the Chukchi Sea continental shelf (Weingartner et al., 2005), although synoptic, seasonal, and inter-annual variations impart considerable temporal variability to the through-flow, including reversals of more than a week in duration (Coachman and Aagaard, 1981; Woodgate et al., 2005; Woodgate et al., 2012; Danielson et al., 2014).

There are two principle water masses contained in the volume flux that passes through Bering Strait into the Chukchi Sea; Bering Sea Water (BSW) and Alaska Coastal Water (ACW) (Coachman et al., 1975). BSW has origins on the Bering Shelf and the Gulf of Anadyr, and is characterized by moderate or relatively high salinity and can be rich with nutrients (Sambrotto et al., 1984). Alaska Coastal Water (ACW) has lower salinity, fewer nutrients and is warmer than BSW in summer months (Coachman et al., 1975; Springer and McRoy, 1993; Weingartner, 1997; Danielson et al., 2011). These water masses are reflected in spatial variations in macronutrients, phytoplankton standing crop, productivity, zooplankton, and fish communities (Walsh et al., 1989; Lee et al., 2007; Norcross et al., 2010). For example, higher primary production and an abundance of large oceanic zooplankton (e.g., *Calanus* spp., *Neocalanus* spp., euphausiids) are associated with BSW, while lower primary production and an abundance of smaller zooplankton taxa (e.g., *Pseudocalanus* spp., *Oithona similis*, meroplankton)are associated with ACW (Springer et al., 1989; Springer and McRoy, 1993; Hopcroft et al., 2010; Matsuno et al., 2011; Eisner et al., 2013). Small demersal fish assemblages in the Chukchi Sea are structured by variation in bottom sediments and near-bottom temperatures and salinities (Barber et al., 1997; Norcross et al., 2010; Norcross et al., 2013).

(ii) 1.3.2 Data collection

Stomach samples were collected from a bottom-trawl survey of the eastern Chukchi Sea during the summer of 2012, conducted as part of the Arctic Ecosystem Integrated Survey (Arctic Eis, https://web.sfos.uaf.edu/wordpress/arcticeis/). Trawling was conducted between 14 August and 18 September during daylight hours. Sample station depth ranged from 12-90 m, with most stations < 50 m (mean 42 m, SD =14.9). Bottom trawling operations were conducted aboard the F/V Alaska Knight with an 83-112 Eastern bottom trawl with 25.3 m headrope and 34.1 m foot rope with a 4.5 mm codend liner, towed for 15 minutes at 1.54 m/s (3 knots). Sample stations were based on a 30 nautical mile square grid pattern, with trawl deployments conducted near the center of the grid cells. All bottom trawl deployments were conducted in accordance with standard NOAA trawling procedures (Stauffer, 2004). Additional stomachs were collected at a limited number of bottom trawl stations with a plumb staff beam trawl which had a 5.1 m footrope, 4.1 m headrope and a 4 mm codend liner. Beam trawl deployments were towed at about 0.77 m/s (1.5 knots) for approximately 5 minutes. See Britt et al. (2013) and Goddard et al. (2014) for a complete description of bottom trawling methods for both gear types.

A total of 1,773 stomachs from 39 species of fish were collected at 72 sampling stations (Figure 1.1). Up to 15 intact fish specimens, per species, were randomly selected for stomach analysis from each trawl deployment, depending on the abundance of fish in the catch. The selected fish were examined for signs of regurgitation and net feeding. These signs include prey items in the mouth or gill rakers, a flaccid stomach, and prey movement. If the fish is determined to have regurgitated or net fed it was discarded and a replacement fish selected. Fish specimens selected for diet analysis were collected whole and preserved in buffered, neutral 10% formalin at sea then shipped back to the Alaska Fisheries Science Center (AFSC) in Seattle. Following arrival at the AFSC, stomach specimens were transferred from 10% formalin to 70% ethanol for storage while awaiting laboratory examination of stomach contents. A detailed description of the stomach sample selection and collection procedure can be found on the AFSC webpage (http://www.afsc.noaa.gov/REFM/REEM/Manuals/StomachChapter.pdf).

(iii) 1.3.3 Diet analysis

Each predator stomach was analyzed individually. For each collected fish, they were weighed and their fork length recorded (mm), prior to having their stomach excised. The contents of each stomach were sorted and identified to the lowest practical taxon, given the digestive state of prey and/or time constraints. Each prey taxa was weighed to the nearest 0.001 g, counted, and when it was possible, the appropriate life history code was identified. A total of 315 unique prey types were identified (see Appendix A for a complete list of prey type/life history stage combinations identified during laboratory analysis). A more detailed description of stomach contents analysis methods can be found on the AFSC webpage (http://www.afsc.noaa.gov/REFM/REEM/Manuals/LabManual.pdf). The diet composition of each predator species was then calculated as the percent wet weight of each prey type, across all non-empty stomachs.

(iv) 1.3.4 Statistical analysis

We used hierarchical cluster analysis on the species diet compositions to identify trophic guilds among the demersal fish community. Only species with sample sizes sufficient to adequately describe diet ($n \geq 10$ stomachs) were included in the cluster analysis. This left 21 species to be included in the subsequent diet analyses (Table 1.1). The diet composition of Arctic cod is known to shift with increasing length (Gray et al., 2015; Marsh et al., this issue); therefore, we divided Arctic cod into length categories. Our Arctic cod specimens ranged in size from 5.7-19.3 cm (FL). We divided this size range into three equal parts to create size bins: small (5.7-10.2 cm), medium (10.3-14.7 cm), and large (14.8-19.3 cm). For the remaining species, we did not separate into size classes due to low sample sizes for most species and because ontogenetic diet shifts have not been previously established for most of the included species.

To simplify analyses and aid interpretation of results, similar prey items were aggregated, reducing the total number of prey types from 315 to 41 (Table 1.2). In general, prey items were aggregated based on taxonomy (e.g., family, order, class); however, in a few instances additional consideration was given to life history stage or association with the pelagic or benthic environment. Planktonic larval life history stages of mollusks (veliger) and decapods (zoea, megalopa) are kept separate from their benthic-oriented adult counterparts (e.g., Gastropoda, Reptantia). The “benthic crustacean” group is a composite group consisting of multiple crustacean taxa that generally associate with the benthic environment (e.g., isopods, ostracods, harpacticoid copepods). “Other worms” is a taxonomically broad category that includes multiple phyla of marine worms (Echiura, Priapula, Rhynchocoela, Sipuncula), all of whom associate with the benthic environment. See Appendix A for a complete list of the taxonomic composition of all aggregated prey groups.

Unidentified prey items seldom accounted for more than 1% of diet composition and are uninformative for clustering. Therefore, prior to clustering, unidentified prey items were removed from diets and the diet compositions normalized to sum to 1. The full diet compositions of the individual species included in clustering are available in Appendix B. For the 18 species not included in clustering, we provide a general description of their food habits from the limited collections (The full diet compositions are available in Appendix C).

Dissimilarity in diet composition was calculated with the Bray-Curtis (B-C) Index (Bray and Curtis, 1957). The B-C index calculates the dissimilarity in diet composition of two predators in terms of the minimum abundance of mutually present prey species, and excludes prey types absent from both diets (double-zero or double-negative). An index that excludes double-zeros is preferred for our analysis, as prey that is absent from both predators’ diets does not necessarily indicate similarity in diet composition or prey preference (Clarke et al., 2006) but may reflect variability in prey abundance and variation in feeding rates.

The observed dissimilarities from the B-C matrix were submitted to cluster analysis performed with Ward's Minimum Variance Method (Ward, 1963). Ward's method is an agglomerative hierarchical approach to clustering that fuses sample units (predator species) into clusters (trophic guilds), while minimizing the sum of squared distances, weighted by cluster size. The clustering structure of the data was evaluated with the agglomerative coefficient. The cluster solution was evaluated with the cophenetic correlation coefficient which provides a measure of how faithfully the output distances in the resulting dendrogram represent the observed dissimilarities from the original B-C matrix. A scree plot of the number of clusters against the output dissimilarity was used to determine where to place a phenon line on the dendrogram. The scree plot depicts the dissimilarity value at a split in the dendrogram against the number of clusters, and indicates where further increases in the number of clusters results in little change in dissimilarity (i.e., increasingly similar clusters).

The composite diets of trophic guilds identified by cluster analysis are reported as the proportion of each prey type (as % weight) of the total stomach contents of all predators within a trophic guild. Prey items that contributed most to dissimilarities between the diets of trophic guilds were identified with similarity percentages (SIMPER, Clarke, 1993). SIMPER reports the cumulative contribution each prey type makes to between-cluster dissimilarity.

To aid the interpretation of clustering results, the species diets and the distances between them are visualized in ordination space with the use of non-metric multidimensional scaling (NMDS). The goodness-of-fit between the ranked distances in the NMDS ordination and the original ranked multivariate distances is expressed as a "stress" value. To ensure convergence on a global solution, a maximum of 500 random starts was used in the NMDS. The significance of the observed stress value is assessed with Monte Carlo simulations (999 random permutations). Stress levels less than 0.15 are considered acceptable. The correlation between the ordination distances (y-axis) and the observed dissimilarities (x-axis) was assessed with a Sheppard plot (linear fit, R2). Variable weights are used to interpret the position of objects in ordination space and are displayed as loading vectors. Prey species with significant loadings on both axes (1,000 permutations, $p < 0.05$) are displayed in the ordination.

We analyzed the composite diets of the trophic guilds identified with cluster analysis using constrained analysis of principal coordinates (CAP, also known as distance-based redundancy analysis [db RDA]). CAP is a constrained ordination technique that can help determine if there is a common structure between two matrices, and can be used on any distance or dissimilarity measure (Legendre and Anderson, 1999; Anderson and Willis, 2003). We calculated a B-C matrix from the diet matrices of each trophic guild prior to being submitted to CAP. The secondary matrix of explanatory variables includes predator length, latitude, longitude, bottom depth (m), and water mass. Latitude, longitude, and depth were recorded at sea during standard trawling operations (see Goddard et al., 2014 for details). The CAP analysis includes categorical and continuous variables. Water mass is treated as categorical variable, and all the remaining variables are continuous. The continuous explanatory variables were log transformed to account for variables recorded on different scales, spanning orders of magnitude. For each CAP we test the significance of all constraints simultaneously with a Monte Carlo global test (199 permutations). Specifically, we test the null hypothesis that there is no significant relationship between variation in the diet matrix and the matrix of explanatory variables.

Water mass designations for bottom trawl locations are taken from Danielson et al. (this issue) and they describe the water characteristics present nearest the sea floor at the bottom trawl sampling stations. The data used to determine water mass was collected during hydrographic operations aboard the F/V Bristol Explorer during the same sampling period (August-September 2012) as bottom trawl operations on the F/V Alaska Knight. The data from CTD sampling stations were linearly interpolated to the bottom trawl sampling stations located within the CTD station bounding polygon. CTD casts were made to a target depth of 5 m above the seafloor, and water mass designations used here describe the identified water mass at the bottom of the sampled water column. For nine bottom trawl stations found outside this sampling polygon, extrapolations were made using a nearest neighbor approach. We briefly review here the water masses present near the sea floor at bottom trawl deployment locations during this study; but see Danielson et al. (this issue) for a complete discussion of Chukchi Sea hydrography and the oceanographic sampling methodology. During the 2012 Arctic Eis bottom trawl survey three water masses were observed in near-bottom waters at bottom trawl locations; Alaska Coastal water (ACW), Chukchi winter water (CWW), and Bering Shelf/Chukchi Shelf Summer Water (BCSW), defined by their temperature (°C) and salinity characteristics (Table 1.3). A variety of processes are responsible for the formation and time evolution of these water masses and their distinct properties, including heating and cooling via air-sea heat fluxes, freezing, brine rejection, coastal runoff, and upwelling. ACW is fresher than the other near-bottom water masses, being influenced by seasonally varying discharges from rivers and streams, resulting in salinities ranging from 20 to 32. We note that melt water from sea ice can also attain salinities well below 30, but these waters are generally found close to the surface and not the seafloor. The ACW is also the warmest of the water masses present during this study, with temperatures ranging from 7 to 12°C. CWW, with temperatures between -2 and 0°C, and with salinities in the range of 30-33.5, is formed on the continental shelf during fall, winter, and spring under the influence of cooling, ice formation, and brine drainage (Weingartner et al., 2005). BCSW can be a mixture of remnant winter waters (possibly warmed by solar heating), BSW, and Anadyr Waters (AW), which originate along the Bering Sea continental slope and passes through the Gulf of Anadyr en route to the Arctic (Coachman et al., 1975). Shelf summer waters exhibit temperatures between 0 and 7°C, cooler than coastal waters but warmer than winter waters. Salinity of the BCSW is generally higher than the freshwater influenced ACW, ranging from 30-33.5, with most in the range of 31-33.

All statistical analyses were performed using the R statistical program (R Core Team, 2014, version 3.0.3) with R packages Vegan (Oksanen et al., 2013) and Cluster (Maechler et al., 2014).

10. 1.4 Results

(v) 1.4.1 Statistical analysis

The data matrix of demersal fish species diets has an agglomerative coefficient of 0.87, indicating a strong clustering structure. The cophenetic correlation coefficient of 0.77 ($p \leq 0.001$, Mantel test, 999 permutations) indicates the distances depicted in the resulting dendrogram (Figure 1.2) are a good representation of the observed dissimilarities from the B-C matrix. The scree plot of cophenetic dissimilarity against the number of clusters indicated that increasing the number of clusters beyond four would not result in clusters that are distinctly dissimilar. Therefore, a phenon line was placed on the dendrogram at a dissimilarity of 1.5 resulting in four clusters (Figure 1.2).

The four distinct clusters reflect the different prey types accounting for the dominant portions of their diets. The composite diets for the four identified feeding guilds are presented in Table 1.2. A limited number of prey types comprised the bulk of guild diets. We assigned names to the four identified feeding guilds based on the dominant prey items (≥10 % wet wt.) in their composite guild diets: gammarid amphipod consumers (GM), benthic invertebrate generalists (BI), fish and shrimp consumers (FS), and zooplankton consumers (ZP). The dendrogram has two distinct branches, each containing two guilds (Figure 1.2). One branch has the ZP and FS guilds and the other has the GM and BI guilds. Based on the guild diet composition, the GM and BI groups can broadly be described as feeding on benthic-oriented invertebrates, while the primary prey types for the ZP and FS guilds are relatively more mobile prey including fish, shrimp, and pelagic invertebrates.

Pairwise SIMPER analysis of guild diet composition identified prey groups that contributed most to dissimilarity between guilds (Table 1.4). The pairwise tests showed that gammarid amphipods contributed most to between guild dissimilarity in all pairwise comparisons between the GM guild and the other three guilds. Polychaete worms contributed most to dissimilarity between the BI guild and both the ZP and FS guilds. And between the FS and ZP guilds, calanoid copepods contributed most to dissimilarity.

The NMDS ordination depicts the distance between predator species in two-dimensional ordination space (Figure 1.3). The observed stress of 0.115 ($p \leq 0.001$) and the correlation from a Sheppard plot (linear fit R2 = 0.935) indicates good interpretive ability. Species are generally located in ordination space nearest to other species from the same guild, and the ordination supports the cluster analysis results. In general, species from the benthic-oriented GM and BI guilds have positive values on the first axis, while species from the FS and ZP guilds, which prey on more mobile and pelagic-oriented prey, have negative values on the first axis. The areas occupied by the four clusters in multivariate space are fairly distinct, with the only clear overlap displayed by the GM and BI guilds.

We used CAP analysis to determine if any of the observed variation in predator guild diets could be explained by water mass and a suite of explanatory variables that are commonly collected during fishery studies. All of the CAP analyses explained a significant (Table 1.5) proportion of the variance in the corresponding diet matrices. The correspondence of the guild diet data with the explanatory variables is depicted in Figure 1.4. The location of the individual stomachs in constrained ordination space indicates their similarity to each other. Stomachs that are clustered closer together have similar contents and are typically dominated by prey species located nearest to them in the ordination space. Vector length for a continuous explanatory variable indicates the importance of that variable to the ordination. The orientation of a vector indicates its correlation with the ordination axes, and the angle between vectors indicates their relationship with other explanatory variables. A 0° angle between vectors is a maximally positive correlation, 90° indicates a null correlation, and 180° is a maximum negative correlation. The categorical variable water mass is represented with points located at the centroid of stomachs that belong to the respective water masses. We present the specific results for each CAP in the following sections.

(vi) 1.4.2 Gammarid amphipod consumer guild

Stomach specimens from the GM guild were collected at 49 of the 71 sampling stations (Figure 1.5). They were generally collected at stations located offshore and were seldom collected from the stations nearest to shore. Sample sizes at collection stations ranged from as few as 1 up to 43 at one station in the northern Chukchi Sea. There were a total of 451 non-empty stomachs for this guild. The GM guild is the most species-rich containing eight species from five families including three sculpins (spatulate sculpin [*Icelus spatula*], hamecon [*Artediellus scaber*], and Arctic staghorn sculpin [*Gymnocanthus tricuspis*]), two eelpouts (Canadian eelpout [*Lycodes polaris*] and marbled eelpout [*L. raridens*]), one snailfish (kelp snailfish [*Liparis tunicatus*]), one alligatorfish (Arctic alligatorfish [*Ulcina olrikii*]), and one prickleback (slender eelblenny [*Lumpenus fabricii*]) (Table 1.1). Gammarid amphipods are the dominant prey item for this guild, comprising 58% of their diet (Table 1.2). In the NMDS plot, species from the GM guild are arranged close together and are found near the loading vector for gammarid amphipods, highlighting the importance of this prey type (Figure 1.3). They are also located near the loading vector for their second most dominant prey type, polychaete worms.

The CAP for the GM guild explained about 6.9% of the total variance in the GM guild diet matrix (Figure 1.4). The first two CAP axes account for 74% of the explained variation (Figure 1.4). Most of the prey types are located near the center of the ordination and do not indicate a strong relationship with any particular explanatory variable. The location of gammarid amphipods in the CAP triplot indicates the proportion of gammarid amphipods in the diet is negatively related to ACW but positively related to depth and latitude. Polychaete worms are the second most important prey to this guild (by % weight) and consumption of polychaetes is also positively associated with latitude and is negatively correlated with the ACW. Consumption of these primary prey groups is greater at higher latitudes and in water masses other than ACW.

(vii) 1.4.3 Benthic invertebrate generalist guild

Five species comprise the BI guild, including two sculpins (Antlered sculpin [*Enophrys diceraus*] and ribbed sculpin [*Triglops pingeli*]), one prickleback (stout eelblenny [*Lumpenus medius*]) and two flatfishes (Arctic flounder [*Liopsetta glacialis*] and yellowfin sole [*Limanda aspera*]). Stomach samples for the BI guild were collected at 24 of the 72 sampling stations (Figure 1.5). These stations were widely scattered across the study area, including multiple nearshore stations. The total number of stomach samples collected at each station ranged from 1 up to 15, and there were a total of 110 non-empty stomachs for this guild. Rather than a single dominant prey type, these species primarily prey on a variety of benthic-oriented invertebrates, including bivalves, crabs (Reptantia), gammarid amphipods, polychaete worms, and anemones (Table 1.2). Other prey groups of lesser importance for the BI guild include Pacific sand lance (*Ammodytes hexapterus*) and Hippolytidae shrimp.

Species from the BI cluster were widely dispersed in the NMDS plot (Figure 1.3). Stout eelblenny, Arctic flounder, and yellowfin sole are closely aligned with the loading vector for polychaete worms. The ribbed sculpin is aligned with zooplankton prey vectors, and the antlered sculpin is not closely associated with any significant prey vectors (Figure 1.3). Ribbed sculpins are the only species from the BI guild to have a negative value on the first NMDS axis, placing them near loading vectors for zooplankton prey. The diet of ribbed sculpin is unique among the species of the BI guild in that it also includes sizeable proportions of zooplankton prey, including hyperiid amphipods (13.5%) and euphausiids (13%). The antlered sculpin is the most distantly located species from the BI guild, having the lowest value on the second axis of all species, from all guilds, and a near zero value on the first axis. The relative isolation of the antlered sculpin reflects the unique composition of its diet, which includes many benthic prey species, similar to other predators from the BI guild, but also includes portions of fish, crabs (Reptantia), and anemones (Appendix B). Species from the FS guild are closest to antlered sculpin in the NMDS plot which reflects the importance to fish to the diet of antlered sculpin (20%). The high proportion of crabs (22%) and the presence of anemones (36%) in the antlered sculpin diet also distinguishes this species' diet from other species within the BI guild. Crabs and anemones are not as prevalent in the diet of any other predator in the BI guild.

CAP explained 25% of the total variation in the diet data for the benthic invertebrate generalist guild. The first two constrained axes represent 76% of the constrained variation (Figure 1.4). Many of the prey groups are located near the center of the triplot and, therefore, do not indicate a strong relationship with any of the explanatory variables, including anemones and bivalves, two of the more dominant prey groups. The location of polychaetes in the constrained ordination space indicates a negative relationship with the ACW and BCSW, and a positive correlation with the cooler CWW. In contrast, the consumption of Reptantia (crabs) is positively correlated with ACW and BCSW, but negatively related to CWW and latitude. The consumption of gammarid amphipods, another important prey group, is positively correlated with depth and latitude, but negatively related to length and longitude. The consumption of important prey groups in different water masses and at different latitudes reflects the generalist nature of this guild and the wide spatial distribution of samples.

(viii) 1.4.4 Fish and shrimp consumer guild

The FS guild is a diverse group including 5 species, each from a different family. Members of the FS guild include, rainbow smelt (Osmeridae, *Osmerus mordax*), saffron cod (Gadidae, *Eleginus gracilis*), shorthorn sculpin (Cottidae, *Myoxocephalus scorpius*), variegated snailfish (Liparidae, *Liparis gibbus*), and Bering flounder (Pleuronectidae, *Hippoglossoides robustus*). Diet samples for the FS guild were collected across the study region at 41 of the 72 sampling stations, with station sample sizes ranging from 1 to 23 (Figure 1.5). There were a total of 315 non-empty stomachs for this guild. The primary prey groups for the FS guild are pricklebacks (Stichaeidae), unidentified fish, and Crangonidae shrimp. All predator species belonging to the FS guild were clustered closely together in the NMDS ordination and all had negative values on both the first and second axis (Figure 1.3). These FS species are all located in the NMDS plot in close proximity to prey vectors for pricklebacks (Stichaeidae) and unidentified fish.

The constrained ordination of the fish and shrimp consumer guild explained about 11% of the total variance in their diet matrix. The first two CAP axes explained about 78% of the constrained variation (Figure 1.4). Most prey groups are clustered together near the center of the ordination indicating they generally do not have strong relationships with any particular explanatory variable. The dominant fish and shrimp prey groups have negative values on the first CAP axis and are located near the vector for predator length, indicating consumption of these prey groups is positively associated with predator length. The location of these dominant prey groups also indicates that consumption of these groups is negatively related to CWW. The consumption of the dominant fish and shrimp prey increases with predator length and is associated with ACW and BCSW.

(ix) 1.4.5 Zooplankton consumer guild

The ZP guild consists of Pacific herring (*Clupea pallasi*), walleye pollock (*Gadus chalcogrammus*), and all three size classes of Arctic cod. Collection of diet specimens for species belonging to this guild were well distributed across the study region being collected at 66 of the 72 stations (Figure 1.5). By station, sample sizes ranged from 1 to 29. The number of specimens collected was generally lower at near shore stations. The total number of non-empty stomachs for this guild was 731. The vast majority of all specimens collected in this guild are Arctic cod. Walleye pollock and Pacific herring account for less than 5% of all ZP stomachs (Table 1.1). The diet of large Arctic cod was most similar with walleye pollock, while the diets of small and medium Arctic cod were more similar to Pacific herring (Figures 1.2 and 1.3). The dominant prey items of the ZP guild are calanoid copepods and euphausiids. In the NMDS ordination, species from the ZP guild all have negative values on the first axis, and all but walleye pollock have positive values on the second axis (Figure 1.3). Pacific herring, small Arctic cod, and medium Arctic cod are located close to significant zooplankton prey vectors, while walleye pollock and large Arctic cod have near zero values on the second axis, placing them close to species from the FS guild. This reflects the relative importance of fish and shrimp in the diets of walleye pollock and large Arctic cod (Appendix B).

The CAP of the zooplankton consumer guild explained 9% of the variation present in the diet data. The first two axes accounted for about 81% of the constrained variation (Figure 1.4). Calanoid copepods are the dominant prey taxa for this guild and their location in the triplot indicates that consumption of calanoids is positively associated with latitude and CWW but negatively related to predator length, longitude, ACW and BCSW. In contrast to copepods, consumption of euphausiids is negatively correlated with latitude and is positively related to longitude and the BCSW. In general, the zooplanktivores consumed copepods at higher latitudes and in the cooler CWW, while consumption of euphausiids was greater at lower latitudes and in association with the BCSW. Presuming that euphausiids are preferred prey items given their higher lipid content, these results suggest that locations and timings of these zooplankton may be important drivers to diet and diet seasonality. This observation supports the notion that euphausiids on the Chukchi shelf are primarily advected northward from the Bering Sea (Berline et al., 2008). The consumption of larvaceans is positively associated with predator length and the ACW.

(x) 1.4.6 Other species

We analyzed the stomach contents from 18 additional demersal fish species that were infrequently encountered and/or were poorly sampled (n < 10 non-empty stomachs) and therefore not included in the trophic guild analysis. The total number of stomach samples per species ranged from 1 to 9 for a total of 75 non-empty stomachs. We have assigned each of these predator species to one of the observed trophic guilds based on the major prey items (by % weight) found in the sampled stomachs (Table 1.6). Major prey was defined as the top two prey categories by % weight, and in all cases these top two prey taxa represented at least 73% of the predator's diet by weight. However, these guild designations are only preliminary and are done for the sake of summarizing the diets of these species in the context of the present trophic guild analysis. The complete diet compositions can be found in Appendix C. Four species fed heavily on gammarid amphipods and were assigned to the GM guild including, the eyeshade sculpin (*Nautichthys pribilovius*), veteran poacher (*Podothecus veternus*), festive snailfish (*Liparis marmaratus*), and Sakhalin sole (*Limanda sakhalinensis*). Five other species of benthic-oriented consumers fed on a mix of polychaetes, crabs, mysids, gammarids and brittle stars (Ophiurida) and were designated to the BI guild including, the half-barred pout (*Gymnelus hemifasciatus*), polar eelpout (*Lycodes turneri*), Arctic shanny (*Stichaeus punctatus*), longhead dab (*Limanda proboscidea*), and Alaska plaice (*Pleuronectes quadrituberculatus*). We added six species to the FS guild who consumed high levels of shrimp and fish including, Pacific cod (*Gadus macrocephalus*), wattled eelpout (*Lycodes palearis*), whitespotted greenling (*Hexagrammos stelleri*), butterfly sculpin (*Hemilepidotus papilio*), plain sculpin (*Myoxocephalus jaok*), and fourhorn sculpin (*M. quadricornis*). Capelin (*Mallotus villosus*), Pacific sand lance, and Greenland turbot (*Reinhardtius hippoglossoides*, also known as Greenland halibut) were added to the ZP guild because they consumed high proportions of euphausiids and calanoid copepods.

11. 1.5 Discussion

The bottom trawl survey conducted in 2012 in support of the Arctic Eis program provided a unique opportunity to systematically sample the feeding habits of demersal fish species across the entire eastern Chukchi Sea continental shelf. We have produced new quantitative diet descriptions for 39 fish species and identified four distinct trophic guilds amongst the demersal fish community. These guilds reflect the major prey items in the diets of fishes during summer. The guild structure and quantitative diet descriptions can contribute to food web and network analyses by providing an ecological framework for grouping trophically similar species together, helping simplify the complex web of predator-prey interactions in the Chukchi Sea.

Through the use of trophic guilds and multivariate statistical techniques we were able to identify some regional patterns in diet composition and relate a portion of the observed variance in guild diet composition to non-diet variables. The cluster analysis and the NMDS both show a distinct separation between the two benthic invertebrate oriented feeding guilds (GM and BI guilds) and the guilds feeding on pelagic prey or larger, more mobile prey (ZP and FS guilds). The first NMDS axis describes this transition from pelagic and off-bottom feeding at the negative end of the axis (ZP and FS) to benthic-oriented feeding at the positive end of the axis (GM and BI). Similar distinctions between benthic and pelagic feeding guilds have been observed in other continental shelf systems (e.g., Garrison and Link, 2000; Marancik and Hare, 2007). In a review of resource partitioning in fish communities, Ross (1986) found trophic gradients, such as that observed here between benthic and pelagic feeders, to be more important than spatial and temporal axes in separating marine species.

The CAP analyses were effective at identifying underlying patterns in the guild diet compositions. All CAP models explained a significant portion of the variance in the guild diet matrices, ranging from 7 to 25% of the total variation ($p = 0.005$, Table 1.5). Previous studies that employed constrained ordination to examine fish diet composition have used canonical correspondence analysis (CCA; ter Braak, 1986). CAP and CCA are both forms of constrained ordination that can be used to determine if there is a common structure between two matrices. An advantage to using CAP is that it can accept any distance or dissimilarity measure (Anderson and Willis, 2003), such as the Bray-Curtis index used in this study. The amount of diet variance for trophic guilds that we could account for with CAP is similar to the results of previous studies that used CCA to explain diet variation for individual species. Jaworski and Ragnarsson (2006) were able to account for 6 to 16% of the variation in diet composition for eight demersal fish species found in Icelandic waters. Similarly, Link et al. (2002) was able to explain 8 to 12% of the variation in the diets of three flatfish species from the northwest Atlantic. Link and Garrison (2002) also used CCA to explain 10% of the variation present in the diet of Atlantic cod (*Gadus morhua*) from the northeast US continental shelf. More recently, Gray et al. (2015) used CCA to describe 8-9% of the total variance in the diets of juvenile Arctic cod from the Beaufort and Chukchi seas, respectively. We found CAP to be a similarly effective method for evaluating sources of variation in the diet of Arctic demersal fishes. Our study and these previous studies used similar explanatory variables: latitude, longitude, depth, and fish size (length in this study). These other studies also included an additional temporal component and included variables for year and/or season. Our study differed from these studies by including a categorical variable for water mass. The range of variation explained by our CAP models (7-25%) overlapped with the range of variation explained in these previous trophic studies using CCA (6-16%). The amount of variation explained by the constrained ordination in our study and these examples may seem low but this is commonly the case with ecological data (Borcard et al., 1992; ter Braak and Verdonschot, 1995). It is not the goal of constrained ordination to explain 100% of the variation in the data because much of that unexplained variation reflects noise (ter Braak, 1986; Borcard et al., 1992). Instead, the goal is to explain a significant amount of variation with a set of constraining variables that highlight informative patterns in the data.

In contrast to the amount of variation explained in our CAP models, Hovde et al. (2002) used CCA to explain 46% of the total variation in the diet of Greenland halibut collected in the Barents Sea when treating all stomachs at a station as a sampling unit, and 30% of the total variation when treating individual stomachs as sampling units (as in this study). Their study differed from ours in several ways; for example their study included three distinct sampling regions (categorical variables), while our study was conducted over a single continuous area which we did not subdivide. Hovde et al. (2002) found this spatial component (sampling region) to be the most important explanatory variable, whether they were looking at the stomachs individually or at the station level. Additionally, their study was conducted over three years and included six distinct sampling periods. We did not have a temporal variable as our study was conducted over a single season. Both their study and ours included variables for latitude, longitude, depth, and predator length; however, their study included additional biotic variables for predator sex, weight, and maturity. The total number of explanatory variables is an important consideration, as increasing the number of explanatory variables will likely increase the amount of explained variation (Borcard et al., 1992). The cumulative effect of the additional biotic and abiotic constraining variables included by Hovde et al. (2002) and their treatment of all stomachs at a station as a sampling unit likely contributed to the additional explained variation in their study (30 to 46%) when compared with ours (7 to 25%).

The explanatory variables that we included in our CAP models (water mass, predator length, depth, latitude, longitude) were informative for all four CAP models. However, there are many other potential explanatory variables that were not included here that could have been informative and may have increased the amount of variation explained, such as the additional biotic and abiotic variables used by Hovde et al. (2002). Future studies that record additional biological information, such as sex, weight, and maturity, or that include additional spatial and temporal variables, may find they can explain more of the variation in the fish diets. Another potentially important explanatory variable that was not included in our analysis is prey abundance. Stomach samples are only a “snapshot” of what a predator is eating at a given time and specific location. Several previous studies in other regions and with different fish predators, have observed a relationship between predator diet composition and local prey abundance (Fahrig et al., 1993; Rachlin and Warkentine, 1997; Frid and Hall, 1999; Link, 2004; Hinz et al., 2005; Link and Ford, 2006). Quantitative data on prey abundance could potentially be an important variable to include in future diet studies of fishes in the Chukchi Sea and may increase the proportion of variation explained with constrained ordination. Future ecosystem studies should aim to collect information on benthic and pelagic prey abundance concurrently with trawl deployments for fish predators to enable more detailed diet analyses, including the partitioning of variance (Borcard et al., 1992) between prey abundance, environmental variables (e.g., water mass), and biological variables (e.g., length, maturity). Variance partitioning is an effective method for evaluating the relative importance of different sets of variables in constrained ordination (Peres-Neto et al., 2006).

A key distinction between our study and these previous studies is that we used constrained ordination to explain diet variation at the level of the trophic guild as opposed to the species level. Because guild members exploit similar prey resources in a similar fashion, we might expect them to have similar relationships with the constraining variables. However, this may not be the case and if species belonging to the same trophic guild respond differently in magnitude or direction to the constraining variables (e.g., water mass) this might have limited the explanatory power of the constrained ordinations. Even though species may be similar enough in diet composition to cluster together as a trophic guild, if their relationships with the available constraining variables are sufficiently different, this can increase the noise in the data at the guild level and possibly limit the variation explained by the constraining variables.

An important limitation of this study was the small sample size for several of the species due to small catches and/or infrequent capture. Sample sizes for 18 of the 39 species of fish collected for diet analysis during this study were too low ($n < 10$) for those species to be included in the cluster analysis (Table 1.6). As a result their diet descriptions are very limited and our guild designations are only preliminary. For those species that were adequately sampled to be included in the trophic guild analyses, the minimum sample size of ten was a generously low threshold and may not have been sufficient to adequately represent diet composition over such a large spatial scale. An example of this limitation from this study is the antlered sculpin from the BI guild. There were 14 non-empty antlered sculpin stomachs and their primary prey items were anemones (36%), crabs (22%), Pacific sand lance (14%), and polychaetes (11%). Anemones are generally an uncommon prey and were only consumed by one antlered sculpin at one station. However, due to the large mass of that particular anemone prey, this prey category accounts for 16% (by weight) of the BI guild diet (Table 1.2). It is possible for the anemone prey to be “washed” into the sculpin’s stomach during the trawling operation; however, a fair amount of digestion was observed on the anemone and it was therefore determined to be a valid prey item. Antlered sculpins have also been observed to consume anemones in the Bering Sea. Collections made in the northern Bering Sea and eastern Bering Sea, showed that anemones occurred in 9% of the non-empty antlered sculpin stomachs (n=55), accounting for 11% of their diet by weight (unpublished data, NOAA/AFSC Food Habits database, http://www.afsc.noaa.gov/REFM/REEM/Data/Default.htm). Although there is good indication from examination of the anemone prey in question and supporting evidence from an adjacent ecosystem that the anemone was a legitimate prey item, the impact this one large prey had on both the species and the guild diet composition highlights the limitations of small sample size. Future stomach collections should focus on these poorly sampled species to develop more robust diet descriptions and a more thorough understanding of trophic guild structure among fishes.

Additionally, this example highlights the influence that a relatively large prey item can have when examining diet composition in terms of percent mass. Several measures and indices are available to describe and quantify diet composition, each with their own limitations and bias (Hyslop, 1980; Hansson, 1998; Brown et al., 2012). For example, measures based on percent prey count may be biased in favor of small prey items, measures based on percent prey mass may be biased in favor of large prey items, as seen here with anemones in the antlered sculpin diet, and the frequency of prey occurrence provides no indication of the mass or numerical importance of consumed prey (Hyslop, 1980). For our analysis we used percent weight of prey to describe diet composition because percent weight provides a measure of the biomass of consumed prey and because biomass is commonly used as currency in ecosystem and bioenergetics models (Christensen and Walters, 2004; Ahlbeck et al., 2012).

The diets of the GM and BI guilds were similar in terms of prey taxa but differed in the relative importance of the prey types. The diet composition of GM species showed a heavy reliance on gammarid amphipods, whereas the generalist diet of the BI guild showed no such reliance on any single prey group. We found that consumption of gammarid amphipods by fishes from the GM guild was negatively related to the presence of ACW and positively related to depth. This observation of the GM guild’s diet is also consistent with what is known about the distribution of gammarid amphipods. Gammarids are widely distributed in the Chukchi Sea and are found in abundance in areas of high organic deposition, overlain by productive nutrient-rich waters (e.g., BCSW) (Grebmeier et al., 1989). It is unclear whether fishes in the GM guild are truly specializing in or exhibiting a preference for gammarid amphipods or if they are consuming an abundant and accessible prey group in the areas they were captured. Continued monitoring of diet composition, and diet analysis at a finer spatial scale and in relation to prey abundance would be required to help resolve this question.

Size is a primary force behind resource partitioning among species (Schoener, 1974), and size-related shifts in diet composition have frequently been observed in fishes (Werner and Gilliam, 1984; Ross, 1986; Mittelbach and Persson, 1998; Marsh et al., this issue). Previous trophic guild analyses have also identified ontogenetic diet shifts as cause for placing different size classes of a single predator species into separate feeding guilds (e.g., Garrison and Link, 2000; Jaworski and Ragnarsson, 2006; Reum and Essington, 2008). A size-based shift in the food habits of Arctic cod has previously been observed for specimens collected in the Alaska Arctic (Gray et al., 2015). In our study all three size classes of Arctic cod were grouped together into the zooplankton guild; however, we did observe separation between the size classes within multivariate space (Figure 1.3). Fish were a more important prey to large Arctic cod than to medium or small Arctic cod (Figure 1.3), placing them closer to the piscivores of the FS guild in the NMDS plot. Size was an important explanatory variable for the FS consumer guild, and the consumption of their most important prey groups (by % wt.) were positively correlated with predator length. This is expected, as fish generally consume small invertebrates when they are juveniles and do not begin consuming fish until they have grown large enough to do so (Werner and Gilliam, 1984; Mittelbach and Persson, 1998). We did not include ontogenetic diet shifts for any other species in our guild analysis other than Arctic cod, which was our most abundantly sampled species. A goal of our trophic guild analysis was to include as many species as possible. For species with few stomach samples, dividing into size classes was not realistic, and for most species in our study, ontogenetic diet shifts are not yet documented. Future studies should focus sampling efforts on these infrequently sampled species, and in particular, emphasis should be placed on acquiring an adequate number of samples across wide size ranges and in multiple seasons to permit identification of ontogenetic diet shifts.

The diet compositions presented here and the related feeding guilds reflect the feeding habits of demersal fishes during mid-to late summer in the eastern Chukchi Sea. Quantitative diet information from other seasons, in particular during ice-covered portions of the year, is not available for most demersal fishes and therefore seasonal dietary shifts or guild switching is unknown. Information on the abundance of prey groups outside of the ice-free summer season is also limited. For predators feeding on prey groups known to have a strong seasonal signal in abundance, guild switching may be a possibility. For example, much of the zooplankton biomass found in the eastern Chukchi Sea during summer are species of Pacific origin and are delivered to the Chukchi Sea by the net northward flow of water through the Bering Strait (Springer et al., 1989; Hopcroft et al., 2010; Matsuno et al., 2011; Questel et al., 2013). The abundance of these Pacific-origin zooplankton species is thought to peak in mid-summer (July/August) in the Chukchi Sea (Springer et al., 1989). During other times of the year, when Pacific-origin zooplankton are less abundant on the continental shelf of the Chukchi Sea and large endemic Arctic copepod species (e.g., *Calanus* spp.) have descended to deeper water to diapause (Ashjian et al., 2003; Falk-Petersen et al., 2009), pelagic consumers may find foraging for zooplankton on the continental shelf less profitable and guild switching may provide improved foraging opportunities. For example, Arctic cod are known to feed on ice-associated invertebrates during ice-covered times of the year (Lønne and Gulliksen, 1989; Gradinger and Bluhm, 2004). For trophic guilds feeding on less mobile, benthic-oriented, taxa, their primary prey may not exhibit a seasonal signal in abundance and the profitability of foraging may not appreciably change between seasons. Guild switching, therefore, may not provide improved foraging opportunities. The lack of data from other times of the year is a common problem for offshore marine Arctic ecological studies, as obtaining representative samples during ice-covered portions of the year is logistically challenging and limited to vessels with ice-breaking capacity. This temporal limitation will be difficult to address for studies that employ traditional fisheries sampling gear (e.g., trawling), and other sampling techniques may need to be employed (Rand and Logerwell, 2009).

Gammarid amphipods are an abundant component of the benthic invertebrate community and can be found throughout the eastern Chukchi Sea (Feder et al., 2007; Schonberg et al., 2014). They are an important part of the diet of all four trophic guilds identified in this study, accounting for no less than 5% of the diet composition (by % wt.). Additionally, they are important prey for seasonally abundant gray whales (*Eschrichtius robustus*) and seabirds (Grebmeier and Harrison, 1992; Highsmith and Coyle, 1992). Some gammarid species are known to live in close association with the underside of sea ice (Poltermann, 2001; Gradinger and Bluhm, 2004). Due to a variety of factors including time constraints and the digestive state of prey, it was not always possible to identify all gammarid amphipods to species, and to isolate those species known to associate with sea ice from other benthic-oriented gammarids. We have made the assumption that the gammarid consumer guild can broadly be considered benthic-oriented. This assumption is based on multiple factors. The predator species included in the GM guild are thought to have a demersal orientation and adult specimens are generally not encountered in the pelagic or near-surface environment (Froese and Pauly, 2014). However, observations of these demersal fishes during ice-covered periods are extremely limited. The clustering and the unconstrained ordination both placed the GM guild closest to the BI guild emphasizing their general trophic similarity and reliance on benthic-oriented prey. Additionally, the stomachs were collected in the summertime coinciding with record low sea ice minimum extent. In consideration of these factors, it does not seem likely that the gammarids consumed by fishes in this study were associating with sea ice at the time they were consumed. See Appendix A for a complete list of taxa identified during laboratory analysis of stomach contents.

Several of the demersal fish species included in our study have been the subject of previous diet studies in the Alaskan Arctic, including Arctic cod (Lowry and Frost, 1981; Craig et al., 1982; Coyle et al., 1997; Cui et al., 2012; Rand et al., 2013; Gray et al., 2015), saffron cod (Coyle et al., 1997), Canadian eelpout (Frost and Lowry, 1983; Gallaway and Norcross, 2011), rainbow smelt (Craig, 1984), Arctic staghorn sculpin (Coyle et al., 1997; Cui et al., 2012; Gray et al., this issue), shorthorn sculpin (Cui et al., 2012; Gray et al., this issue), fourhorn sculpin (Craig, 1984), hamecon (Frost and Lowry, 1983), spatulate sculpin (Frost and Lowry, 1983), Arctic alligatorfish (Frost and Lowry, 1983; Cui et al., 2012), stout eelblenny (Gallaway and Norcross, 2011), and Bering flounder (Coyle et al., 1997; Gallaway and Norcross, 2011; Cui et al., 2012). The species-specific diet compositions that we observed here (Appendices B and C) are in general agreement with the findings of these previous works. For example, the diet composition of snailfishes (*Liparis* spp.) has previously been described in the northern Bering Sea (Cui et al., 2012) and in the Chukchi and Beaufort seas (Frost and Lowry, 1983). The primary prey items for those unidentified snailfishes were amphipods and polychaetes, followed by fishes and zooplankton. In this study, we present species-specific diet descriptions for variegated snailfish, kelp snailfish, and festive snailfish. We found variegated snailfish to primarily consume fish, while both the kelp snailfish and festive snailfish primarily consumed gammarid amphipods. Where minor differences in diet composition between our study and the previous studies exist they may reflect differences in the timing and location of sampling, predator size, spatial variation in prey abundance, flexibility in the predator diets, and small sample sizes in some cases. Continued monitoring of fish diets will be required to determine the extent of inter-annual variation in diet composition and to identify any potential effects from climate change or industrial activity in the Alaska Arctic.

To the best of our knowledge this study presents the first diet descriptions for several species from within the Alaska Arctic (northern Bering Sea, eastern Chukchi Sea, and western Beaufort Sea), including, Pacific herring, capelin, walleye pollock, Pacific cod, marbled eelpout, polar eelpout, wattled eelpout, half-barred pout, whitespotted greenling, eyeshade sculpin, antlered sculpin, ribbed sculpin, butterfly sculpin, plain sculpin, veteran poacher, slender eelblenny, Arctic shanny, Pacific sand lance, Alaska plaice, yellowfin sole, Sakhalin sole, longhead dab, and Greenland turbot. These species are generally less abundant in the Alaska Arctic than other species, such as Arctic cod, or are infrequently encountered and captured with traditional fish sampling gear (e.g., bottom trawl).

The present analysis is a start to identifying functional units of demersal fishes in the Chukchi Sea. Analyses that have greater sample sizes and take ontogenetic diet shifts into consideration will be required for a more comprehensive picture of trophic guild structure. For many of the predator species included in this study, these are the first diet records from this region. This paper focused solely on fishes collected with a benthic trawl and did not address the food habits of fishes that occupy the pelagic realm. Future studies of fish food habits in this region should include an additional component focused on the collection and analysis of fish diet data from pelagic waters. This would contribute to a more comprehensive view of fish trophic guilds and may provide additional insight to predator species distributions and spatial variation in diet compositions.

An ecosystem-based approach to marine resource management requires an understanding of the trophic relationships among species in an ecosystem (Link, 2002; Clement et al., 2013; Travis et al., 2014). The trophic guilds identified here can be used to reduce the complexity of the Chukchi Sea food web to a less complex network of ecologically meaningful trophic groups, and can support the development of management strategies that include broader ecosystem considerations. These trophic guilds can also be used to establish nodes in network and ecosystem models (Yodzis and Winemiller, 1999; Gauzens et al., 2013), and can facilitate comparative analyses with other ecosystems containing ecologically equivalent groups (Megrey et al., 2009). The study of fish food habits in the Alaska Arctic has been sporadic over the last few decades and limited in scope. Regular monitoring of the food habits of the demersal fish community (e.g., every few years) will be required to improve our understanding of the spatial, temporal, and interannual variation in diet composition. Additionally, regular sampling will improve our ability to identify and predict the impacts of climate change and commercial development on the structure and functioning of the Chukchi Sea ecosystem.

12. 1.6 Acknowledgements

This work was conducted as part of the Arctic Ecosystem Integrated Survey (Arctic Eis) and was funded [in part] by the U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM) through Cooperative Agreement M12PG00018 between BOEM, Alaska Outer Continental Shelf Region and the Alaska Fisheries Science Center. We are especially grateful to Richard Hibpshman, Caroline Robinson, Sean Rohan, and Kimberly Sawyer of the University of Washington (UW/SAFS) for laboratory analysis of stomachs. Thanks to Geoff Lang (NOAA) for data management. Thank you to all Arctic Eis survey participants who helped with stomach sample collection and the collection of oceanographic data. We would also like to extend our thanks to the Captain and crew of the F/V Alaska Knight, and the Captain and crew of the F/V Bristol Explorer for their efforts. Special thanks to Kirstin Holsman, Stephani Zador, and Kerim Aydin from NOAA for reviewing an earlier version of this manuscript. We also thank two anonymous reviewers for their constructive criticism and comments. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service. This publication is [partially] funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement No. NA10OAR4320148, Contribution No. 2433.

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Table 1.1. Total stomachs analyzed for species included in cluster analysis. All stomachs were collected from the 2012 summer bottom-trawl survey of the eastern Chukchi Sea. The trophic guilds were identified from the cluster analysis. The abbreviations are used in the NMDS ordination.

Trophic guild	Species name	Common name	Abbreviation	Non-empty stomachs	Empty stomachs	Size range (cm)
Gammarid consumers						
	Lycodes polaris	Canadian eelpout	CANAPOUT	16	3	4.2-22
	Lycodes raridens	Marbled eelpout	MRBLPOUT	11	1	3.5-30
	Icelus spatula	Spatulate sculpin	SPATSCUL	21	0	3.2-11
	Artediellus scaber	Hamecon	HAMECON	21	1	6-8
	Gymnocanthus tricuspis	Arctic staghorn sculpin	ASTAGSCL	102	6	3-17
	Ulcina olrikii	Arctic alligatorfish	ARCALGTR	43	4	3.6-6.1
	Liparis tunicatus	Kelp snailfish	KELPSNLF	94	4	2.8-15.6
	Lumpenus fabricii	Slender eelblenny	SLNDREBL	143	5	5.6-27
Benthic invert consumers						
	Enophrys diceraus	Antlered sculpin	ANTLSCUL	14	6	9.2-18
	Triglops pingeli	Ribbed sculpin	RIBDSCUL	46	2	3.8-15
	Lumpenus medius	Stout eelblenny	STOUTEBL	24	1	5.2-14
	Limanda aspera	Yellowfin sole	YLWFNSOL	13	0	7.5-18
	Liopsetta glacialis	Arctic flounder	ARCTFLND	13	0	10.1-16
Fish/Shrimp consumers						
	Osmerus mordax	Rainbow smelt	RAINSMLT	28	4	10-30
	Eleginus gracilis	Saffron cod	SAFRNCOD	82	2	6.4-31
	Myoxocephalus scorpius	Shorthorn sculpin	SHTHRNSC	57	7	7.4-29
	Liparis gibbus	Variegated snailfish	VARISNLF	54	0	8.2-31
	Hippoglossoides robustus	Bering flounder	BERIFLND	94	20	3.4-24
Zooplankton consumers						
	Clupea pallasi	Pacific herring	PHERRING	21	2	12-26
	Gadus chalcogrammus	Walleye pollock	WPOLLOCK	13	0	8-12
	Boreogadus saida	Small Arctic cod	SMARCCOD	224	6	5.7-10.2
	Boreogadus saida	Medium Arctic cod	MDARCCOD	435	10	10.3-14.7
	Boreogadus saida	Large Arctic cod	LGARCCOD	38	1	14.8-19.3

Table 1.2. The composite diets of the four trophic guilds identified from the cluster analysis. Trace prey items are less than 0.01% of the diet.

Prey	Gammarid cons. (n=451)	Benthic invert cons. (n=110)	Fish/shrimp cons. (n=315)	Zooplankton cons. (n=731)
Gadidae			1.42%	0.55%
Zoarcoidei			0.53%	0.15%
Zoarcidae			0.30%	
Cottoidei			0.55%	
Cottidae	0.42%		6.81%	0.41%
Cyclopteridae	0.02%		0.15%	
Liparidae	0.79%		4.68%	0.12%
Stichaeidae			19.18%	0.25%
Pacific sand lance	0.89%	6.32%	1.06%	2.13%
Flatfish	0.38%		0.41%	0.26%
Unidentified fish	3.13%	3.65%	15.04%	4.46%
Bivalvia	0.46%	12.05%	0.17%	trace
Pteropoda				0.44%
Gastropoda	0.02%	1.63%	0.08%	
Mollusca (veliger)	trace	0.20%		
Crangonidae	0.10%	0.62%	12.52%	0.04%
Pandalidae	0.29%		5.30%	2.32%
Hippolytidae	2.45%	6.07%	6.41%	7.19%
Unidentified Shrimp	1.62%	0.05%	7.11%	5.71%
Reptantia	2.70%	11.66%	4.03%	0.11%
Decapod larvae	0.13%	0.24%	0.03%	0.30%
Larvacean	1.00%	0.14%	0.44%	7.26%
Thaliacea				0.03%
Chaetognatha	0.02%	1.82%	trace	3.29%
Euphausiidae	0.05%	3.56%	1.09%	10.10%
Mysida	0.45%	trace	0.98%	1.99%
Calanoida	0.02%		0.01%	35.36%
Hyperiidea	0.01%	3.56%	0.15%	6.07%
Gammaridea	58.19%	8.72%	5.37%	9.09%
Caprellidae	0.12%		trace	
Echinozoa		1.62%		
Ophiurida	0.01%	1.60%	trace	
Pycnogonida		0.67%		
Benthic crustacean	0.71%	3.51%	0.14%	1.15%
Polychaeta	21.58%	15.29%	3.00%	0.43%
Nematoda	0.05%			
Other worms	3.84%		2.30%	
Anemone		16.22%		
Foraminiferida	trace			
Unidentified Invertebrate	0.33%	0.23%	0.05%	0.75%
Unidentified prey	0.22%	0.57%	0.65%	0.03%

Table 1.3. Temperature (°C) and salinity (psu) boundaries for water masses present at bottom trawl stations during the 2012 summer bottom trawl survey. The information in this table and the water mass names are from Danielson et al. (this issue).

Water mass	Temperature (°C)	Salinity (psu)
Alaska Coastal Water (ACW)	7-12	20-32
Bering/Chukchi Shelf Summer Water (BCSW)	0-7	30-33.5
Chukchi Winter Water (CWW)	-2-0	30-33.5

Table 1.4. SIMPER analysis of diet dissimilarities between trophic guilds identified in the cluster analysis. Below the diagonal are the groups that contributed most to dissimilarity in the pairwise comparison. Above the diagonal is the cumulative contribution the identified prey type made to between cluster dissimilarity. The guilds are GM (gammarid amphipod consumers), BI (benthic invertebrate consumers), FS (fish and shrimp consumers), and ZP (zooplankton consumers).

Cluster	GM	BI	FS	ZP
GM		0.33	0.30	0.28
BI	Gammaridea		0.21	0.22
FS	Gammaridea	Polychaeta		0.17
ZP	Gammaridea	Polychaeta	Calanoida	

Table 1.5. The proportion of variance present in the guild diet matrices explained by the corresponding matrices of explanatory variables. Also, the test statistic and p-values from the Monte Carlo global permutation test (199 permutations).

Cluster	Proportion of variance explained	Pseudo-F	*P*
GM	0.069	5.473	0.005
BI	0.251	5.755	0.005
FS	0.106	6.083	0.005
ZP	0.086	11.359	0.005

Table 1.6. Preliminary trophic guild designations based on the dominant prey items from the diet composition of poorly sampled (n < 10 non-empty stomachs) demersal fish species.

Guild	Species name	Common name	Major prey	Proportion (% wt)	Non-empty stomachs	Size range (cm)
Gammarid consumers						
	Nautichthys pribilovius	Eyeshade sculpin	Gammaridea	78	9	2.3-4.5
			Caprellidae	9		
	Podothecus veternus	Veteran poacher	Gammaridea	76	5	10-15
			Benthic crustacean	22		
	Liparis marmaratus	Festive snailfish	Gammaridea	50	7	4.6-10.7
			Polychaeta	33		
	Limanda sakhalinensis	Sakhalin sole	Gammaridea	55	6	7.3-16
			Polychaeta	42		
Benthic invertebrate generalists						
	Gymnelus hemifasciatus	Half-barred pout	Mysida	45	1	6.5
			Polychaeta	45		
	Lycodees turneri	Polar eelpout	Polychaeta	74	2	16.4-17
			Gammaridea	14		
	Stichaeus punctatus	Arctic shanny	Reptantia	59	2	10.8-14
			Gammaridea	25		
	Limanda proboscidea	Longhead dab	Polychaeta	72	7	10.9-21
			Gammaridea	21		
	Pleuronectes quadrituberculatus	Alaska plaice	Polychaeta	82	7	13-22
			Ophiurida	12		
Fish/shrimp consumers						
	Gadus macrocephalus	Pacific cod	Unidentified shrimp	81	1	12.4
			Polychaeta	19		
	Lycodes palearis	Wattled eelpout	Stichaeidae	48	6	14-24
			Cottidae	25		
	Hexagrammos stelleri	Whitespotted greenling	Unidentified shrimp	70	5	13-15
			Hippolytidae	29		
	Hemilepidotus papilio	Butterfly sculpin	Hippolytidae	50	1	18
			Gammaridea	50		
	Myoxocephalus jaok	Plain sculpin	Cottidae	89	1	18
			Unidentified fish	11		
	Myoxocephalus quadricornis	Four-horned sculpin	Zoarcidae	90	2	15-27
			Stichaeidae	10		
Zooplankton consumers						
	Mallotus villosus	Capelin	Euphausiidae	97	8	11-13
			Calanoida	02		
	Ammodytes hexapterus	Pacific sand lance	Calanoida	93	4	8.1-12.4
			Unidentified invert	07		
	Reinhardtius hippoglossoides	Greenland turbot	Euphausiidae	58	1	10.2
			Benthic crustacean	42		

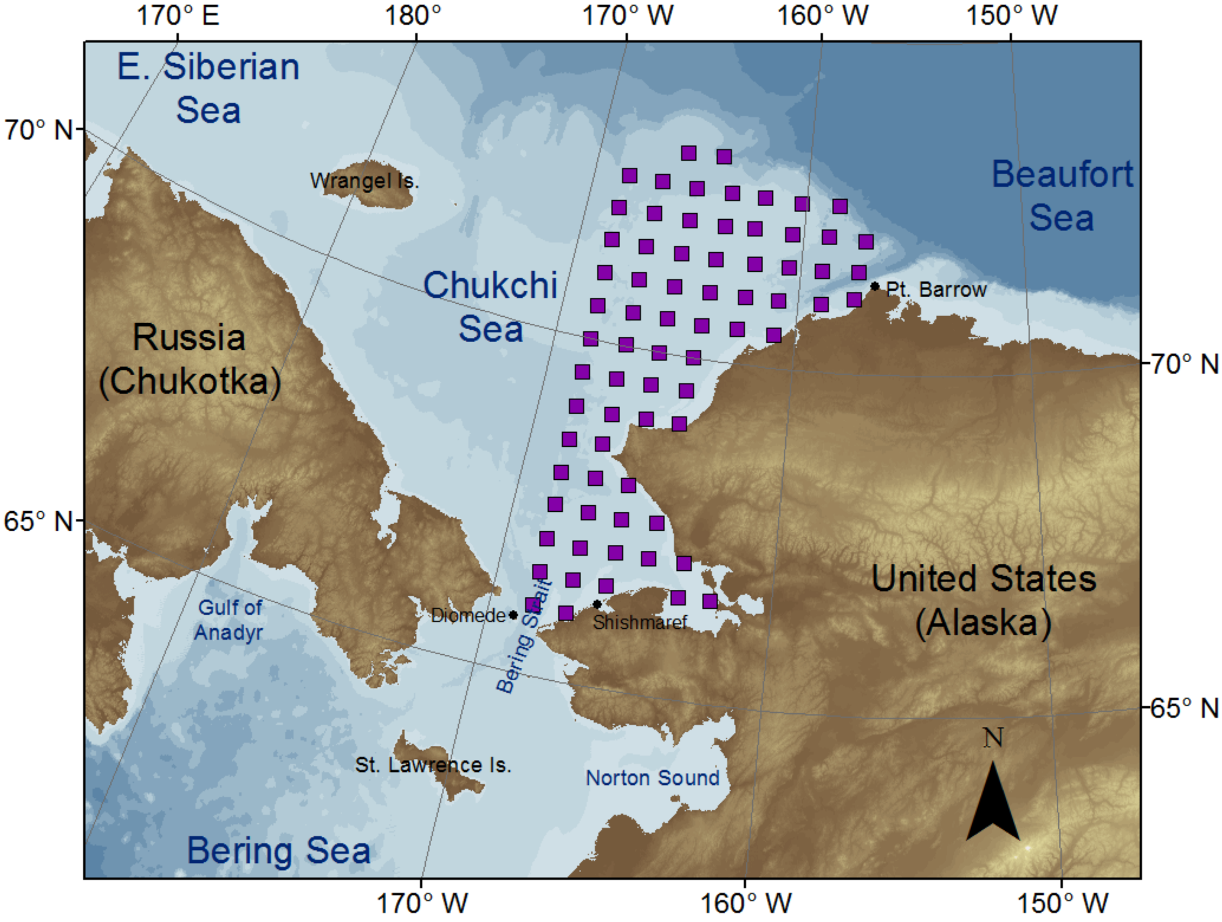

Figure 1.1. Sample locations for stomach samples collected during the 2012 Arctic Eis bottom trawl survey of the eastern Chukchi Sea.

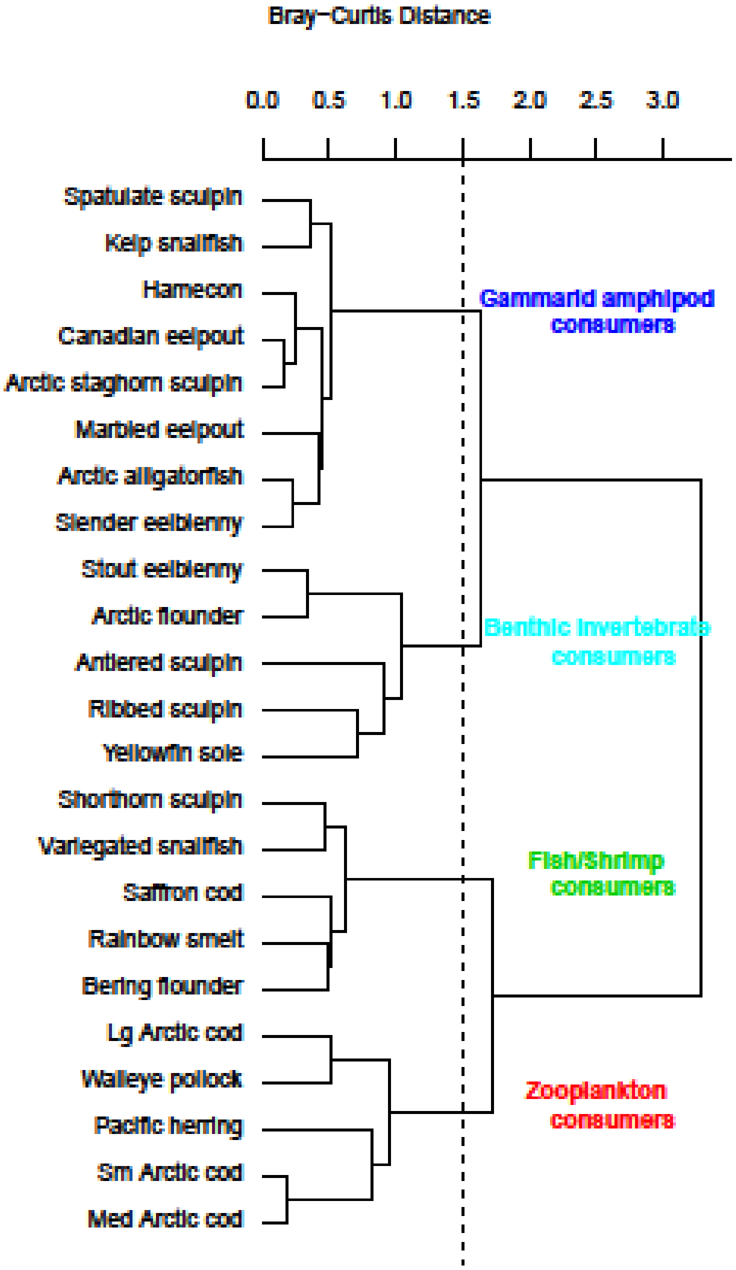

Figure 1.2. Ward's minimum variance dendrogram depicting the results of cluster analysis of the species diet compositions using Ward's Minimum Distance Method (cophenetic correlation 0.75, p<0.001). Following the results of the scree plot, a phenon line is placed at a dissimilarity of 1.5, identifying the four significant clusters. The clusters names reflect their dominant prey type (see Table 1.2): fish and shrimp consumers, zooplankton consumers, gammarid amphipod consumers, and benthic invertebrate consumers.

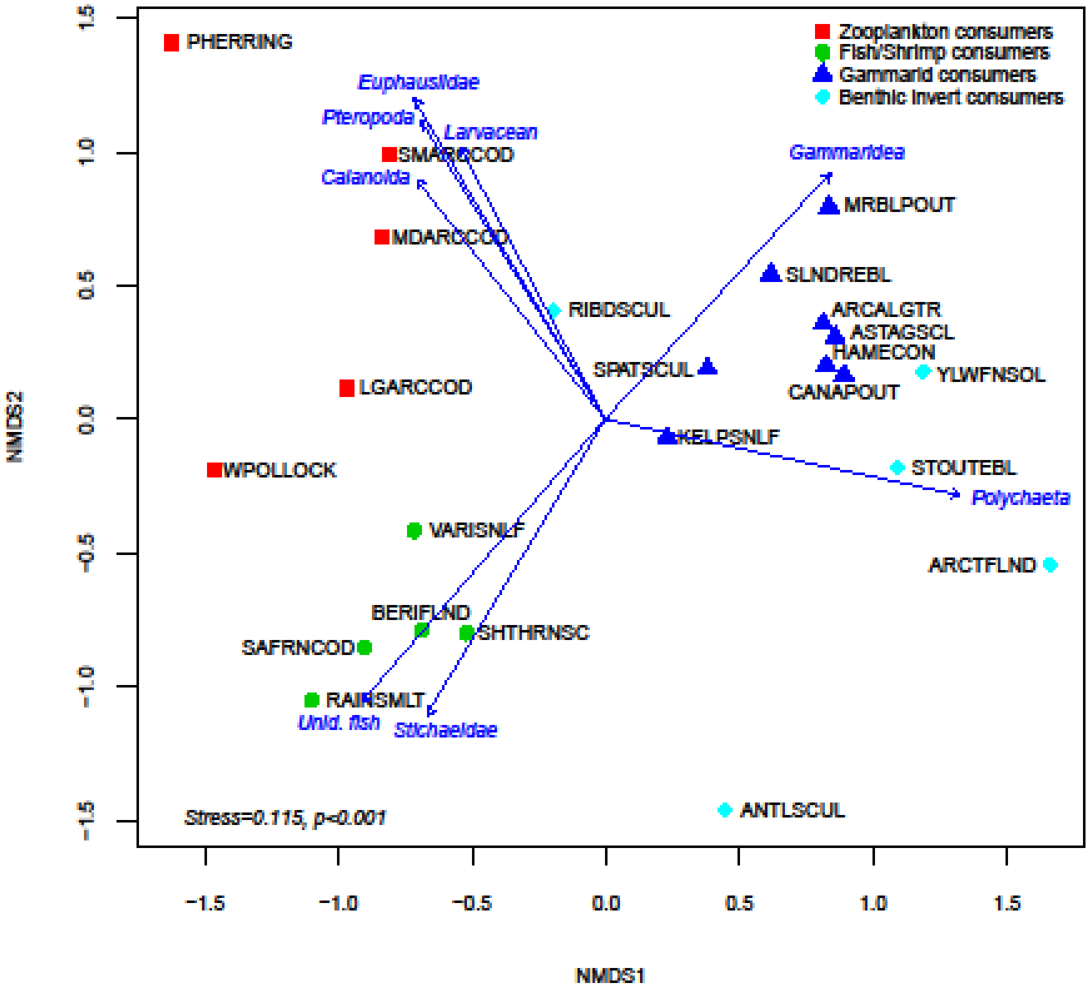

Figure 1.3. NMDS ordination constructed from the B-C matrix of diet dissimilarities. The four guilds identified in the cluster analysis are highlighted with red squares (ZP), green circles (FS), blue triangles (GM), and cyan diamonds (BI). Loading vectors of significant prey types ($p \leq 0.01$) are included (blue vectors and prey names) to aid interpretation of ordination results.

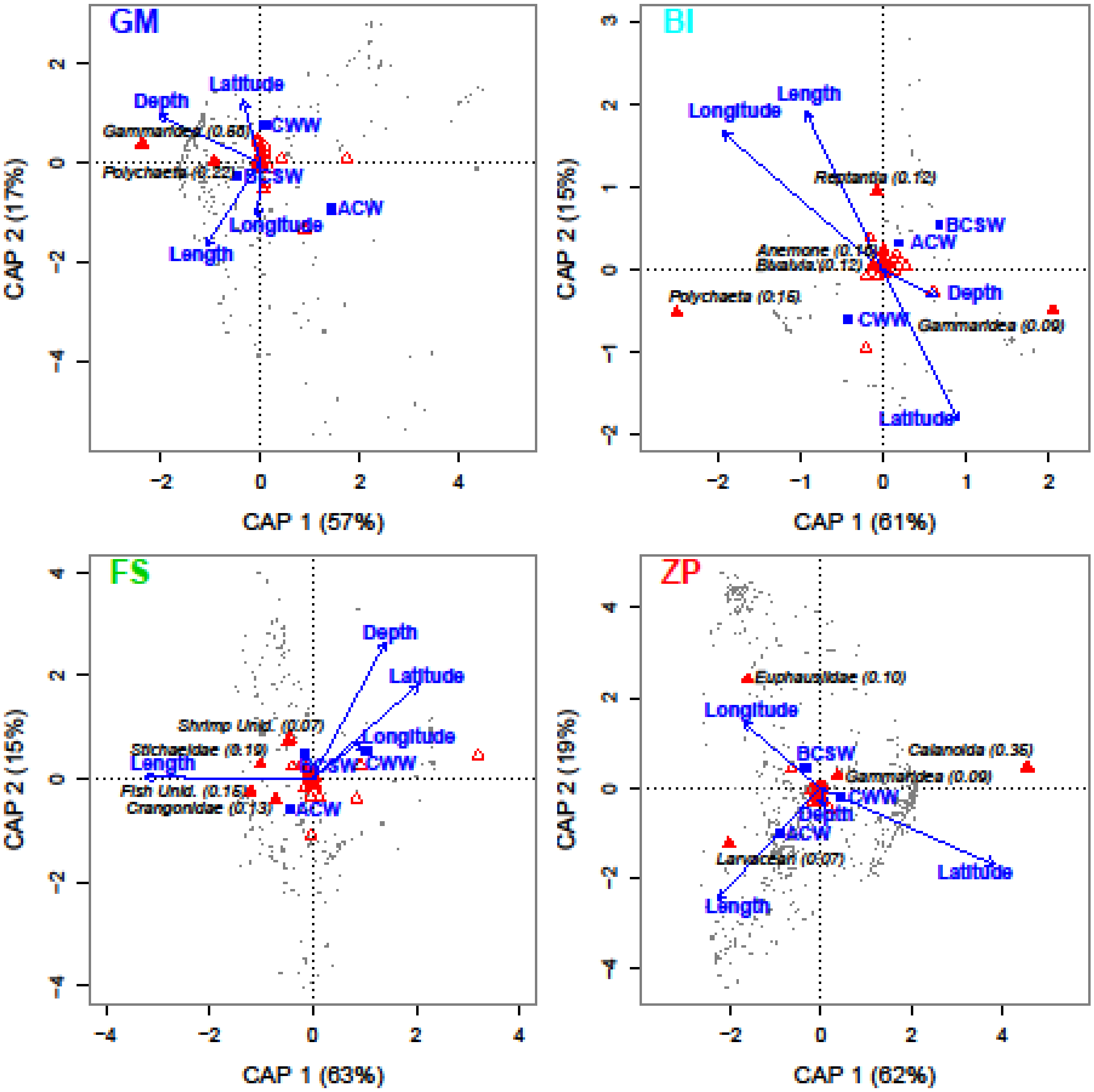

Figure 1.4. Constrained analysis of principal coordinates (CAP) on the predator diets of the four trophic guilds identified with cluster analysis (GM=gammarid amphipod consumers, BI=benthic invertebrate consumers, FS=fish and shrimp consumers, ZP=zooplankton consumers). The grey dots represent the individual predator stomachs. The red triangles are for prey taxa. To ease figure interpretation we have only labeled the dominant prey taxa (by % weight) with italicized lettering and solid red triangles. Prey groups of lesser importance are unlabeled and their location is shown with hollow red triangles. The blue arrows and blue bolded text represent the continuous explanatory non-diet variables. The length of the vector indicates its importance to the ordination and the direction indicates its correlation with the CAP axes and the other vectors. Water masses are a factorial variable and the centroids are shown with blue squares. The amount of constrained variation explained by each axis is given in parentheses of the axis labels.

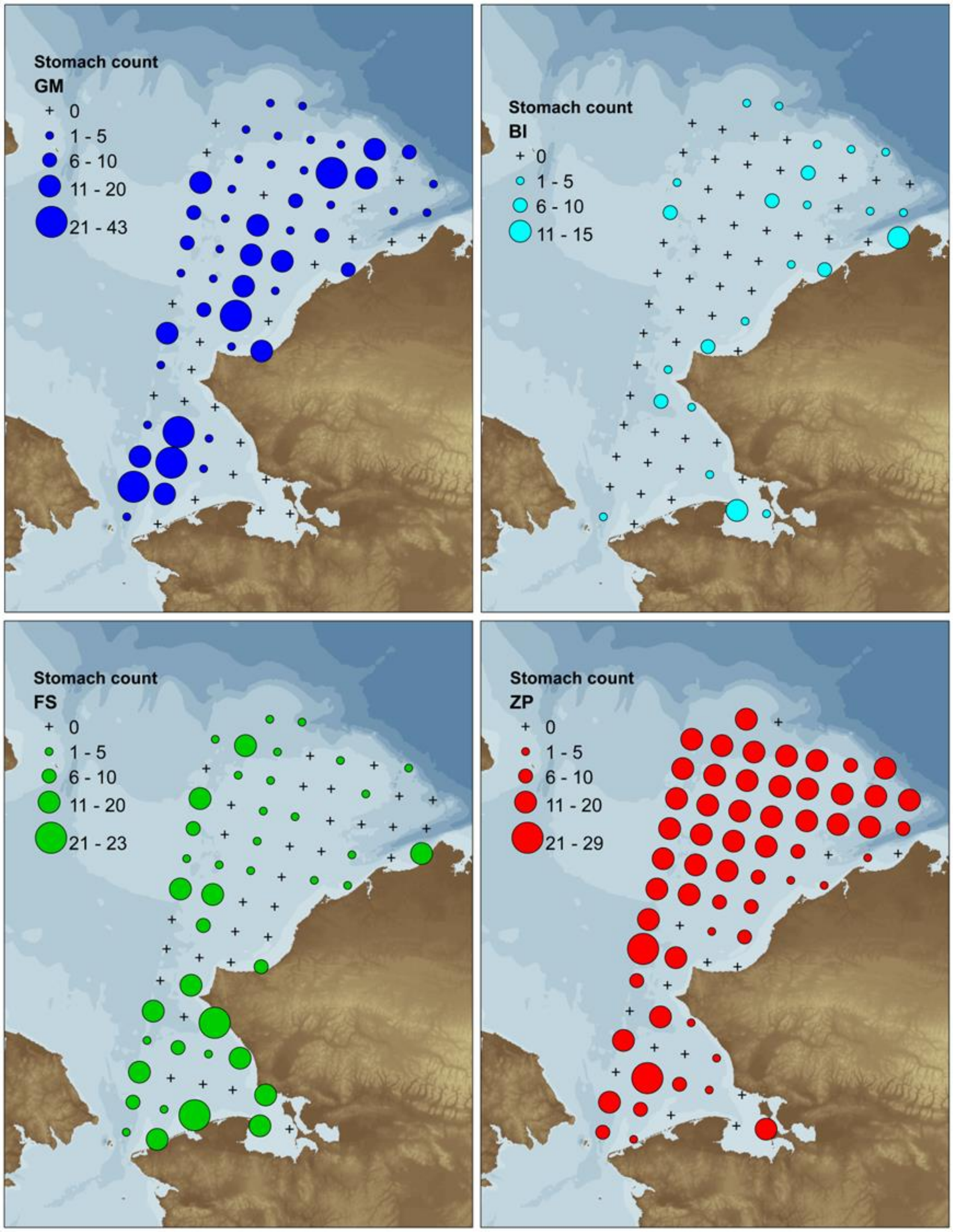

Figure 1.5. The spatial distribution of stomach samples from the four trophic guilds. Note the different scales for bubble sizes in each map. ZP=zooplankton consumers, FS=Fish and shrimp consumers, GM=gammarid consumers, BI=Benthic invertebrate generalists.

14. 1.8 Appendix A

Caption: Prey types and life history stage identified during laboratory analysis of stomach contents. Aggregated prey group is the prey category used in diet descriptions and multivariate analyses. Species names are provided for prey taxa identified to the species level. When distinct life history stages could be identified they are provided.

Table A1. Prey types and life history stage identified during laboratory analysis of stomach contents. Aggregated prey group is the prey category used in diet descriptions and multivariate analyses. Species names are provided for prey taxa identified to the species level. When distinct life history stages could be identified they are provided.

Aggregated prey group	SpeciesName	CommonName	Life history stage
Anemone		Anthozoa (anemone)	unknown
Arrow worm		Chaetognatha (arrow worm)	unknown
Benthic crustacean	Cyclopoida	(copepod)	unknown
Benthic crustacean		Cirripedia (barnacle)	unknown
Benthic crustacean		Cumacea (cumacean)	unknown
Benthic crustacean		Flabellifera (isopod)	unknown
Benthic crustacean		Harpactacoida - Benthic (copepod)	unknown
Benthic crustacean		Harpacticoida (copepod)	unknown
Benthic crustacean		Isopoda (isopod)	unknown
Benthic crustacean	Nebalia bipes	Malacostraca Leptostraca	unknown
Benthic crustacean		Malacostraca Leptostraca	unknown
Benthic crustacean		Malacostraca Phyllocarida	unknown
Benthic crustacean		Myodocopa (ostracoda)	unknown
Benthic crustacean		Ostracoda	unknown
Benthic crustacean		Tanaidacea (peracaridan)	unknown
Brittle star	Amphipholis sp.	Amphiuridae (brittle star)	unknown
Brittle star		Chilophiurina (brittle star)	unknown
Brittle star	Ophiopholis aculeata	Ophiactidae (brittle star)	unknown
Brittle star		Ophiurida (brittle star)	unknown
Brittle star	Ophiura sarsi	Ophiuridae (brittle star)	unknown
Brittle star		Ophiuridae (brittle star)	unknown
Calanoida	Gaidius sp.	Aetideidae (copepod)	unknown
Calanoida	Calanus glacialis/marshallae	Calanidae (copepod)	unknown
Calanoida	Calanus hyperboreus	Calanidae (copepod)	unknown
Calanoida	Calanus sp.	Calanidae (copepod)	unknown
Calanoida	Neocalanus cristatus	Calanidae (copepod)	unknown
Calanoida	Neocalanus flemingeri/plumchrus	Calanidae (copepod)	unknown
Calanoida		Calanidae (copepod)	unknown
Calanoida		Calanoida (copepod)	unknown
Calanoida	Centropages abdominalis	Centropagidae (copepod)	unknown
Calanoida		Copepoda	unknown
Calanoida		Large calanoid (copepod) > 5mm	unknown
Calanoida		Medium calanoid (copepod) 2-5mm	unknown
Calanoida	Epilabidocera longipedata	Pontellidae (copepod)	unknown
Calanoida	Pseudocalanus sp.	Pseudocalanidae (copepod)	unknown
Calanoida		Small calanoid (copepod) < 2mm	unknown
Calanoida	Tortanus discaudatus	Tortanidae (copepod)	unknown
Caprellidea	Caprella sp.	Caprellidae (amphipod)	unknown
Caprellidea		Caprellidae (amphipod)	unknown
Clam		Bivalvia (clam)	unknown
Clam		Cardiidae (cockle)	unknown
Clam		Ennucula tenuis (clam)	unknown
Clam	Nuculana pernula	Nuculanidae (clam)	unknown
Clam	Macoma sp.	Tellinidae (clam)	unknown
Clam		Tellinidae (clam)	unknown
Clam	Yoldia sp.	Yoldiidae (clam)	unknown
Cottidae	Gymnocanthus tricuspis	Arctic staghorn sculpin	unknown
Cottidae		Cottidae (sculpin)	unknown
Cottidae	Artediellus sp.	Cottoidei (sculpin)	unknown
Cottidae	Gymnocanthus sp.	Cottoidei (sculpin)	unknown

Cottidae	Myoxocephalus sp.	Cottoidei (sculpin)	unknown
Cottidae	Artediellus scaber	hamecon	unknown
Cottidae	Myoxocephalus scorpius	shorthorn sculpin	unknown
Cottidae	Icelus spatula	Spatulate sculpin	unknown
Cottoidei		Cottoidei (sculpin)	unknown
Crab	Hyas coarctatus	Arctic lyre crab	unknown
Crab		Chionoecetes Hybrid (Tanner hybrid)	unknown
Crab		Decapoda brachyura (crab)	unknown
Crab	Pagurus trigonocheirus	Fuzzy hermit	unknown
Crab	Telmessus cheiragonus	Helmet crab	juvenile
Crab	Telmessus cheiragonus	Helmet crab	unknown
Crab	Erimacrus isenbeckii	Korean horsehair crab	juvenile
Crab	Erimacrus isenbeckii	Korean horsehair crab	unknown
Crab	Pagurus rathbuni	Longfinger hermit	unknown
Crab	Hyas sp.	Lyre crab	unknown
Crab		Majidae (spider crab)	juvenile
Crab		Majidae (spider crab)	unknown
Crab	Pagurus sp.	Paguridae (hermit crab)	unknown
Crab		Paguridae (hermit crab)	juvenile
Crab		Paguridae (hermit crab)	unknown
Crab		Reptantia (crab)	juvenile
Crab		Reptantia (crab)	larva and juvenile
Crab		Reptantia (crab)	unknown
Crab	Chionoecetes opilio	Snow crab	juvenile
Crab	Chionoecetes opilio	Snow crab	unknown
Crab	Chionoecetes sp.	Snow or Tanner crab	unknown
Crab	Oregonia bifurca	Splitnose crab decorator crab	unknown
Crangonidae	Argis dentata	Arctic argid (shrimp)	unknown
Crangonidae	Crangon communis	Common two-spined crangon (shrimp)	unknown
Crangonidae	Argis sp.	Crangonidae (shrimp)	unknown
Crangonidae	Crangon sp.	Crangonidae (shrimp)	juvenile
Crangonidae	Crangon sp.	Crangonidae (shrimp)	unknown
Crangonidae		Crangonidae (shrimp)	unknown
Crangonidae	Argis lar	Northern argid (shrimp)	unknown
Crangonidae	Sclerocrangon boreas	Sculptured shrimp	unknown
Cyclopteridae		Cyclopteridae (snailfish)	unknown
Decapod larvae		Anomura (crab)	zoea
Decapod larvae		Atelecyclidae (crab)	megalops
Decapod larvae		Caridea (shrimp)	larva
Decapod larvae		Decapoda (shrimp and crab)	zoea
Decapod larvae	Telmessus cheiragonus	Helmet crab	megalops
Decapod larvae	Erimacrus isenbeckii	Korean horsehair crab	megalops
Decapod larvae	Paralithodes sp.	Lithodidae (king crab)	megalops
Decapod larvae	Paralithodes sp.	Lithodidae (king crab)	zoea
Decapod larvae		Lithodidae (king crab)	megalops
Decapod larvae		Majidae (spider crab)	zoea
Decapod larvae		Natantia (shrimp)	larva
Decapod larvae	Pagurus sp.	Paguridae (hermit crab)	zoea
Decapod larvae		Paguridae (hermit crab)	larva
Decapod larvae		Paguridae (hermit crab)	megalops
Decapod larvae		Paguridae (hermit crab)	zoea
Decapod larvae		Pandalidae (shrimp)	larva
Decapod larvae		Reptantia (crab)	larva
Decapod larvae		Reptantia (crab)	megalops
Decapod larvae		Reptantia (crab)	zoea
Decapod larvae	Chionoecetes opilio	Snow crab	megalops
Echinozoa		Holothuroidea (sea cucumber)	unknown
Echinozoa	Echinarachnius parma	Sand dollar	unknown

Euphausiidae	Thysanoessa inermis	Euphausiidae (euphausiid)	unknown
Euphausiidae	Thysanoessa longipes	Euphausiidae (euphausiid)	unknown
Euphausiidae	Thysanoessa raschi	Euphausiidae (euphausiid)	juvenile
Euphausiidae	Thysanoessa raschi	Euphausiidae (euphausiid)	unknown
Euphausiidae	Thysanoessa sp.	Euphausiidae (euphausiid)	juvenile
Euphausiidae	Thysanoessa sp.	Euphausiidae (euphausiid)	unknown
Euphausiidae		Euphausiidae (euphausiid)	juvenile
Euphausiidae		Euphausiidae (euphausiid)	larva and juvenile
Euphausiidae		Euphausiidae (euphausiid)	unknown
Flatfish	Hippoglossoides robustus	Bering flounder	unknown
Flatfish		Pleuronectoidei (flatfish)	unknown
Flatfish	Platichthys stellatus	Starry flounder	unknown
Foraminiferida		Foraminiferida (protozoan)	unknown
Gadidae	Boreogadus saida	Arctic cod	unknown
Gadidae		Gadidae (gadid fish)	unknown
Gammaridea	Lysianassoidea	(Gammarid Amphipod)	unknown
Gammaridea	Ampelisca eschrichti	Ampeliscidae (amphipod)	unknown
Gammaridea	Ampelisca macrocephala	Ampeliscidae (amphipod)	unknown
Gammaridea	Ampelisca sp.	Ampeliscidae (amphipod)	unknown
Gammaridea	Byblis gaimardi	Ampeliscidae (amphipod)	egg-carrying
Gammaridea	Byblis gaimardi	Ampeliscidae (amphipod)	unknown
Gammaridea	Byblis sp.	Ampeliscidae (amphipod)	unknown
Gammaridea	Haploops laevis	Ampeliscidae (amphipod)	unknown
Gammaridea	Haploops sp.	Ampeliscidae (amphipod)	unknown
Gammaridea		Ampeliscidae (amphipod)	unknown
Gammaridea		Amphilochidae (amphipod)	unknown
Gammaridea	Aoridae	Aoridae (amphipod)	unknown
Gammaridea	Apherusa sp.	Calliopiidae (amphipod)	unknown
Gammaridea	Paracalliopiella sp.	Calliopiidae (amphipod)	unknown
Gammaridea	Weyprechtia heugleni	Calliopiidae (amphipod)	unknown
Gammaridea		Calliopiidae (amphipod)	unknown
Gammaridea		Corophiidae (amphipod)	unknown
Gammaridea	Paramphithoe sp.	Epimeriidae (amphipod)	unknown
Gammaridea	Rhachotropis aculeata	Eusiridae (amphipod)	unknown
Gammaridea	Rhachotropis sp.	Eusiridae (amphipod)	unknown
Gammaridea	Rozinante fragilis	Eusiridae (amphipod)	unknown
Gammaridea		Eusiridae (amphipod)	unknown
Gammaridea	Gammarus sp.	Gammaridae (amphipod)	unknown
Gammaridea		Gammaridae (amphipod)	unknown
Gammaridea		Gammaridea (amphipod)	unknown
Gammaridea		Haustoriidae (amphipod)	unknown
Gammaridea	Gammaropsis sp.	Isaeidae (amphipod)	unknown
Gammaridea	Photis fischmanni	Isaeidae (amphipod)	unknown
Gammaridea	Photis reinhardi	Isaeidae (amphipod)	unknown
Gammaridea	Photis sp.	Isaeidae (amphipod)	unknown
Gammaridea	Protomedeia fasciata	Isaeidae (amphipod)	egg-carrying
Gammaridea	Protomedeia fasciata	Isaeidae (amphipod)	unknown
Gammaridea	Protomedeia grandimana	Isaeidae (amphipod)	unknown
Gammaridea	Protomedeia sp.	Isaeidae (amphipod)	unknown
Gammaridea		Isaeidae (amphipod)	unknown
Gammaridea	Ericthonius sp.	Ischyroceridae (amphipod)	unknown
Gammaridea	Ericthonius tolli	Ischyroceridae (amphipod)	unknown
Gammaridea	Ischyrocerus sp.	Ischyroceridae (amphipod)	egg-carrying
Gammaridea	Ischyrocerus sp.	Ischyroceridae (amphipod)	unknown
Gammaridea		Ischyroceridae (amphipod)	unknown
Gammaridea		Liljeborgiidae (amphipod)	unknown
Gammaridea	Hippomedon sp.	Lysianassidae (amphipod)	unknown
Gammaridea		Lysianassidae (amphipod)	unknown

Gammaridea	Maera danae	Maeridae (amphipod)	unknown
Gammaridea		Maeridae (amphipod)	unknown
Gammaridea	Megamoera dentata	Melitidae (amphipod)	unknown
Gammaridea	Megamoera mikulitschae	Melitidae (amphipod)	unknown
Gammaridea	Megamoera sp.	Melitidae (amphipod)	unknown
Gammaridea	Melita sp.	Melitidae (amphipod)	unknown
Gammaridea	Melitoides makarovi	Melitidae (amphipod)	unknown
Gammaridea	Quasimelita formosa	Melitidae (amphipod)	unknown
Gammaridea		Melitidae (amphipod)	unknown
Gammaridea	Aceroides latipes	Oedicerotidae (amphipod)	unknown
Gammaridea	Bathymedon sp.	Oedicerotidae (amphipod)	unknown
Gammaridea	Monoculodes sp.	Oedicerotidae (amphipod)	unknown
Gammaridea		Oedicerotidae (amphipod)	larva
Gammaridea		Oedicerotidae (amphipod)	unknown
Gammaridea	Harpiniinae (subfamily)	Phoxocephalidae (amphipod)	unknown
Gammaridea		Phoxocephalidae (amphipod)	unknown
Gammaridea		Pleustidae (amphipod)	unknown
Gammaridea	Dyopedos sp.	Podoceridae (amphipod)	unknown
Gammaridea		Podoceridae (amphipod)	unknown
Gammaridea	Pontoporeia femorata	Pontoporeiidae (amphipod)	unknown
Gammaridea	Priscillina armata	Pontoporeiidae (amphipod)	unknown
Gammaridea		Pontoporeiidae (amphipod)	unknown
Gammaridea	Metopa sp.	Stenothoidae (amphipod)	unknown
Gammaridea	Metopella longimanna	Stenothoidae (amphipod)	unknown
Gammaridea		Stenothoidae (amphipod)	unknown
Gammaridea	Stilipes distincta	Stilipedidae (amphipod)	unknown
Gammaridea	Syrrhoe crenulata	Synopiidae (amphipod)	unknown
Gammaridea	Tiron spiniferum	Synopiidae (amphipod)	unknown
Gammaridea		Synopiidae (amphipod)	unknown
Gammaridea	Urothoe sp.	Urothoidae (amphipod)	unknown
Gammaridea		Urothoidae (amphipod)	unknown
Hippolytidae	Eualus fabricii	Arctic eualid (shrimp)	unknown
Hippolytidae	Eualus avinus	Beaked eualid (shrimp)	unknown
Hippolytidae	Eualus gaimardii	Hippolytidae (shrimp)	egg-carrying
Hippolytidae	Eualus gaimardii	Hippolytidae (shrimp)	unknown
Hippolytidae	Eualus macilentus	Hippolytidae (shrimp)	unknown
Hippolytidae	Eualus sp.	Hippolytidae (shrimp)	unknown
Hippolytidae	Eualus stoneyi	Hippolytidae (shrimp)	unknown
Hippolytidae	Lebbeus sp.	Hippolytidae (shrimp)	unknown
Hippolytidae	Spirontocaris sp.	Hippolytidae (shrimp)	unknown
Hippolytidae		Hippolytidae (shrimp)	juvenile
Hippolytidae		Hippolytidae (shrimp)	unknown
Hirudinea		Hirudinea (leech)	unknown
Hyperidea	Hyperia medusarum	Hyperiidae (amphipod)	unknown
Hyperidea	Hyperia sp.	Hyperiidae (amphipod)	unknown
Hyperidea	Parathemisto libellula	Hyperiidae (amphipod)	unknown
Hyperidea	Themisto abyssorum	Hyperiidae (amphipod)	unknown
Hyperidea	Themisto pacifica	Hyperiidae (amphipod)	unknown
Hyperidea	Themisto sp.	Hyperiidae (amphipod)	unknown
Hyperidea		Hyperiidae (amphipod)	unknown
Hyperidea		Hyperiidea (amphipod)	egg-carrying
Hyperidea		Hyperiidea (amphipod)	unknown
Larvacean		Copelata (larvacea)	unknown
Larvacean	Oikopleura sp.	Oikopleuridae (larvacea)	unknown
Liparidae	Liparis tunicatus	kelp snailfish	unknown
Liparidae	Liparidae	Liparidae (snailfish)	unknown
Liparidae	Liparis sp.	Liparidae (snailfish)	unknown
Liparidae	Liparis gibbus	Variegated snailfish	unknown

Mollusca (veliger)		Gastropoda (snail)	veliger
Mollusca (veliger)		Mollusca	veliger
Mysida		Mysida (mysid)	unknown
Mysida	Mysis oculata	Mysidae	unknown
Mysida	Disacanthomysis dybowskii	Mysidae (mysid)	unknown
Mysida	Erythrops erythrophthalma	Mysidae (mysid)	egg-carrying
Mysida	Erythrops erythrophthalma	Mysidae (mysid)	unknown
Mysida	Neomysis awatschensis	Mysidae (mysid)	unknown
Mysida	Neomysis rayii	Mysidae (mysid)	unknown
Mysida	Neomysis sp.	Mysidae (mysid)	unknown
Mysida	Pseudomma sp.	Mysidae (mysid)	unknown
Mysida	Pseudomma truncatum	Mysidae (mysid)	unknown
Mysida	Stilomysis grandis	Mysidae (mysid)	unknown
Mysida		Mysidae (mysid)	unknown
Nematoda		Nematoda (worm)	unknown
Other worms		Echiura (marine worm)	unknown
Other worms	Priapulus caudatus	Priapulidae	unknown
Other worms		Rhynchocoela	unknown
Other worms		Sipuncula (peanut worm)	unknown
Pacific sand lance	Ammodytes hexapterus	Pacific sandlance	unknown
Pandalidae	Pandalus goniurus	Flexed pandalid (shrimp)	unknown
Pandalidae	Pandalus sp.	Pandalidae (shrimp)	unknown
Pandalidae		Pandalidae (shrimp)	unknown
Pandalidae	Pandalus eous	Pink shrimp	unknown
Pandalidae	Pandalus tridens	Yellow-leg pandalid (shrimp)	unknown
Pelagic salp		Thaliacea (pelagic salp)	unknown
Polychaeta	Ampharete sp.	Ampharetidae (polychaete)	unknown
Polychaeta		Ampharetidae (polychaete)	unknown
Polychaeta		Aphroditiformia (polychate)	unknown
Polychaeta		Arabellidae (polychaete)	unknown
Polychaeta		Capitellidae (polychaete)	unknown
Polychaeta		Cirratulidae (polychaete)	unknown
Polychaeta		Flabelligeridae (polychaete)	unknown
Polychaeta		Glyceridae (polychaete)	unknown
Polychaeta		Glyceriformia	unknown
Polychaeta		Goniadidae (polychaete)	unknown
Polychaeta		Lumbrineridae (polychaete)	unknown
Polychaeta	Magelona sp.	Magelonidae (polychaete)	unknown
Polychaeta		Maldanidae (polychaete)	unknown
Polychaeta		Nephtyidae (polychaete)	unknown
Polychaeta		Nereidae (polychaete)	unknown
Polychaeta		Onuphidae (polychaete)	unknown
Polychaeta		Opheliidae (polychaete)	unknown
Polychaeta		Orbiniidae (polychaete)	unknown
Polychaeta		Oweniidae (polychaete)	unknown
Polychaeta		Pectinariidae (polychaete)	unknown
Polychaeta		Phyllodocida (polychaete)	unknown
Polychaeta	Eteone sp.	Phyllodocidae (polychaete)	unknown
Polychaeta	Phyllodoce sp.	Phyllodocidae (polychaete)	unknown
Polychaeta		Phyllodocidae (polychaete)	unknown
Polychaeta		Polychaeta (polychaete)	larva
Polychaeta		Polychaeta (polychaete)	unknown
Polychaeta	Eunoe nodosa	Polynoidae (polychaete)	unknown
Polychaeta	Polyeunoa sp.	Polynoidae (polychaete)	unknown
Polychaeta		Polynoidae (polychaete)	unknown
Polychaeta		Sabellidae (polychaete)	unknown
Polychaeta		Spionidae (polychaete)	unknown
Polychaeta		Sternaspidae (polychaete)	unknown

Polychaeta		Syllidae (polychaete)	unknown
Polychaeta		Terebellidae (polychaete)	unknown
Pteropoda		Gymnosomata (naked pteropod)	unknown
Pteropoda		Pteropoda	unknown
Pteropoda		Thecosomata (shelled pteropod)	unknown
Pycnogonida		Pycnogonida (sea spider)	unknown
Snail		Gastropoda (snail)	unknown
Snail		Lamellariidae (snail)	unknown
Snail	Solariella sp.	Trochidae	unknown
Stichaeidae	Stichaeus punctatus	Arctic shanny	unknown
Stichaeidae	Lumpenus fabricii	Slender eelblenny	unknown
Stichaeidae		Stichaeidae (prickleback)	unknown
Stichaeidae	Lumpenus medius	Stout eelblenny	unknown
Unidentified fish		Gnathostomata	unknown
Unidentified fish		Non-gadoid fish remains	larva
Unidentified fish		Non-gadoid fish remains	unknown
Unidentified fish		Teleostei (fish)	unknown
Unidentified Invertebrate		Amphipoda (amphipod)	unknown
Unidentified Invertebrate		Crustacea	larva and juvenile
Unidentified Invertebrate		Crustacea	unknown
Unidentified Invertebrate		Decapoda (shrimp and crab)	unknown
Unidentified Invertebrate		Malacostraca	unknown
Unidentified Invertebrate		Mollusca	unknown
Unidentified prey		Unidentified eggs	unknown
Unidentified prey		Unidentified organic material	unknown
Unidentified prey		Unidentified tube	unknown
Unidentified prey		Unidentified worm-like organism	unknown
Unidentified Shrimp		Caridea (shrimp)	juvenile
Unidentified Shrimp		Caridea (shrimp)	unknown
Unidentified Shrimp		Natantia (shrimp)	unknown
Zoarcidae	Lycodes polaris	Canadian eelpout	unknown
Zoarcidae	Lycodes sp.	Zoarcidae (eelpout)	unknown
Zoarcoidei		Zoarcoidei	unknown

15. 1.9 Appendix B

Caption: Diet composition by percent weight for the 21 predator species included in hierarchical cluster analysis.

Table B1. Diet composition by percent weight for the 21 predator species included in hierarchical cluster analysis. Predators are columns and prey groups are rows. 'Trace' denotes prey present in amounts comprising <0.01% of diet composition.

Prey	Pacific herring	Rainbow smelt	Small Arctic cod	Medium Arctic cod	Large Arctic cod	Saffron cod
Ammodytidae				0.49%	7.44%	
Anemone						
Benthic crustacean	0.07%	0.06%	1.08%	1.47%	0.60%	0.05%
Bivalvia				0.01%		trace
Calanoida	9.97%	0.06%	46.26%	40.90%	21.65%	trace
Caprellidae						
Chaetognatha			3.76%	4.83%	0.20%	trace
Cottidae	3.38%			0.50%		
Cottoidei		1.08%				
Crangonidae		0.79%		0.07%		30.50%
Cyclopteridae						
Decapoda larvae	0.21%	0.22%	0.56%	0.31%		0.01%
Echinozoa						
Euphausiidae	27.60%	0.70%	20.37%	10.23%	1.04%	1.92%
Foraminiferida						
Gadidae					1.94%	
Gammaridea		2.37%	12.50%	10.26%	6.15%	3.75%
Gastropoda						0.22%
Hippolytidae		0.36%	1.90%	4.16%	18.50%	2.41%
Hirudinea						
Hyperiidea	2.23%	0.77%	3.99%	5.96%	8.40%	0.05%
Larvacean	51.97%	1.05%	4.47%	6.40%	3.73%	0.98%
Liparidae				0.22%		
Mollusca veliger						
Mysida		1.54%	1.00%	3.35%	0.03%	0.51%
Nematoda						
Ophiurida						
Other worms						5.90%
Pandalidae		3.79%	0.55%	2.88%	2.67%	8.90%
Pleuronectidae					1.05%	
Polychaeta		3.86%	0.07%	0.12%	1.41%	3.32%
Pteropoda	0.51%		0.35%	0.62%	0.11%	
Pycnogonida						
Reptantia	0.17%		0.22%	0.13%		0.06%
Stichaeidae	3.83%	43.06%	0.60%			16.88%
Thaliacea				0.05%		
Unidentified fish	0.01%	40.10%	0.60%	1.96%	11.29%	17.86%
Unidentified invertebrate			0.53%	1.20%		0.10%
Unidentified shrimp	0.04%	0.18%	1.09%	3.57%	13.79%	5.45%
Unidentified			0.10%	0.03%		1.11%
Zoarcidae						
Zoarcoidei				0.28%		

Table B1 continued

Prey	Walleye pollock	Canadian eelpout	Marbled eelpout	Spatulate sculpin	Hamecon	Antlered sculpin
Ammodytidae						14.10%
Anemone						36.18%
Benthic crustacean	3.34%	0.03%		0.01%	1.14%	
Bivalvia		0.27%	0.09%		0.49%	
Calanoida	14.31%	0.00%				
Caprellidae						
Chaetognatha	2.98%					0.71%
Cottidae		0.83%				
Cottoidei						
Crangonidae						
Cyclopteridae		0.36%				
Decapoda larvae	4.29%		0.11%		6.62%	0.18%
Echinozoa						
Euphausiidae	0.66%	0.47%		0.25%		0.08%
Foraminiferida						
Gadidae	6.50%					
Gammaridea	4.17%	52.79%	91.24%	42.96%	46.35%	
Gastropoda					0.57%	3.62%
Hippolytidae		0.79%		34.30%		
Hirudinea						
Hyperiidea	1.43%					
Larvacean						
Liparidae						
Mollusca veliger						0.44%
Mysida				1.04%	10.85%	
Nematoda						
Ophiurida					1.16%	2.86%
Other worms						
Pandalidae				6.36%		
Pleuronectidae						
Polychaeta		40.68%	8.56%	15.05%	31.87%	10.50%
Pteropoda						
Pycnogonida						1.49%
Reptantia		2.86%			0.95%	21.91%
Stichaeidae						
Thaliacea						
Unidentified fish	47.17%	0.34%				6.33%
Unidentified invertebrate	1.31%			0.03%		0.40%
Unidentified shrimp	13.83%	0.59%				
Unidentified						1.21%
Zoarcidae						
Zoarcoidei						

Table B1 continued

Prey	Arctic staghorn sculpin	Shorthorn sculpin	Ribbed sculpin	Arctic alligatorfish	Variegated snailfish	Kelp snailfish
Ammodytidae					2.86%	3.06%
Anemone						
Benthic crustacean	0.17%	0.70%	8.37%	1.71%	0.06%	0.56%
Bivalvia	0.17%		0.04%	17.39%	0.37%	0.03%
Calanoida				0.02%	trace	0.03%
Caprellidae					0.01%	0.40%
Chaetognatha	trace		5.67%			0.04%
Cottidae		5.57%			16.39%	1.32%
Cottoidei		2.43%			0.38%	
Crangonidae	trace	1.71%	2.34%		2.43%	0.33%
Cyclopteridae		1.10%				
Decapoda larvae	0.05%	0.02%	0.60%	0.97%	0.03%	0.18%
Echinozoa						
Euphausiidae	0.03%	0.08%	13.34%		0.86%	0.01%
Foraminiferida						
Gadidae					1.17%	
Gammaridea	60.23%	7.70%	19.85%	53.11%	7.14%	48.94%
Gastropoda	0.03%					
Hippolytidae		7.03%	22.92%		10.61%	4.62%
Hirudinea						
Hyperiidea			13.45%		0.18%	0.03%
Larvacean	0.82%		0.42%		trace	
Liparidae					12.67%	2.71%
Mollusca veliger						
Mysida	0.08%		0.02%	4.64%	0.18%	0.97%
Nematoda						
Ophiurida	trace	trace				
Other worms	7.79%			2.46%	0.03%	
Pandalidae		3.81%			2.90%	0.32%
Pleuronectidae					1.12%	1.32%
Polychaeta	27.30%	1.21%	5.79%	17.20%	2.88%	14.20%
Pteropoda						
Pycnogonida						
Reptantia	2.42%	25.93%	3.73%		1.31%	4.72%
Stichaeidae		17.73%			16.34%	
Thaliacea						
Unidentified fish	0.02%	17.17%	3.07%		6.53%	10.70%
Unidentified invertebrate	0.59%	0.13%	0.20%			0.01%
Unidentified shrimp		2.25%	0.21%		12.72%	5.50%
Unidentified	0.31%	1.50%		2.49%		
Zoarcidae					0.81%	
Zoarcoidei		3.93%				

Table B1 continued

Prey	Slender eelblenny	Stout eelblenny	Bering flounder	Yellowfin sole	Arctic flounder
Ammodytidae					
Anemone					
Benthic crustacean	9.33%	10.08%		4.89%	0.04%
Bivalvia	5.93%	12.93%	0.72%	49.20%	0.42%
Calanoida	0.15%		trace		
Caprellidae					
Chaetognatha					
Cottidae					
Cottoidei					
Crangonidae			2.61%		
Cyclopteridae					
Decapoda larvae					
Echinozoa				6.69%	
Euphausiidae			0.17%		
Foraminiferida	trace				
Gadidae			19.45%		
Gammaridea	53.72%	10.70%	2.50%	13.60%	1.86%
Gastropoda	0.05%				0.13%
Hippolytidae			12.29%		
Hirudinea					
Hyperiidea					
Larvacean	12.32%	2.89%			
Liparidae					
Mollusca veliger	trace				
Mysida	0.05%		11.86%		
Nematoda	1.12%				
Ophiurida				1.32%	
Other worms	0.25%		2.44%		
Pandalidae			3.11%		
Pleuronectidae					
Polychaeta	14.76%	61.95%	4.93%	20.73%	97.54%
Pteropoda					
Pycnogonida					
Reptantia	0.15%			3.52%	
Stichaeidae			24.34%		
Thaliacea					
Unidentified fish			13.18%		
Unidentified invertebrate	0.80%				
Unidentified shrimp			1.61%		
Unidentified	1.36%	1.46%	0.77%	0.05%	
Zoarcidae					
Zoarcoidei					

16. 1.10 Appendix C

Caption: Diet composition by percent weight for the 18 predator species that were not included in hierarchical cluster analysis due to low sample size (n<10). Predators are columns and prey groups are rows. ‘Trace’ denotes prey present in amounts comprising <0.01% of diet composition.

Table C1. Diet composition by percent weight for the 18 predator species that were not included in hierarchical cluster analysis due to low sample size (n<10). Predators are columns and prey groups are rows. 'Trace' denotes prey present in amounts comprising <0.01% of diet composition.

Prey	Capelin	Pacific cod	Half-barred pout	Wattled eelpout	Polar eelpout	Whitespotted greenling
Ammodytidae						
Anemone						
Benthic crustacean				0.02%	0.13%	
Bivalvia				0.02%		
Calanoida	2.39%					
Caprellidae					0.26%	
Chaetognatha						
Cottidae				25.23%		
Cottoidei				4.09%		
Crangonidae				8.85%		
Cyclopteridae						
Decapoda larvae					1.83%	
Echinozoa						
Euphausiidae	97.34%			0.21%		
Foraminiferida					0.13%	
Gadidae						
Gammaridea			10.00%	11.34%	14.36%	0.58%
Gastropoda						
Hippolytidae						29.15%
Hirudinea						
Hyperiidea	0.27%					
Larvacean						
Liparidae						
Mollusca veliger						
Mysida			45.00%			
Nematoda						
Ophiurida						
Other worms						
Pandalidae						
Pleuronectidae						
Polychaeta		18.87%	45.00%	2.10%	74.15%	
Pteropoda						
Pycnogonida						
Reptantia						
Stichaeidae				48.14%		
Thaliacea						
Unidentified fish						
Unidentified invertebrate						
Unidentified shrimp		81.13%				70.27%
Unidentified					9.14%	
Zoarcidae						
Zoarcoidei						

Table C1 continued:

Prey	Butterfly sculpin	Plain sculpin	Four-horned sculpin	Eyeshade sculpin	Veteran poacher	Festive snailfish
Ammodytidae						
Anemone						
Benthic crustacean					22.13%	0.04%
Bivalvia						0.04%
Calanoida						
Caprellidae				9.09%		1.50%
Chaetognatha						
Cottidae		89.48%				
Cottoidei						
Crangonidae					1.39%	
Cyclopteridae						
Decapoda larvae						0.39%
Echinozoa						
Euphausiidae						
Foraminiferida						
Gadidae						
Gammaridea	49.88%			78.41%	76.31%	50.43%
Gastropoda						
Hippolytidae	50.12%					5.06%
Hirudinea						
Hyperiidea						
Larvacean						
Liparidae						
Mollusca veliger						
Mysida						
Nematoda						
Ophiurida						
Other worms						
Pandalidae						
Pleuronectidae						
Polychaeta				0.58%	0.17%	32.84%
Pteropoda						
Pycnogonida						
Reptantia				8.89%		6.35%
Stichaeidae			9.76%			
Thaliacea						
Unidentified fish		10.52%				2.96%
Unidentified invertebrate						
Unidentified shrimp						0.39%
Unidentified				3.03%		
Zoarcidae			90.24%			
Zoarcoidei						

Table C1 continued:

Prey	Arctic shanny	Pacific sand lance	Longhead dab	Sakhalin sole	Alaska plaice	Greenland turbot
Ammodytidae						
Anemone						
Benthic crustacean			0.09%	0.10%		42.42%
Bivalvia			0.02%	0.83%		
Calanoida		93.33%				
Caprellidae						
Chaetognatha						
Cottidae						
Cottoidei						
Crangonidae						
Cyclopteridae						
Decapoda larvae						
Echinozoa			1.31%			
Euphausiidae						57.58%
Foraminiferida						
Gadidae						
Gammaridea	25.05%		21.05%	54.68%	1.26%	
Gastropoda					0.27%	
Hippolytidae	6.48%					
Hirudinea					4.73%	
Hyperiidea						
Larvacean			4.75%			
Liparidae						
Mollusca veliger						
Mysida			0.52%	0.93%		
Nematoda						
Ophiurida				0.05%	11.59%	
Other worms						
Pandalidae						
Pleuronectidae						
Polychaeta	9.72%		72.26%	41.57%	82.14%	
Pteropoda						
Pycnogonida						
Reptantia	58.75%			1.85%		
Stichaeidae						
Thaliacea						
Unidentified fish						
Unidentified invertebrate		6.67%				
Unidentified shrimp						
Unidentified						
Zoarcidae						
Zoarcoidei						

2 Chapter 2 - Results of the fish food habits collections during the 2012 surface/midwater trawl survey of the eastern Chukchi Sea and northern Bering Sea

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2.1 Abstract

Scientists from the NOAA Alaska Fisheries Science Center (AFSC) participated in the 2012 Arctic Ecosystem Integrated Survey (Arctic Eis) surface/midwater trawl survey of the eastern Chukchi Sea and northern Bering Sea. One of the goals of this trawl survey was to collect fish specimens to assess their food habits in the pelagic environment within these regions. This report documents the collection of stomach contents data from common pelagic fish species encountered during the survey and provides summarized descriptions of the stomach contents. Fish stomachs were collected from a total of 91 trawl deployments during the survey, of which 37 trawl deployments were in the northern Bering Sea and 54 in the eastern Chukchi Sea. A total of 948 stomach samples were collected from eight species; Pacific herring (*Clupea pallasi*, n=170), capelin (*Mallotus villosus*, n=196), rainbow smelt (*Osmerus mordax*, n=115), Arctic cod (*Boreogadus saida*, n=114), saffron cod (*Eleginus gracilis*, n=204), walleye pollock (*Gadus chalcogrammus*, n=64), shorthorn sculpin (*Myoxocephalus scorpius*, n=1), and Pacific sandlance (*Ammodytes hexapterus*, n=84). These collections, followed by laboratory analysis of stomach specimens produced geo-referenced quantitative diet compositions of predator species with prey identified to the lowest taxonomic level possible. We provide summarized diet descriptions for the eastern Chukchi Sea and northern Bering Sea separately for the sampled species, and describe the spatial distribution of the collected stomach samples across the study region. The complete geo-referenced diet compositions will be made available through the Alaska Ocean Observing System Workspace (AOOS, http://www.aoos.org/).

2.2 Introduction

Scientists from the NOAA Alaska Fisheries Science Center (AFSC) participated in the 2012 Arctic Ecosystem Integrated Survey (Arctic Eis) summer trawl surveys of the eastern Chukchi Sea and northern Bering Sea. A goal of these trawl surveys was to collect fish specimens to assess their food habits in the demersal and pelagic environments. Accurate descriptions of predator food habits are an essential part of incorporating ecosystem considerations into the management of living marine resources (Link and Browman 2014, Travis et al. 2014) and are of central importance to food web modeling. The collection of stomach samples during the 2012 Chukchi Sea and northern Bering Sea surveys will produce region-specific quantitative diet descriptions for commonly encountered fish species. The addition of these data to the food habits database at the AFSC's Resource Ecology and Ecosystem Modeling (REEM) Program, along with updated biomass estimates, can greatly improve the accuracy of our current modeling efforts (Whitehouse and Aydin in review). Further development of food web models and other decision support tools will improve our understanding of trophic relationships in this ecosystem and their sensitivity to human activities, such as fishing and energy extraction.

Fishes are an important component of Arctic ecosystems, channeling production from lower trophic levels to upper level predators, such as seabirds, seals, belugas, and people (Welch et al. 1992, Whitehouse et al. 2014). In the Alaskan Arctic, fishes are known to consume a variety of pelagic and benthic invertebrates and other fishes (Coyle et al. 1997, Cui et al. 2012, Whitehouse et al. Accepted). There are a limited number of studies focused on the food habits of fishes in the Alaskan Arctic, and many of these studies have been qualitative in nature and focused on demersally-caught specimens.

Rand et al. (2013) examined the diets of pelagic-caught Arctic cod (*Boreogadus saida*) in the western Beaufort Sea and found euphausiids to be the most dominate prey group, by percent weight and number. Other important prey groups were copepods and larvaceans. Craig et al. (1982) made under-ice, near-surface collections of Arctic cod during spring in the western Beaufort Sea and found copepods, amphipods, and fish to be the most important prey items.

The objectives of this report are to (1) document the collection of stomach contents data from common pelagic fish species encountered in the eastern Chukchi Sea and northern Bering Sea during the 2012 Arctic Eis surface/midwater summer trawl survey, and (2) to document the contents of those collected stomachs. These collections, followed by laboratory analysis of stomach specimens, produced geo-referenced quantitative diet compositions of predator species (by percent weight) with prey identified to the lowest taxonomic level possible. Here we detail the methods of specimen collection in the field and the analysis of stomach contents in the laboratory. I provide summarized diet descriptions for the eastern Chukchi Sea and northern Bering Sea separately for the sampled species, and describe the spatial distribution of the collected stomach samples across the study region.

2.3 Methods

Stomach samples were collected during the 2012 Arctic Ecosystem Integrated Survey's (Arctic Eis) surface/midwater trawl and oceanographic survey in the northern Bering Sea and eastern Chukchi Sea from August 6 to September 26 (Andrews, 2012). Trawling operations were conducted aboard the chartered fishing vessel F/V *Bristol Explorer* during daylight hours. Sampling stations in the Chukchi Sea were based on the Arctic Eis 30 nautical mile (nm) square grid pattern, as followed in other field components of the Arctic Eis (e.g., Goddard et al. 2014). Stations in the northern Bering Sea were based on a square grid pattern along longitudinal transects with stations spaced north to south 30 nm, as were previous surveys conducted in that region (Andrews, 2012). Additional stomach samples were collected from the catch of midwater trawls that were conducted opportunistically, between the gridded stations, to verify acoustic backscatter (DeRobertis et al. this issue).

Following each trawl deployment, intact fish specimens were selected from as wide a size range as possible. Selected specimens were checked for signs of regurgitation and were rejected if stomach contents were evident in the mouth or gills. Fish specimens selected for diet analysis were collected whole and preserved in buffered, neutral 10% formalin at sea then shipped back to the Alaska Fisheries Science Center (AFSC) in Seattle. Stomach specimens were then transferred from 10% formalin to 70% ethanol for storage while awaiting laboratory examination of stomach contents. A detailed description of the stomach sample selection and collection procedure can be found on the AFSC webpage (http://www.afsc.noaa.gov/REFM/REEM/Manuals/StomachChapter.pdf).

Each stomach was analyzed individually. The contents of each stomach were sorted and the prey items were identified to the lowest practical taxon, given the digestive state of prey and/or time constraints. Each prey taxa was weighed to the nearest 0.001 g, counted, and when possible, the appropriate life history code was identified. For more details on diet analysis, a detailed description of laboratory methods for stomach contents analysis can be found on the AFSC webpage (http://www.afsc.noaa.gov/REFM/REEM/Manuals/LabManual.pdf).

A total of 134 unique prey type/life history code combinations were identified during diet analysis (see Appendix D). To aid the interpretation of diet compositions in this report, similar prey items were grouped taxonomically into 14 aggregated prey types. Several uncommon prey types were grouped into the larger general prey categories of "other prey", "other zooplankton", and "unidentified". The other prey category consists of benthic-oriented invertebrate prey, such as polychaetes, isopods, bivalves, and brittle stars. "Other zooplankton" are other pelagic invertebrates that do not fit into any of the other groups (e.g., pteropods). Appendix D contains a complete list of the identified prey taxa/life history code combinations and their assigned aggregated prey groups.

The diet composition of each species are presented here as the percent weight of each prey type, across all non-empty stomachs within the study regions. We use percent weight of prey to describe diet composition because this metric provides a measure of the biomass of consumed prey and because biomass is commonly used as currency in ecosystem and bioenergetics models (Christensen and Walters, 2004; Ahlbeck et al., 2012). The complete geo-referenced diet compositions will be made available through the Alaska Ocean Observing System Workspace (AOOS, http://www.aoos.org/).

2.4 Results

Fish stomachs were collected from 91 trawl deployments during the trawl survey, which included 37 trawl deployments in the northern Bering Sea and 54 in the eastern Chukchi Sea. A total of 948 stomach samples were collected from eight species: Pacific herring (*Clupea pallasi*), capelin (*Mallotus villosus*), rainbow smelt (*Osmerus mordax*), Arctic cod (*Boreogadus saida*), saffron cod (*Eleginus gracilis*), walleye pollock (*Gadus chalcogrammus*), shorthorn sculpin (*Myoxocephalus scorpius*), and Pacific sandlance (*Ammodytes hexapterus*) (Table 2.1). The number of stomachs sampled per trawl deployment varied from 1 to 69 (Figure 2.1), and the total number of stomachs sampled per species ranged from 1 (shorthorn sculpin) to 204 (saffron cod) (Table 2.1). Walleye pollock were only sampled in the northern Bering Sea, and the single shorthorn sculpin was collected in the eastern Chukchi Sea. The following sections note diet composition and the spatial distribution of stomach samples for each species. Species diet composition are displayed separately for the two study regions, the eastern Chukchi Sea and the northern Bering Sea.

2.4.1 Pacific herring

Pacific herring stomach samples were collected from 32 trawl deployments, including seven in the eastern Chukchi Sea and 25 in the northern Bering Sea (Figure 2.2). A total of 170 stomach samples were collected, with the majority of stomachs collected in the northern Bering Sea (Table 2.2). The mean size of Pacific herring sampled in the northern Bering Sea (18.1 cm) was significantly less (Welch's t-test, $p < 0.001$) than in the eastern Chukchi Sea (23.5 cm) (Figure 2.3). The specimens collected in the northern Bering Sea included several fish with total lengths less than 10 cm, whereas the minimum size in the eastern Chukchi Sea was 19 cm.

Pacific herring diet composition was dominated by calanoid copepods (> 40% wt) in both the northern Bering Sea and eastern Chukchi Sea (Table 2.3). Euphausiids were of secondary importance in the northern Bering Sea but were of relatively little importance in the eastern Chukchi Sea. Hyperiid amphipods and larvaceans were important prey groups in both regions. Fishes were a more important prey type in the eastern Chukchi Sea (12.5 %) than in the northern Bering Sea (3.9 %). Pricklebacks (Stichaeidae) were of particular importance, accounting for 9% of the diet.

(xi) 2.4.2 Capelin

The collection of capelin stomachs was widely distributed across the study area. Stomach samples were obtained from 15 trawl deployments in the northern Bering Sea and 23 in the eastern Chukchi Sea (Figure 2.4). A total of 196 capelin stomachs were sampled, with 72 from the northern Bering Sea and 124 coming from the eastern Chukchi Sea (Table 2.4). The sampled capelin ranged in size from 5.9 to 13.7 cm (Table 2.4, Figure 2.5), and the mean size of all sampled specimens in the Chukchi Sea (8.92 cm) was less than in the northern Bering Sea (10.52 cm) (Welch's t-test, $p < 0.001$).

The diet composition of capelin was dominated by calanoid copepods in both regions, accounting for 58% of the diet in the northern Bering Sea and 71% in the eastern Chukchi Sea (Table 2.5). Euphausiids were of secondary importance in both regions. Other less important prey groups in both regions included Chaetognaths (arrow worms), larvaceans, and hyperiid amphipods.

(xii) 2.4.3 Rainbow smelt

Rainbow smelt stomachs were primarily obtained from trawl deployments in the northern Bering Sea and were only collected from one trawl in the eastern Chukchi Sea (Figure 2.6). 105 of the 115 total stomachs came from the northern Bering Sea (Table 2.6). Sampled fishes ranged in size from 7.4 cm to 24 cm. The mean sizes of the sampled specimens from the two study regions were not significantly different (Welch's t-test, $p = 0.31$) (Figure 2.7).

The co-dominant prey types in the northern Bering Sea were mysids and fish, both accounting for 45% of the diet composition by weight (Table 2.7). Fish prey included Osmeridae (smelts, 9.3%), Pacific herring (8.7%), sandlance (*Ammodytes* sp., 8.6%), capelin (7.4%), and Arctic cod (4.97%). In the eastern Chukchi Sea the singularly dominant prey type was gammarid amphipods, whom accounted for 63% of the diet by weight. Prey of lesser importance in the Chukchi Sea included mysids (25.3%), shrimp (5.6%), and fish (3.7%). It is important to note when comparing diet composition between the two study regions that all 10 of the rainbow smelt samples from the eastern Chukchi Sea are from a single trawl deployment, and do not represent region-wide variation in diet composition.

(xiii) 2.4.4 Arctic cod

Arctic cod were collected from 28 trawl deployments; the majority occurred in the eastern Chukchi Sea (Figure 2.8). Of 114 stomachs collected, 92 of them were from 21 trawl deployments in the eastern Chukchi Sea (Table 2.8). The specimens ranged from 3.4 cm to 14.6 cm. In the northern Bering Sea the mean size of collected specimens (7.91 cm) was significantly larger (Welch's t-test, $p < 0.01$) than those specimens collected from the eastern Chukchi Sea (4.59 cm) (Figure 2.9). The largest Arctic cod collected for stomach analysis from the eastern Chukchi Sea (7.1 cm) was smaller than the mean length of specimens from the northern Bering Sea (7.91 cm), where the largest specimen was 14.6 cm.

In the northern Bering Sea, the dominant prey groups were fish (40.86%), mysids (32.52%), and calanoid copepods (19.34%) (Table 2.9). In contrast, in the eastern Chukchi Sea the overwhelmingly dominant prey type was calanoid copepods, accounting for 90.35% of the diet composition. The other prey taxa in the eastern Chukchi Sea were euphausiids (6.29%) and chaetognaths (3.36%).

Fish prey were only consumed by a single Arctic cod in the northern Bering Sea. However, this specimen was the largest collected in this study (14.6 cm), and it’s stomach contents accounted for more than 40% of the total prey (by weight) for all Arctic cod specimens collected in the northern Bering Sea. The particular fish prey was a 49 mm Pacific herring. This example highlights the bias toward large prey items that may be present when using percent weight to describe diet composition and the large influence a single but massive stomach may have when working with small sample sizes.

(xiv) 2.4.5 Saffron cod

Saffron cod were collected from 11 trawl deployments in the northern Bering Sea and 19 in the eastern Chukchi Sea (Figure 2.10). In total, 204 stomachs were collected: 153 in the northern Bering Sea and 51 in the eastern Chukchi Sea (Table 2.10). In the northern Bering Sea the distribution of collected stomachs across the sampled stations was uneven with sample sizes by station ranging from 1 to 40. Four of the stations in the northern Bering Sea had sample sizes of 18, 38, 39, and 40; and collectively accounted for more than 66% of the total saffron cod collections (Figure 2.10). In the eastern Chukchi Sea the sample sizes were generally smaller but more evenly distributed across the study area. The sampled fish ranged in size from 3.2 to 13.9 cm in the eastern Chukchi Sea and from 4.7 to 31 cm in the northern Bering Sea (Figure 2.11). The mean size of the sampled fish was significantly larger in the northern Bering Sea (13.7 cm) than in the eastern Chukchi Sea (5.7 cm) (Welch’s t-test, $p < 0.001$).

The dominant prey group in the diet composition of saffron cod in the northern Bering Sea was the ‘other prey’ category, which comprised 43% of the diet by weight (Table 2.11). Some of the important taxa in the ‘other prey’ category were echiuran worms (25.8 %) and polychaete worms (12.4%). Other important prey groups in the northern Bering Sea were shrimps (26.9%), gammarid amphipods (14.4%), cumaceans (6.2%), and fish (6.1%). The most dominant prey category in the diet composition of saffron cod collected in the eastern Chukchi Sea was shrimp (53.2%), in particular, Crangonidae shrimp account for 99.8% of the shrimp prey. Prey of lesser importance included calanoid copepods (15.8%), gammarid amphipods (11.1%), and ‘other prey’ (6.7%).

(xv) 2.4.6 Walleye pollock

Walleye pollock were only collected for stomach analysis in the northern Bering Sea (Figure 2.12). Collections were made from five trawl deployments totaling in 64 stomachs (Table 2.12). The collected specimens ranged in size from 9.2 to 20.5 cm, with a mean size of 13.7 cm (Figure 2.13).

The diet composition of walleye pollock was dominated by calanoid copepods (49.9%) and mysids (24.3%) (Table 2.13). Prey of lesser importance included, gammarid amphipods (8.4%), larvaceans (6.2%), shrimp (4.7%), and hyperiid amphipods (2.6%).

(xvi) 2.4.7 Shorthorn sculpin

A single shorthorn sculpin stomach was collected from a station in the eastern Chukchi Sea (Figure 2.14). This specimen was 4.5 cm in length and its stomach contained calanoid copepods (95%) and chaetognaths (5%).

(xvii) 2.4.8 Pacific sandlance

Pacific sandlance were collected for stomach analysis from 7 trawl deployments in the northern Bering Sea and 11 in the eastern Chukchi Sea (Figure 2.15). The sample size by trawl ranged from 2 to 5 stomachs. In the northern Bering Sea the collected specimens ranged in size from 5.5 to 15.5 cm and in the eastern Chukchi Sea they ranged from 3.6 to 13.5 cm (Table 2.14). The mean size in the northern Bering Sea (11.7 cm) was significantly larger than in the eastern Chukchi Sea (7.3 cm) (Welch's t-test, $p < 0.001$) (Figure 2.16).

In the northern Bering Sea, the two dominant prey groups were Chaetognaths (42.9%) and calanoid copepods (32.8%) (Table 2.15). Of secondary importance were fish (11.0%) and larvaceans (9.7%). The fish prey primarily consisted of larval yellowfin sole (*Limanda aspera*). In the eastern Chukchi Sea the diet composition consisted of calanoid copepods (85.7%), euphausiids (13.5%), and Chaetognaths (0.8%).

2.1 Acknowledgements

Special thanks to Richard Hibpshman, Caroline Robinson, Sean Rohan, and Kimberly Sawyer from the University of Washington for laboratory analysis of stomach contents. Thanks to Geoff Lang (AFSC) for providing access to the data. Thank you to all Arctic Eis survey participants for their help in collecting stomach specimens. Thanks to the captain and crew of the F/V *Bristol Explorer* for their efforts. This work was conducted as part of the Arctic Ecosystem Integrated Survey (Arctic Eis) and was funded [in part] by the U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM) through Cooperative Agreement M12PG00018 between BOEM, Alaska Outer Continental Shelf Region and the Alaska Fisheries Science Center. The findings and conclusions in this report are those of the author and do not necessarily represent the views of the National Marine Fisheries Service. This publication is [partially] funded by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement No. NA10OAR4320148, Contribution No. 2608.

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Table 2.1. The total number of stomach samples collected for each predator species and the total by sampling region (ECS = eastern Chukchi Sea, NBS = northern Bering Sea).

Common name	Species	ECS	NBS	Total
Pacific herring	*Clupea pallasi*	34	136	170
Capelin	*Mallotus villosus*	124	72	196
Rainbow smelt	*Osmerus mordax*	10	105	115
Arctic cod	*Boreogadus saida*	92	22	114
Saffron cod	*Eleginus gracilis*	51	153	204
Walleye pollock	*Gadus chalcogrammus*	0	64	64
Shorthorn sculpin	*Myoxocephalus scorpius*	1	0	1
Pacific sandlance	*Ammodytes hexapterus*	53	31	84
	Total	365	583	948

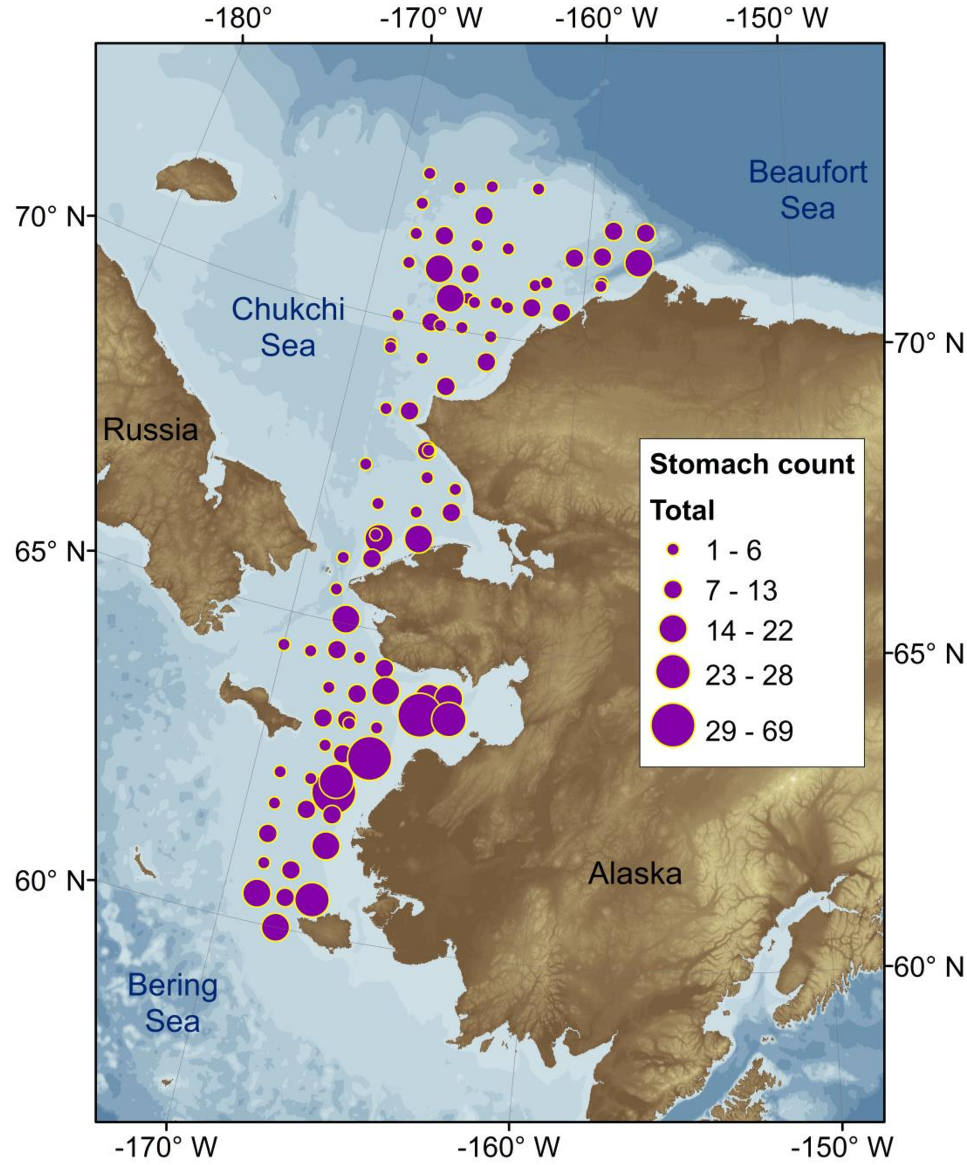

Figure 2.1. The location of trawl deployments where fish stomach samples were collected during the 2012 surface/midwater trawl survey. The size of the bubble is scaled to the number of stomachs collected from a trawl deployment. Sample sizes by trawl ranged from 1 to 69.

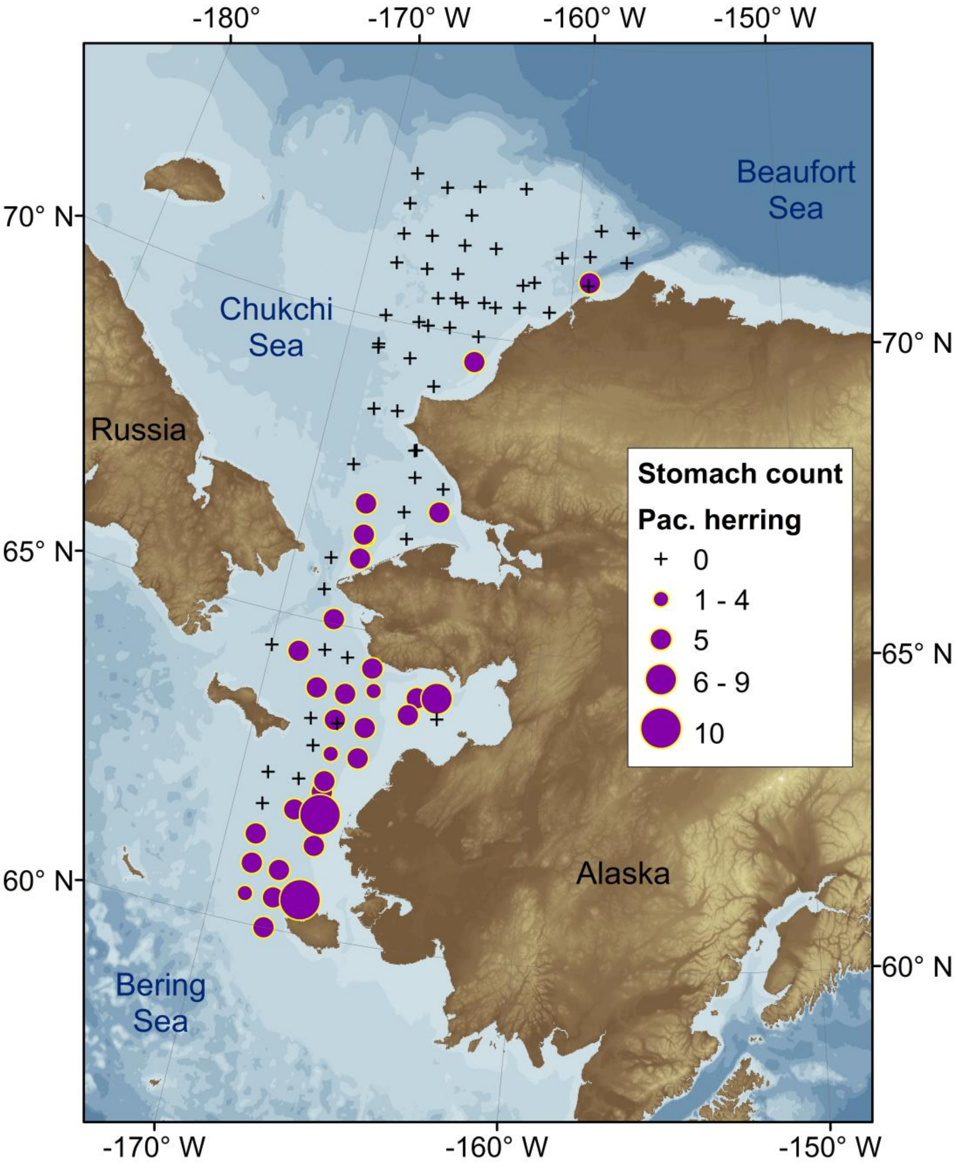

Figure 2.2. Sample locations where Pacific herring stomachs were collected. The size of the bubble corresponds to sample size. Please note two of the trawl locations in the eastern Chukchi Sea are in close proximity and only appear as a single bubble on this map (stations CH B02 and Mid1, see Appendix E for locations). The sample sizes for those two trawls were four and five, respectively.

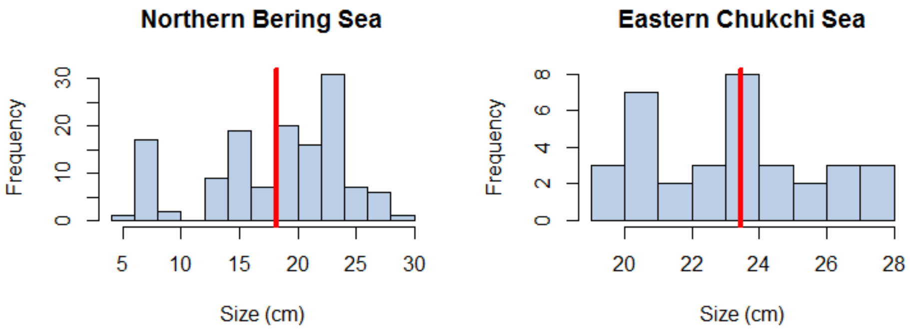

Figure 2.3. Length frequency distribution for Pacific herring selected for diet analysis from the northern Bering Sea and eastern Chukchi Sea (including empty stomachs). The vertical red line is the mean length of selected specimens from the respective regions.

Table 2.2. Sample sizes, size range (cm), and mean size (cm) for Pacific herring collected in the eastern Chukchi Sea and northern Bering Sea.

Region	**N. Bering Sea**		**E. Chukchi Sea**	
	Full	Empty	Full	Empty
Number	101	35	31	3
Size range (cm)	5.1 - 26.6	6.4 - 29	19 - 28	21 - 28
Mean (SD)	18.09 (5.59)	18.41 (6.73)	23.31 (2.53)	25 (3.61)

Table 2.3. Diet compositions (% weight) for Pacific herring in the northern Bering Sea (NBS) and eastern Chukchi Sea (ECS).

Prey	**NBS**	**ECS**
Calanoida	40.75	42.24
Chaetognatha	0.90	0.00
Cumacea	0.02	0.00
Decapod larvae	0.51	6.69
Euphausiidae	21.92	0.99
Gammaridea	0	0
Hyperiidea	19.89	25.53
Larvacean	6.08	10.70
Mysidae	5.26	0.01
Shrimp	0.34	0.41
Other prey	0	0.06
Other zooplankton	0.48	0.87
Teleostei	3.86	12.50
Unidentified	0	0

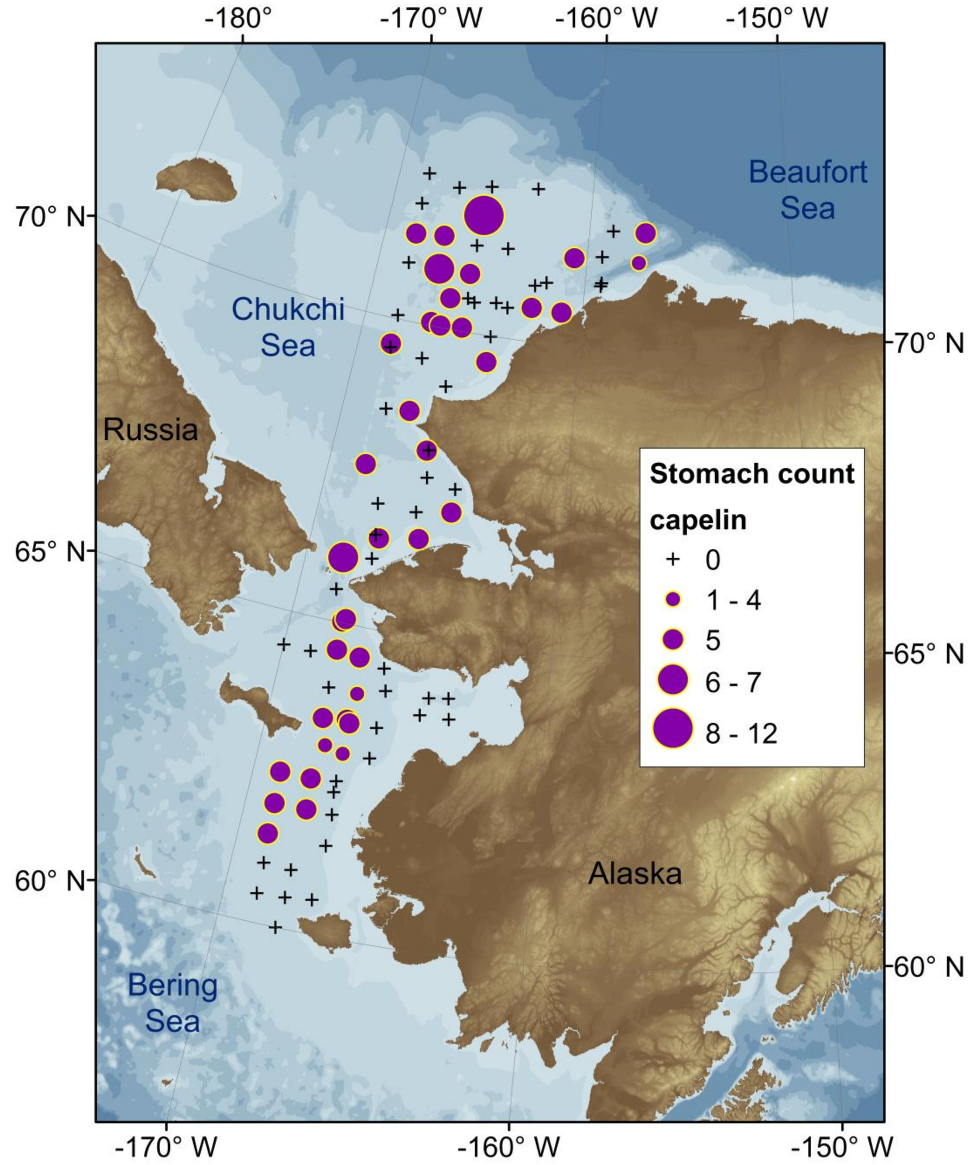

Figure 2.4. Sample locations where capelin stomachs were collected. The size of the bubble corresponds to sample size.

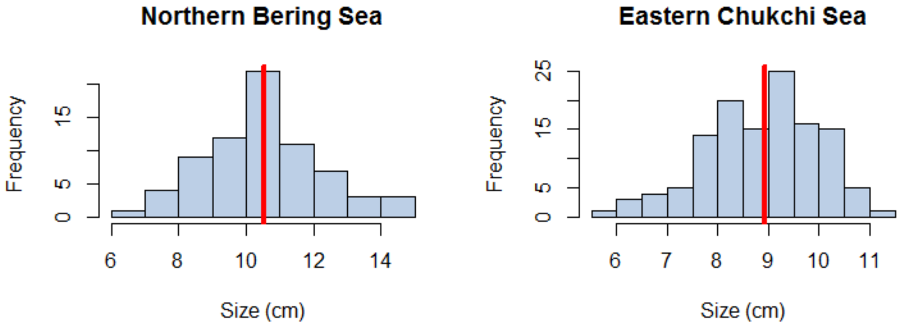

Figure 2.5. Length frequency distribution for capelin selected for diet analysis from the northern Bering Sea and eastern Chukchi Sea (including empty stomachs). The vertical red line is the mean length of selected specimens from the respective regions.

Table 2.4. Sample sizes, size range (cm), and mean size (cm) for capelin collected in the eastern Chukchi Sea and northern Bering Sea.

Region	**N. Bering Sea**		**E. Chukchi Sea**	
	Full	Empty	Full	Empty
Number	57	15	101	23
Size range (cm)	6.9 - 14.8	7.7 - 13.7	6.4 - 11.2	5.9 - 10.7
Mean (SD)	10.63 (1.84)	10.07 (1.47)	8.88 (1.06)	9.07 (1.25)

Table 2.5. Diet compositions (% weight) for capelin in the northern Bering Sea (NBS) and eastern Chukchi Sea (ECS).

Prey	**NBS**	**ECS**
Calanoida	57.91	71.17
Chaetognatha	8.53	3.69
Cumacea	0	0
Decapod larvae	0.16	0.01
Euphausiidae	32.97	18.77
Gammaridea	0.02	0
Hyperiidea	0.24	0.76
Larvacean	0.18	1.54
Mysidae	0	2.97
Shrimp	0	0
Other prey	0	1.08
Other zooplankton	0	0
Teleostei	0	0
Unidentified	0	0

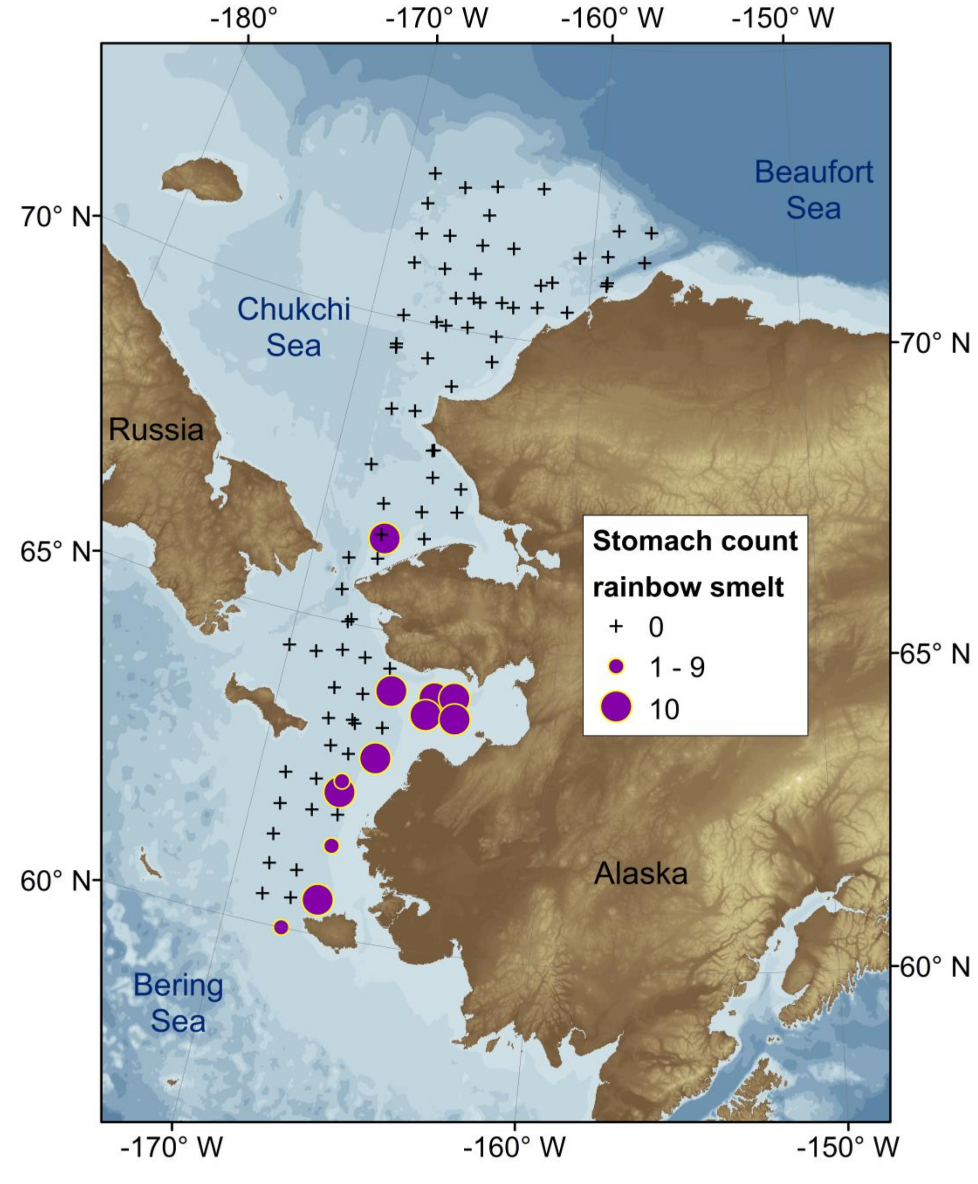

Figure 2.6. Sample locations where rainbow smelt stomachs were collected. The size of the bubble corresponds to sample size.

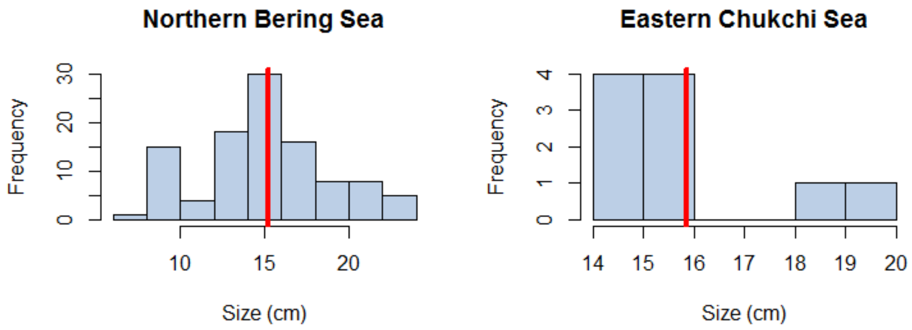

Figure 2.7. Length frequency distribution for rainbow smelt selected for diet analysis from the northern Bering Sea and eastern Chukchi Sea (including empty stomachs). The vertical red line is the mean length of selected specimens from the respective regions.

Table 2.6. Sample sizes, size range (cm), and mean size (cm) for rainbow smelt collected in the eastern Chukchi Sea and northern Bering Sea.

Region	**N. Bering Sea**		**E. Chukchi Sea**	
	Full	Empty	Full	Empty
Number	76	29	9	1
Size range (cm)	8.2 - 24	7.9 - 22.2	14.2 - 18.2	19.4
Mean (SD)	15.43 (3.95)	14.53 (3.56)	15.47 (1.19)	-

Table 2.7. Diet compositions (% weight) for rainbow smelt in the northern Bering Sea (NBS) and eastern Chukchi Sea (ECS).

Prey	**NBS**	**ECS**
Calanoida	1.33	0
Chaetognatha	0.06	0
Cumacea	1.09	0.24
Decapod larvae	0.68	0
Euphausiidae	0	0
Gammaridea	1.05	63.36
Hyperiidea	0.52	1.63
Larvacean	1.77	0
Mysidae	45.41	25.31
Shrimp	3.46	5.56
Other prey	0.02	0.23
Other zooplankton	0	0
Teleostei	44.61	3.66
Unidentified	0	0

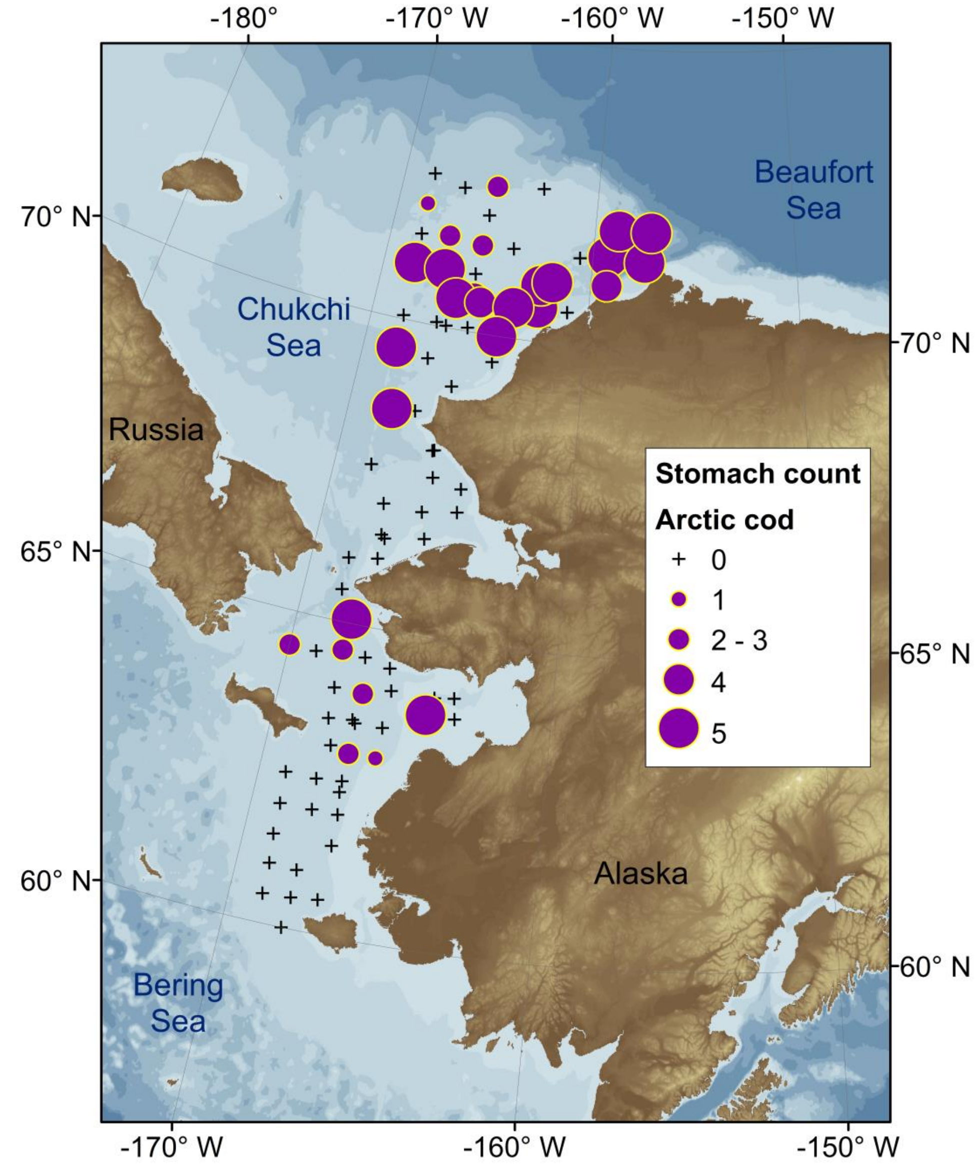

Figure 2.8. Sample locations where Arctic cod stomachs were collected. The size of the bubble corresponds to sample size.

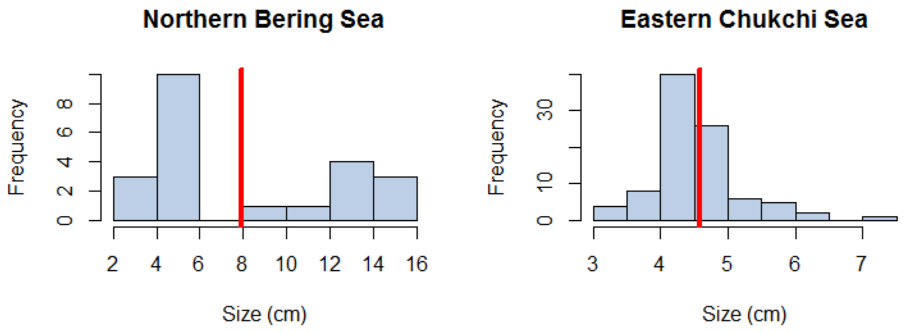

Figure 2.9. Length frequency distribution for Arctic cod selected for diet analysis from the northern Bering Sea and eastern Chukchi Sea (including empty stomachs). The vertical red line is the mean length of selected specimens from the respective regions.

Table 2.8. Sample sizes, size range (cm), and mean size (cm) for Arctic cod collected in the eastern Chukchi Sea and northern Bering Sea.

Region	**N. Bering Sea**		**E. Chukchi Sea**	
	Full	Empty	Full	Empty
Number	19	3	85	7
Size range (cm)	3.9 - 14.6	9.2 - 13.4	3.4 - 7.1	3.4 - 4.6
Mean (SD)	7.37 (4.52)	11.33 (2.10)	4.62 (0.65)	4.16 (0.44)

Table 2.9. Diet compositions (% weight) for Arctic cod in the northern Bering Sea (NBS) and eastern Chukchi Sea (ECS).

Prey	**NBS**	**ECS**
Calanoida	19.34	90.35
Chaetognatha	0.32	3.36
Cumacea	0	0
Decapod larvae	0	0
Euphausiidae	0.30	6.29
Gammaridea	0	0
Hyperiidea	0	0
Larvacean	6.65	0
Mysidae	32.52	0
Shrimp	0	0
Other prey	0	0
Other zooplankton	0	0
Teleostei	40.86	0
Unidentified	0	0

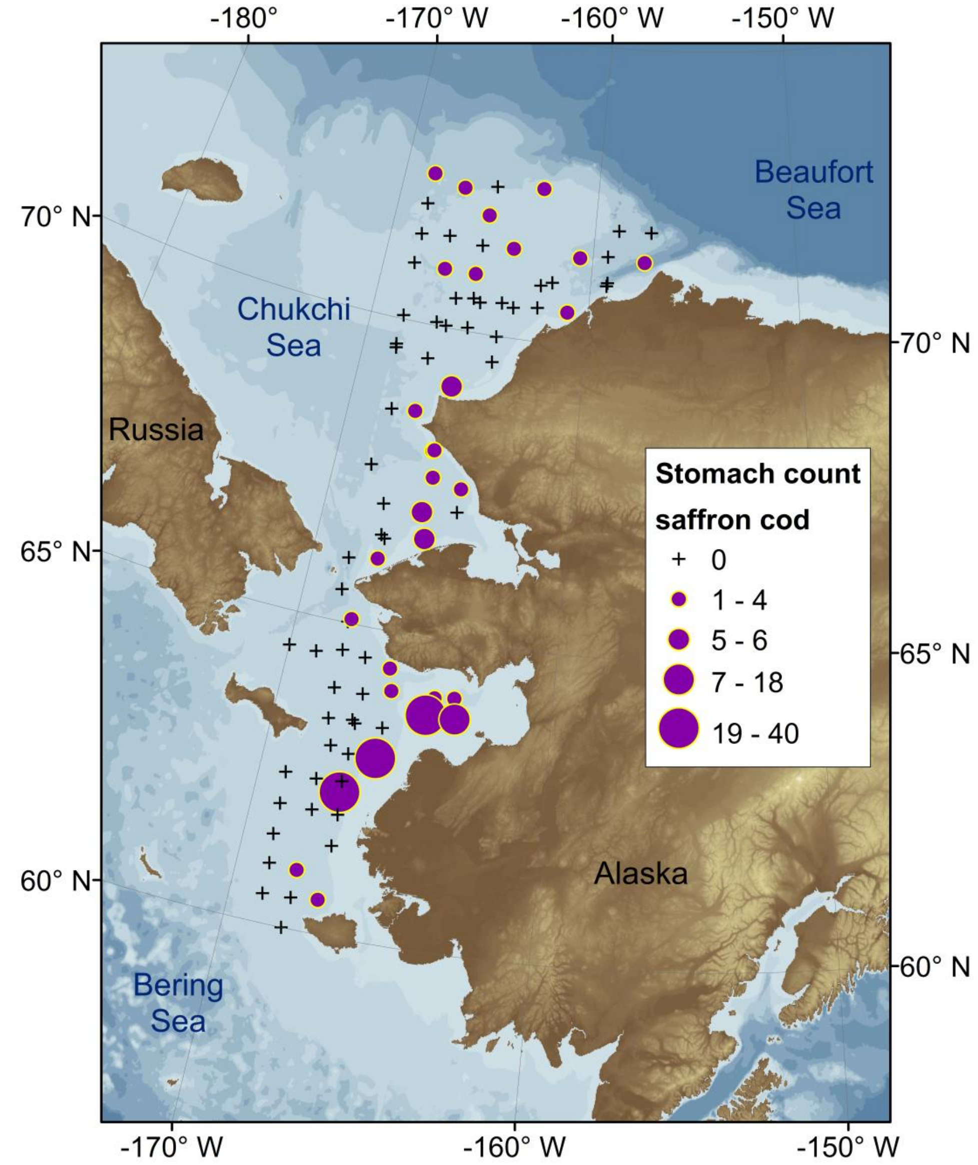

Figure 2.10. Sample locations where saffron cod stomachs were collected. The size of the bubble corresponds to sample size.

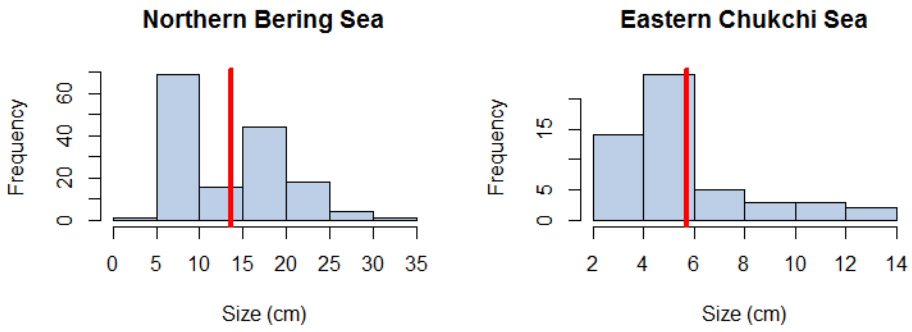

Figure 2.11. Length frequency distribution for saffron cod selected for diet analysis from the northern Bering Sea and eastern Chukchi Sea (including empty stomachs). The vertical red line is the mean length of selected specimens from the respective regions.

Table 2.10. Sample sizes, size range (cm), and mean size (cm) for saffron cod collected in the eastern Chukchi Sea and northern Bering Sea.

Region	**N. Bering Sea**		**E. Chukchi Sea**	
	Full	Empty	Full	Empty
Number	138	15	51	0
Size range (cm)	4.7 - 31	7.5 - 16.1	3.2 - 13.9	-
Mean (SD)	14.14 (5.88)	9.69 (2.32)	5.69 (2.68)	-

Table 2.11. Diet compositions (% weight) for saffron cod in the northern Bering Sea (NBS) and eastern Chukchi Sea (ECS).

Prey	**NBS**	**ECS**
Calanoida	0.24	15.76
Chaetognatha	0.08	0.32
Cumacea	6.15	0
Decapod larvae	0.06	0.59
Euphausiidae	0	0
Gammaridea	14.42	11.07
Hyperiidea	0.20	0.14
Larvacean	0.80	0.8
Mysidae	2.10	4.69
Shrimp	26.88	53.22
Other prey	43.00	6.65
Other zooplankton	0	2.65
Teleostei	6.05	4.09
Unidentified	0.01	0.03

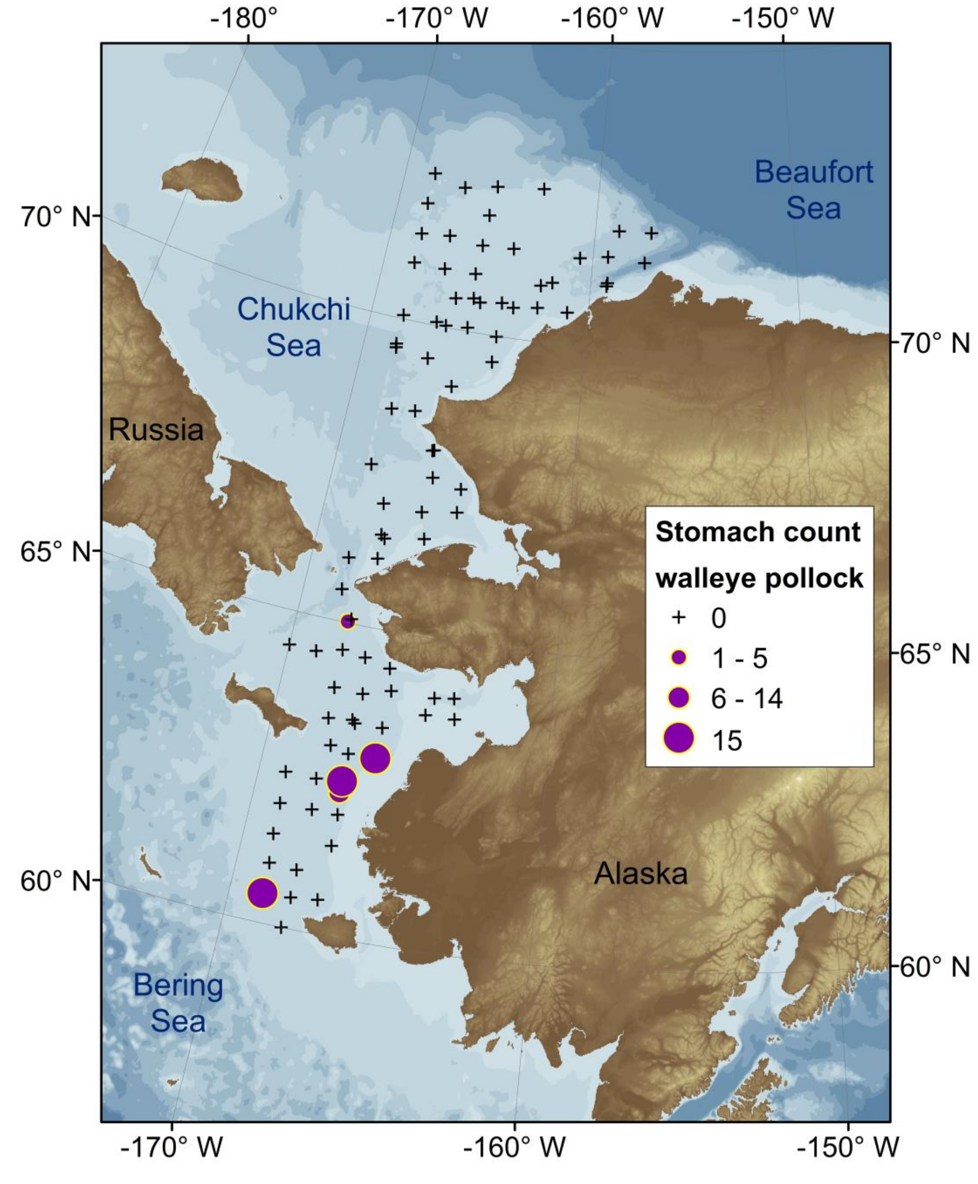

Figure 2.12. Sample locations where walleye pollock stomachs were collected. The size of the bubble corresponds to sample size.

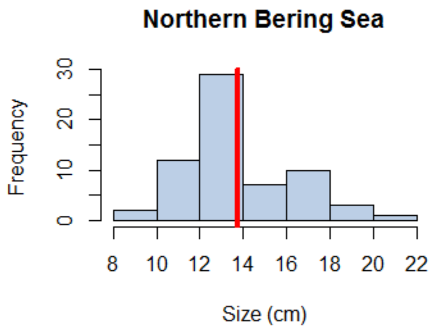

Figure 2.13. Length frequency distribution for walleye pollock selected for diet analysis from the northern Bering Sea (including empty stomachs). The vertical red line is the mean length of selected specimens.

Table 2.12. Sample sizes, size range (cm), and mean size (cm) for walleye pollock collected in the northern Bering Sea.

Region	**N. Bering Sea**		**E. Chukchi Sea**	
	Full	Empty	Full	Empty
Number	63	1	0	0
Size range (cm)	9.2 - 20.5	12.8	-	-
Mean (SD)	13.73 (2.43)	-	-	-

Table 2.13. Diet compositions (% weight) for walleye pollock in the northern Bering Sea (NBS).

Prey	**NBS**
Calanoida	49.86
Chaetognatha	1.11
Cumacea	0.39
Decapod larvae	0.75
Euphausiidae	0.20
Gammaridea	8.44
Hyperiidea	2.63
Larvacean	6.23
Mysidae	24.30
Shrimp	4.71
Other prey	0.05
Other zooplankton	0
Teleostei	1.33
Unidentified	0

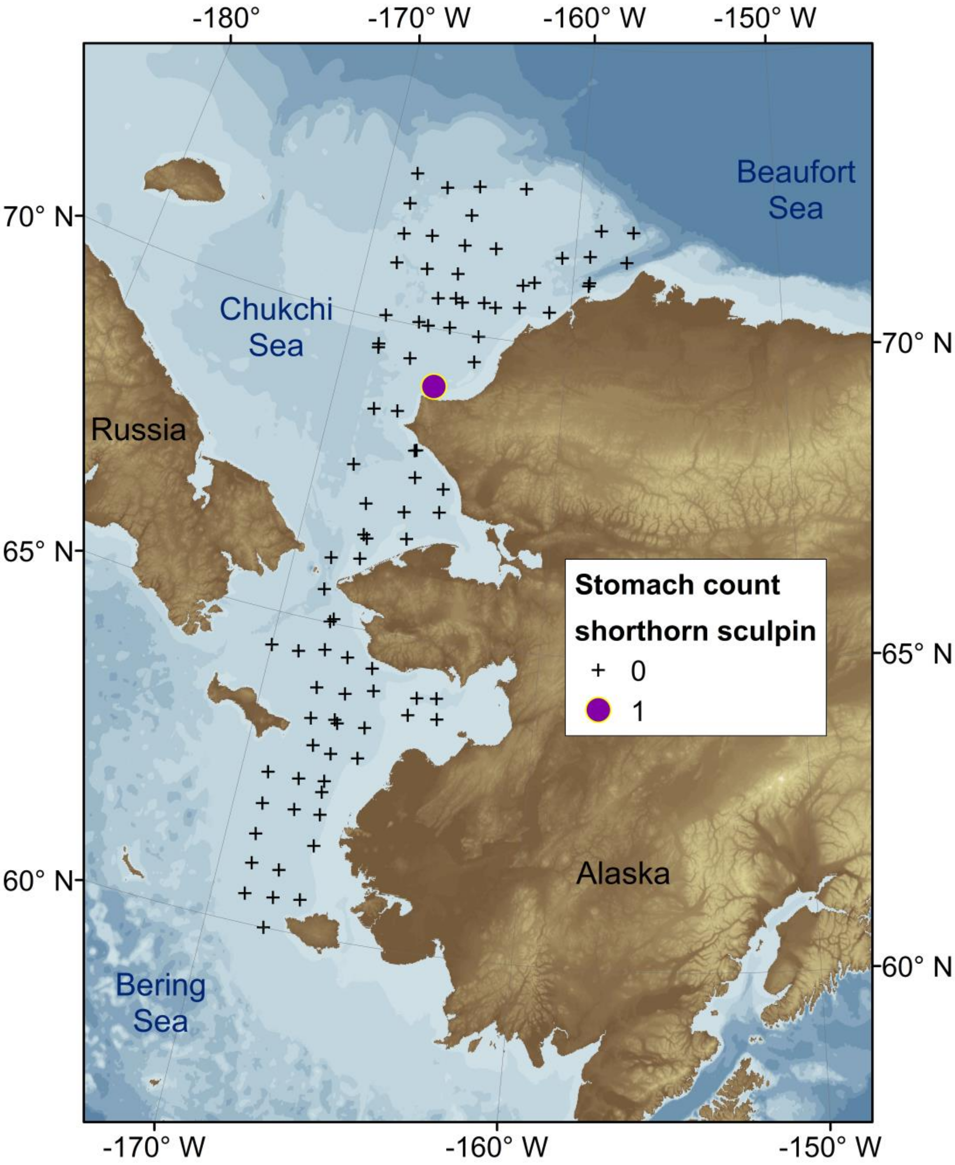

Figure 2.14. Sample location where the lone shorthorn sculpin stomach was collected.

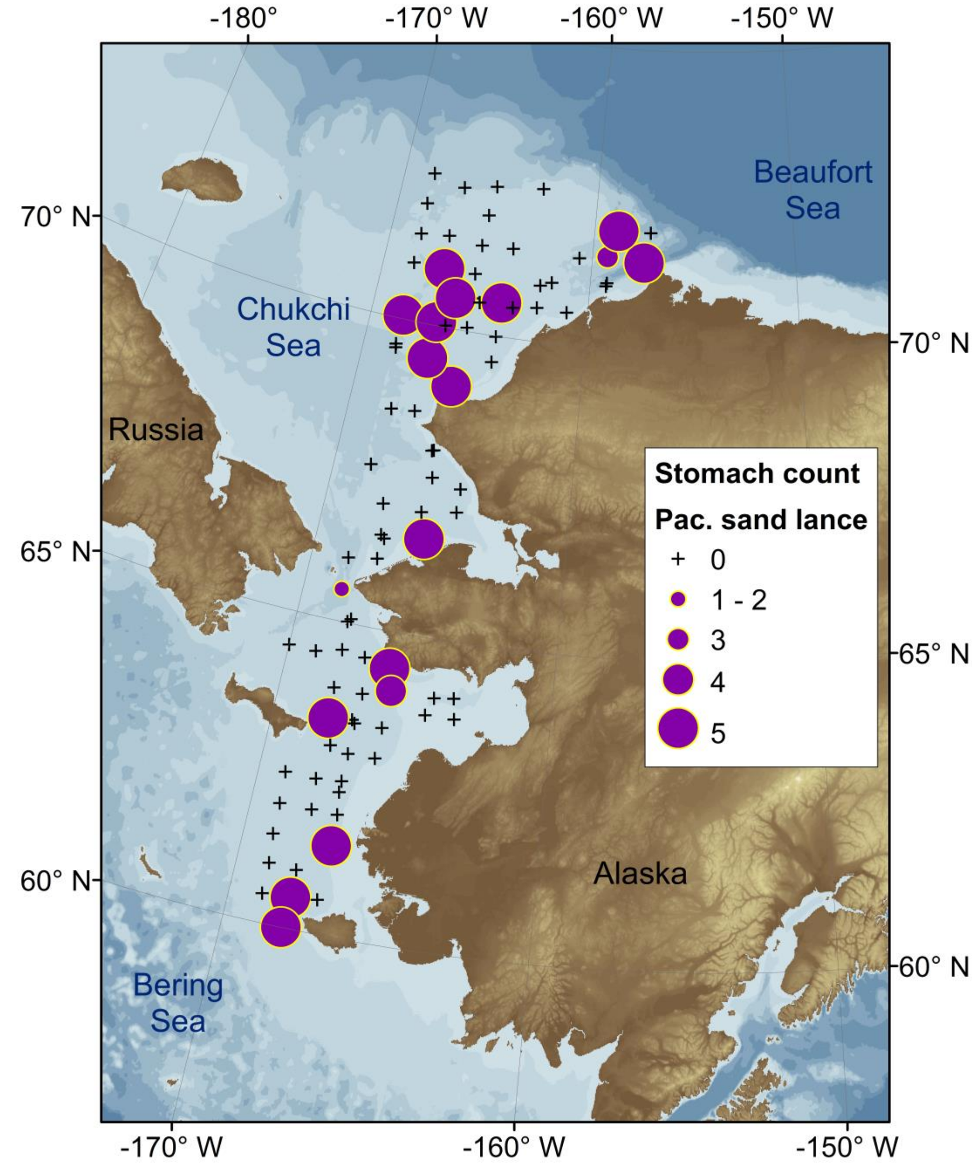

Figure 2.15. Sample locations where Pacific sandlance stomachs were collected. The size of the bubble corresponds to sample size.

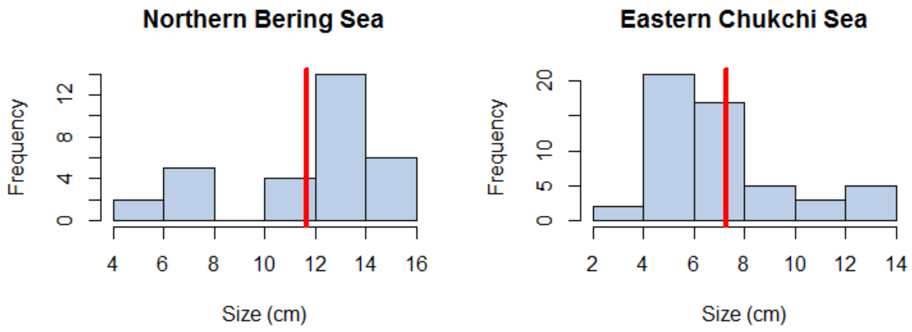

Figure 2.16. Length frequency distribution for Pacific sandlance selected for diet analysis from the northern Bering Sea and eastern Chukchi Sea (including empty stomachs). The vertical red line is the mean length of selected specimens from the respective regions.

Table 2.14. Sample sizes, size range (cm), and mean size (cm) for Pacific sandlance collected in the eastern Chukchi Sea and northern Bering Sea.

Region	**N. Bering Sea**		**E. Chukchi Sea**	
	Full	Empty	Full	Empty
Number	26	5	36	17
Size range (cm)	5.7 - 15.5	5.5 - 13.9	3.6 - 13.5	3.6 - 13.4
Mean (SD)	12.43 (2.70)	7.76 (3.46)	7.23 (2.66)	7.32 (2.54)

Table 2.15. Diet compositions (% weight) for Pacific sandlance in the northern Bering Sea (NBS) and eastern Chukchi Sea (ECS).

Prey	**NBS**	**ECS**
Calanoida	32.79	85.76
Chaetognatha	42.86	0.78
Cumacea	0	0
Decapod larvae	0.76	0
Euphausiidae	0.30	13.46
Gammaridea	0	0
Hyperiidea	0	0
Larvacean	9.68	0
Mysidae	0.99	0
Shrimp	0.10	0
Other prey	1.51	0
Other zooplankton	0	0
Teleostei	11.02	0
Unidentified	0	0

2.3 Appendix D

Caption: Prey types and life history stage identified during laboratory analysis of stomach contents. Aggregated prey group is the prey category used in the diet descriptions. Species names are provided for prey taxa identified to the species level. When distinct life history stages could be identified they are provided. The life history codes are; C=unknown, 3=zoea, 4=megalops, 6=larva, 7=juvenile.

Table D1. Prey types and life history stage identified during laboratory analysis of stomach contents. Aggregated prey group is the prey category used in the diet descriptions. Species names are provided for prey taxa identified to the species level. When distinct life history stages could be identified they are provided. The life history codes are; C=unknown, 3=zoea, 4=megalops, 6=larva, 7=juvenile.

Common Name	Species Name	Life history code	Aggregated group
Anthozoa (anemone)		C	Other prey
Polychaeta (polychaete)		C	Other prey
Phyllodocidae (polychaete)		C	Other prey
Syllidae (polychaete)		C	Other prey
Nephtyidae (polychaete)		C	Other prey
Glyceridae (polychaete)		C	Other prey
Goniadidae (polychaete)		C	Other prey
Sternaspidae (polychaete)		C	Other prey
Oweniidae (polychaete)		C	Other prey
Aphroditiformia (polychaete)		C	Other prey
Mollusca		C	Other prey
Pteropoda		C	Other zooplankton
Gymnosomata (naked pteropod)		C	Other zooplankton
Bivalvia (clam)		C	Other prey
Ostracoda		C	Other prey
Copepoda		C	Calanoida (copepod)
Calanoida (copepod)		C	Calanoida (copepod)
Calanidae (copepod)		C	Calanoida (copepod)
Calanidae (copepod)	Calanus sp.	C	Calanoida (copepod)
Calanidae (copepod)	Calanus hyperboreus	C	Calanoida (copepod)
Calanidae (copepod)	Calanus glacialis/marshallae	C	Calanoida (copepod)
Calanidae (copepod)	Neocalanus sp.	C	Calanoida (copepod)
Calanidae (copepod)	Neocalanus cristatus	C	Calanoida (copepod)
Calanidae (copepod)	Neocalanus flemingeri/plumchrus	C	Calanoida (copepod)
Eucalanidae (copepod)	Eucalanus bungii	C	Calanoida (copepod)
Pseudocalanidae (copepod)	Pseudocalanus sp.	C	Calanoida (copepod)
Metridiidae (copepod)		C	Calanoida (copepod)
Metridiidae (copepod)	Metridia sp.	C	Calanoida (copepod)
Metridiidae (copepod)	Metridia princeps	C	Calanoida (copepod)
Metridiidae (copepod)	Metridia lucens/pacifica	C	Calanoida (copepod)
Centropagidae (copepod)	Centropages sp.	C	Calanoida (copepod)
Centropagidae (copepod)	Centropages abdominalis	C	Calanoida (copepod)
Pontellidae (Calanoid Copepod)		C	Calanoida (copepod)

Table D1 (continued).

Common Name	Species Name	Life history code	Aggregated group
Pontellidae (copepod)	Epilabidocera sp.	C	Calanoida (copepod)
Pontellidae (copepod)	Epilabidocera longipedata	C	Calanoida (copepod)
Acartiidae (copepod)	Acartia sp.	C	Calanoida (copepod)
Tortanidae (copepod)		C	Calanoida (copepod)
Tortanidae (copepod)	Tortanus discaudatus	C	Calanoida (copepod)
Medium calanoid (copepod) 2-5mm		C	Calanoida (copepod)
Small calanoid (copepod) < 2mm		C	Calanoida (copepod)
Mysidae (mysid)		C	Mysidae (mysid)
Mysidae (mysid)	Disacanthomysis dybowskii	C	Mysidae (mysid)
Mysidae (mysid)	Acanthomysis stelleri	C	Mysidae (mysid)
Mysidae	Mysis oculata	C	Mysidae (mysid)
Mysidae (mysid)	Neomysis sp.	C	Mysidae (mysid)
Mysidae (mysid)	Neomysis awatschensis	C	Mysidae (mysid)
Mysidae (mysid)	Pseudomma sp.	C	Mysidae (mysid)
Mysidae (Mysid)	Michthyops sp.	C	Mysidae (mysid)
Cumacea (cumacean)		C	Cumacea (cumacean)
Isopoda (isopod)		C	Other prey
Gammaridea (amphipod)		C	Gammaridea (amphipod)
Ampeliscidae (amphipod)		C	Gammaridea (amphipod)
Ampeliscidae (amphipod)	Ampelisca sp.	C	Gammaridea (amphipod)
Ampeliscidae (amphipod)	Byblis sp.	C	Gammaridea (amphipod)
Calliopiidae (amphipod)		C	Gammaridea (amphipod)
Eusiridae (amphipod)		C	Gammaridea (amphipod)
Eusiridae (amphipod)	Rhachotropis sp.	C	Gammaridea (amphipod)
Haustoriidae (amphipod)	Eohaustorius eous	C	Gammaridea (amphipod)
Isaeidae (amphipod)		C	Gammaridea (amphipod)
Ischyroceridae (amphipod)		C	Gammaridea (amphipod)
Lysianassidae (amphipod)		C	Gammaridea (amphipod)
Oedicerotidae (amphipod)		C	Gammaridea (amphipod)
Oedicerotidae (amphipod)	Monoculodes sp.	C	Gammaridea (amphipod)
Phoxocephalidae (amphipod)		C	Gammaridea (amphipod)
Pleustidae (amphipod)		C	Gammaridea (amphipod)
Podoceridae (amphipod)		C	Gammaridea (amphipod)

Table D1 (continued).

Common Name	Species Name	Life history code	Aggregated group
Podoceridae (amphipod)	Dyopedos sp.	C	Gammaridea (amphipod)
Stenothoidae (amphipod)		C	Gammaridea (amphipod)
Stenothoidae (amphipod)	Metopa sp.	C	Gammaridea (amphipod)
Synopiidae (amphipod)		C	Gammaridea (amphipod)
(Gammarid Amphipod)	Lysianassoidea	C	Gammaridea (amphipod)
Uristidae (amphipod)		C	Gammaridea (amphipod)
Pontoporeiidae (amphipod)		C	Gammaridea (amphipod)
Pontoporeiidae (amphipod)	Priscillina armata	C	Gammaridea (amphipod)
Melitidae (amphipod)		C	Gammaridea (amphipod)
Hyperiidea (amphipod)		C	Hyperiidea (amphipod)
Hyperiidea (amphipod)		C	Hyperiidea (amphipod)
Hyperiidae (amphipod)	Themisto sp.	C	Hyperiidea (amphipod)
Hyperiidae (amphipod)	Themisto libellula	C	Hyperiidea (amphipod)
Hyperiidae (amphipod)	Themisto pacifica	C	Hyperiidea (amphipod)
Caprellidae (amphipod)		C	Other prey
Euphausiidae (euphausiid)		C	Euphausiidae (euphausiid)
Euphausiidae (euphausiid)	Thysanoessa sp.	C	Euphausiidae (euphausiid)
Euphausiidae (euphausiid)	Thysanoessa inermis	C	Euphausiidae (euphausiid)
Euphausiidae (euphausiid)	Thysanoessa raschi	C	Euphausiidae (euphausiid)
Natantia (shrimp)		3	Decapod larvae
Natantia (shrimp)		6	Decapod larvae
Natantia (shrimp)		C	Natantia (shrimp)
Caridea (shrimp)		6	Decapod larvae
Caridea (shrimp)		7	Natantia (shrimp)
Caridea (shrimp)		C	Natantia (shrimp)
Hippolytidae (shrimp)		7	Natantia (shrimp)
Hippolytidae (shrimp)		C	Natantia (shrimp)
Pandalidae (shrimp)		3	Decapod larvae
Pandalidae (shrimp)		C	Natantia (shrimp)
Pandalidae (shrimp)	Pandalus sp.	C	Natantia (shrimp)
Crangonidae (shrimp)		7	Natantia (shrimp)
Crangonidae (shrimp)		C	Natantia (shrimp)
Ridged crangon (shrimp)	Crangon dalli	C	Natantia (shrimp)
Northern argid (shrimp)	Argis lar	C	Natantia (shrimp)

Table D1 (continued).

Common Name	Species Name	Life history code	Aggregated group
Crangon complex (Crangon, Neocrangon,Lissocrangon)		7	Natantia (shrimp)
Crangon complex (Crangon, Neocrangon,Lissocrangon)		C	Natantia (shrimp)
Reptantia (crab)		3	Decapod larvae
Reptantia (crab)		4	Decapod larvae
Paguridae (hermit crab)		3	Decapod larvae
Paguridae (hermit crab)		4	Decapod larvae
Paguridae (hermit crab)		6	Decapod larvae
Paguridae (hermit crab)		C	Other prey
Decapoda brachyura (crab)		3	Decapod larvae
Decapoda brachyura (crab)		4	Decapod larvae
Majidae (spider crab)		3	Decapod larvae
Majidae (spider crab)		4	Decapod larvae
Atelecyclidae (crab)		4	Decapod larvae
Korean horsehair crab	Erimacrus isenbeckii	4	Decapod larvae
Echiura (marine worm)		C	Other prey
Priapulida (marine worm)		C	Other prey
Ophiurida (brittle star)		C	Other prey
Chaetognatha (arrow worm)		C	Chaetognatha (arrow worm)
Copelata (larvacea)		C	Copelata (larvacean)
Teleostei (fish)		C	Teleostei (fish)
Non-gadoid fish remains		C	Teleostei (fish)
Pacific herring	Clupea pallasii	C	Teleostei (fish)
Osmeridae (smelt)		C	Teleostei (fish)
Capelin	Mallotus villosus	C	Teleostei (fish)
Gadidae (gadid fish)		C	Teleostei (fish)
Arctic cod	Boreogadus saida	C	Teleostei (fish)
Stichaeidae (prickleback)		C	Teleostei (fish)
Daubed shanny	Leptoclinus maculatus	C	Teleostei (fish)
Ammodytidae (sandlance)	Ammodytes sp.	C	Teleostei (fish)
Pleuronectidae (flatfish)		6	Teleostei (fish)
Pleuronectidae (flatfish)		C	Teleostei (fish)
Yellowfin sole	Limanda aspera	6	Teleostei (fish)
Unidentified organic material		C	Unidentified
Unidentified tube		C	Unidentified

17. 2.8 Appendix E

Caption: The location and station identification number for trawl deployments where stomach specimens were collected during the 2012 Arctic Eis surface/midwater summer trawl survey. Station ID's beginning with 'NB' are located in the northern Bering Sea, and station ID's starting with 'CH' are in the Chukchi Sea. Station ID's beginning with 'Mid', are midwater trawling locations which were sampled opportunistically between the gridded sampling stations.

Table E1. The location and station identification number for trawl deployments where stomach specimens were collected during the 2012 Arctic Eis surface/midwater summer trawl survey. Station ID's beginning with 'NB' are located in the northern Bering Sea, and station ID's starting with 'CH' are in the Chukchi Sea. Station ID's beginning with 'Mid', are midwater trawling locations which were sampled opportunistically between the gridded sampling stations.

Station ID	Haul number	Latitude	Longitude
NB-ZZ02	377	60	-168.08
NB-Z01	371	60.47	-168.91
NB-Z02	366	60.5	-167.98
NB-Z03	374	60.55	-167.1
NB-Y02	365	60.95	-167.98
NB-Y01	362	60.97	-168.91
NB-X01	350	61.44	-169
NB-X03	356	61.44	-167
NB-W01	347	61.94	-169.01
NB-W03	341	61.95	-167
NB-W02	344	61.95	-167.9
Mid21	338	62.31	-167.09
NB-V01	331	62.45	-169.06
NB-V02	334	62.45	-167.97
NB-V03	337	62.49	-167.08
NB-U03	323	62.94	-167.05
NB-U04	322	62.95	-166.08
NB-U02	328	63.02	-167.72
NB-T02	300	63.44	-168
NB-T03	304	63.44	-167.03
NB-T04	307	63.45	-166.03
Mid20	301	63.49	-167.14
NB-T06	314	63.77	-163.5
NB-T05	319	63.77	-164.57
NB-SO3	294	63.93	-166.96
NB-S02	291	63.94	-168.02
NB-SO4	297	64.06	-165.95
NB-S05	313	64.06	-164.34
NB-S06	310	64.1	-163.62
NB-R04	269	64.41	-166.15
NB-R01	278	64.45	-168.97
NB-R00	281	64.45	-169.99
NB-R03	272	64.51	-167.13
NB-R02	275	64.56	-168.02
Mid18	265	65.02	-168.05
NB-Q02	266	65.07	-167.93
NB-P02	257	65.51	-168.53
CH-A01	3	66.03	-168.54
CH-A02	7	66.11	-167.42
CH_B02	14	66.45	-167.31
Mid1	15	66.5	-167.46

Table E1 continued.

Station ID	Haul number	Latitude	Longitude
CH-B03	10	66.56	-165.74
CH-C03	31	66.98	-166.03
Mid2	24	67	-167.63
CH-C04	35	67.07	-164.61
CH-D04	38	67.45	-164.6
CH-D03	42	67.56	-165.84
CH-D01	51	67.58	-168.47
CH-E03	62	67.99	-166.06
Mid4	63	68	-165.98
Mid5	66	68.53	-168.13
CH-F02	70	68.57	-167.11
CH-G03	74	69.07	-165.74
CH-H02	90	69.45	-167.02
Mid7	87	69.52	-168.52
CH-H04	98	69.57	-164.13
CH-H01	86	69.58	-168.54
Mid8	102	69.99	-164.11
Mid9	108	70.03	-166.49
CH-I03	106	70.06	-165.49
CH-I02	111	70.06	-166.94
CH-I01	115	70.06	-168.5
Mid11	125	70.5	-166.27
Mid12	129	70.5	-165.11
Mid13	135	70.5	-163.53
CH-J06	142	70.53	-160.98
CH-J03	128	70.55	-165.44
CH-J04	133	70.55	-164.09
CH-J05	138	70.55	-162.4
CH-K05	159	70.92	-162.37
CH-K02	171	70.94	-167.05
CH-K01	177	70.94	-168.54
CH-K03	167	70.95	-165.55
Mid15	156	70.99	-161.84
Mid14	151	71.02	-159.23
CH-K07	150	71.07	-159.19
CH-L01	180	71.43	-168.5
CH-L03	228	71.43	-165.45
CH-L06	237	71.44	-160.63
CH-L08	251	71.44	-157.45
CH-L04	229	71.46	-163.91
CH-L02	222	71.49	-167.12
CH-L07	254	71.5	-159.26
CH-M03	188	71.94	-165.37
CH-M01	217	71.94	-168.53
CH-M07	243	71.94	-158.8
CH-M08	248	71.94	-157.19
CH-N02	209	72.32	-166.83
CH-N03	205	72.43	-165.2
CH-N01	214	72.45	-168.49
CH-N05	197	72.51	-162.82

Appendix Y.

Capelin (*Mallotus villosus*) Genetics in the Alaskan Arctic

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Date

November 28, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game
DNA	deoxyribonucleic acid
mtDNA	mitochondrial DNA
PCR	polymerase chain reaction
GOA	Gulf of Alaska

List of Oral and Poster Presentations

None

Proposed Objectives and Study Chronology

Objectives

The primary objective of this project was to examine the genetic structure of capelin (*Mallotus villosus*) in the waters surrounding northern Alaska: the Bering Sea, Chukchi Sea, and Arctic Ocean. The second objective was to compare the genetic structure of capelin from the Arctic and Gulf of Alaska. The data gathered from these samples will form the initial genetic baseline of the Arctic region that can be used to monitor stock structure over time.

Study Chronology

In 2005, we began genetic analysis of capelin in the Gulf of Alaska with microsatellite (Msat) markers. We submitted a proposal to BOEM in 2011 to expand capelin genetic studies to the Arctic. Arctic capelin samples were first received September 2012. After the samples were processed in late 2012, they were shipped to the AFSC, Seattle, for ageing studies. Optimization of the capelin microsatellite markers on the ABI 3130*xl* DNA Analyzer was completed by mid-2013. DNA was isolated and genotypes of the 2012 samples were generated in late 2013. Samples collected in the 2013 survey were received in October 2013. Tissue samples were processed, DNA was isolated, and microsatellite genotypes were generated in 2014. Microsatellite data analysis began in 2015. An opportunity to obtain mitochondrial DNA (mtDNA) information on the samples arose and a subset of samples was sequenced, with the data added to the emerging report. The report was finalized in November 2016. Microsatellite genotypes and mtDNA haplotypes accompany this report as supplemental material.

Abstract

The conclusions of this study are based on a survey of microsatellite markers and mtDNA sequences of capelin in northern Alaskan waters. Non-spawning adult capelin were collected from the northeastern Bering Sea, Chukchi Sea, and Arctic Ocean near Barrow, Alaska in 2012 and 2013 (N=1600). Data from 192 Gulf of Alaska capelin from a previous study were added for comparison. Data were obtained from 16 microsatellite markers, and a subset of individuals was sequenced at the cytochrome b region of the mtDNA (N=300). Genetic differentiation was not detected geographically or temporally among the collections of Arctic samples, however, significant departure from Hardy-Weinberg proportions was observed at 7 of the 16 microsatellite loci after correction for multiple tests in the Arctic population as a whole. Further, a log likelihood of data partitioned into two theoretical groups by STRUCTURE, indicated that the tails of the distribution, half of the samples, had a high (75-95%) individual assignment to one of the two partitioned populations. Distribution of allele frequencies were not a smooth or unimodal distribution in half of the loci examined. These indices suggest weak structure among capelin in the Arctic, or remnants of past structure, which may now be introgressing. Comparison with Gulf of Alaska (GOA) samples confirms a previously described historic divergence of mtDNA between the GOA and the Arctic, and examination of nuclear loci from this study indicate the divergence is contemporary.

Introduction

Capelin *(Mallotus villosus)* is a major forage species, providing an ecological link between upper and lower components of the food web. Capelin is found in the circumpolar north, distributed approximately above the 15°C thermocline in the Pacific, and is important to a wide variety of marine organisms, including marine mammals (Sinclair & Zeppelin, 2002; and Womble & Sigler, 2006), predatory fish (Rose & Rowe, 2015) and birds (Thayer et al, 2006; Jodice, et al., 2006; Sinclair et al, 2008; and Davoren et al, 2010).

Capelin respond quickly and consistently to temperature changes and hence act as an early warning sea 'canary' for changes that may also affect other species and the ecosystem (Rose, 2005). Capelin require a narrow temperature range of 2-10°C for maturation. Small changes in temperature (as little as 1°C) can result in large scale distribution shifts of hundreds of kilometers in a single year, and would directly impact the many species that feed on this keystone fish (Rose, 2005). The temperature related shift in capelin in the Atlantic affected specifically weight, abundance and recruitment variation in cod, but also shifts in distribution of salmon, halibut, seabirds and marine mammals (Rose, 2005; Drinkwater, 2006; Hjermann et al, 2007; Burke, 2008; Wilhelm et al, 2008; Burke & Montevecchi, 2009; Orlova et al., 2009; Regular, 2009; and Rose & Rowe, 2015). It is one of the few truly circumpolar species (Vilhjalmsson, 2004) and has been used as a key indicator for an ecosystem based research program in the northwest Atlantic (Davoren, 2007) and as a model for climate change analysis in the Atlantic (Huse & Ellingsen, 2008).

There is a general recognition that a long term ocean climate shift in the Gulf of Alaska has been partially responsible for the observed reorganization of the community structure and a decline in capelin abundance in Alaskan waters (Anderson & Piatt, 1999; Yang, 2004). Periods of high adult capelin abundance have been linked to a cold phase in the oceanographic environment of Alaska (Doyle et al., 2002; Mueter & Norcross, 2002; Logerwell, 2006; Logerwell, et al., 2007), and proximity to tidewater glaciers and those areas distinguished by lower temperature (Arimitsu et al., 2008).

In the Atlantic, two spawning strategies are utilized by capelin: beach spawners are thought to be iteroparous (multi- season spawners), while offshore spawners are semelparous (death of both genders after a single spawning event) (Christiansen et al, 2007), and patterns of larval emergence at demersal sites are different from those reported for beach spawners (Penton & Davoren, 2008). Spawning in the Gulf of Alaska is thought to be primarily on sandy beaches (Dodson et al., 1991) at temperatures of 5-9° (Pahlke 1985), with the peak of spawning around Kodiak Island in June-July (Doyle, 2002).

Previous circumpolar wide genetic studies indicate that strong population structuring of capelin likely exists in the waters around the state of Alaska, yet no comprehensive genetic studies have yet been reported for the Gulf of Alaska, Bering Sea, Chukchi Sea, and Arctic Ocean. Population structure of capelin stocks in the Atlantic Ocean have been genetically elucidated as early as 1976 (Payne), and numerous studies have followed (Birt et al., 1995, Dodson et al., 1991 & 2007, Praebel et al., 2008, and Kenchington et al., 2015). The cytochrome b (cyt-b) gene in mitochondrial DNA was used to identify four distinct genetic clades of capelin: the northeast and central Atlantic Ocean, northwest Atlantic Ocean, Arctic

Ocean, and North Pacific Ocean (Dodson et al., 2007). The present geographical isolation of the four clades, apparently maintained over many glacial cycles, may warrant species status. The Arctic clade includes the Arctic Ocean and Bering Sea, and the north Pacific clade encompasses the Gulf of Alaska. The mtDNA variation in the Dodson (et al., 2007) study indicated some genetic structuring within both clades, particularly in the north Pacific clade. The mtDNA (maternal) variation provides a view of historic divergence, whereas nuclear variation (both parents) can provide insight into stock structure on a more recent time scale. The application of nuclear markers is warranted to detect current restricted areas of sympatry or introgression. Because the Pacific Rim experienced less change in environmental conditions, due to refugia (Stergiou, 1989), and some immature ocean Atlantic capelin often migrate to feeding grounds, while other local populations complete their entire life cycle in nearshore waters and fjords (Praebel et al., 2008), we hypothesize that there are multiple, capelin stocks in Alaskan waters. The primary objective of this study is to genetically analyze capelin collected in Alaskan Arctic waters, including the northern Bering Sea and Chukchi Sea. A second objective is to quantify the extent of introgression of Bering Sea and Gulf of Alaska capelin. This is the first comprehensive population genetic study of capelin done in Alaska.

Methods

Sample Collections

Non-spawning adult capelin were collected by midwater and surface trawls from the northeastern Bering Sea, Chukchi Sea, and Arctic Ocean near Barrow, Alaska in 2012 and 2013 (Table 1, Fig. 1). Approximately 150 fish per haul were retained (or collections of fish over several hauls in an area, such as Norton and Kotzebue Sounds). Whole fish were frozen at sea. Lengths and weights were obtained in the laboratory, and a fin clip and piece of heart tissue were extracted for genetic research. Extracted tissue was preserved in 95% ethanol.

Table 1. Collections of capelin including year, latitude, longitude, number of microsatellite genotypes, number of mtDNA sequences, and mean fork length (mm). Values from regions are in bold.

Area of Collection	Year	Latitude (N)	Longitude (W)	Number msats	Number mtDNA	Mean length (mm)
Nunivak Island (Haul 157)	**2012**	**61.98**	**-169.01**	**142**	**144**	**10.44**
Norton Sound	**2012**			**143**	**0**	**9.90**
Haul 130		64.51	-167.05	15	0	8.03
Haul 131		64.52	-168.01	24	0	10.4
Haul 138		63.97	-166.98	48	0	9.45
Haul 140		63.48	-168.00	12	0	11.96
Haul 141		63.50	-167.12	44	0	9.89
Bering Strait (Haul 153)	**2013**	**65.00**	**-168.97**	**153**	**0**	**9.4**
Kotzebue	**2012**			**146**	**0**	**8.92**
Haul 18		67.49	-164.59	78	0	9.02
Haul35		68.54	-167.14	68	0	8.77
Kotzebue (Haul 17)	**2013**	**67.01**	**-166.00**	**116**	**0**	**6.40**
Cape Lisbon (Haul 43)	**2013**	**69.06**	**-165.68**	**134**	**0**	**7.80**
Point Lay (Haul 50)	**2013**	**69.51**	**-164.18**	**143**	**0**	**6.70**
Chukchi Sea	**2012**			**146**	**0**	**9.08**
Haul 86		70.97	-165.47	47	0	8.97
Haul 88		70.98	-167.00	49	0	9.12
Haul 93		71.47	-168.49	50	0	9.15
Icy Point (Haul 75)	**2013**	**70.52**	**-161.04**	**164**	**0**	**9.50**
Point Barrow (Haul 123)	**2012**	**71.48**	**-157.46**	**134**	**145**	**7.23**
Barrow_juv (Haul 106)	**2013**	**71.00**	**-159.35**	**146**	**0**	**6.20**
Kodiak - GOA	**2007**			**190**	**40**	
station 52		55.52	-157.2	95	40	
station 26		57.03	-152.31	95	0	

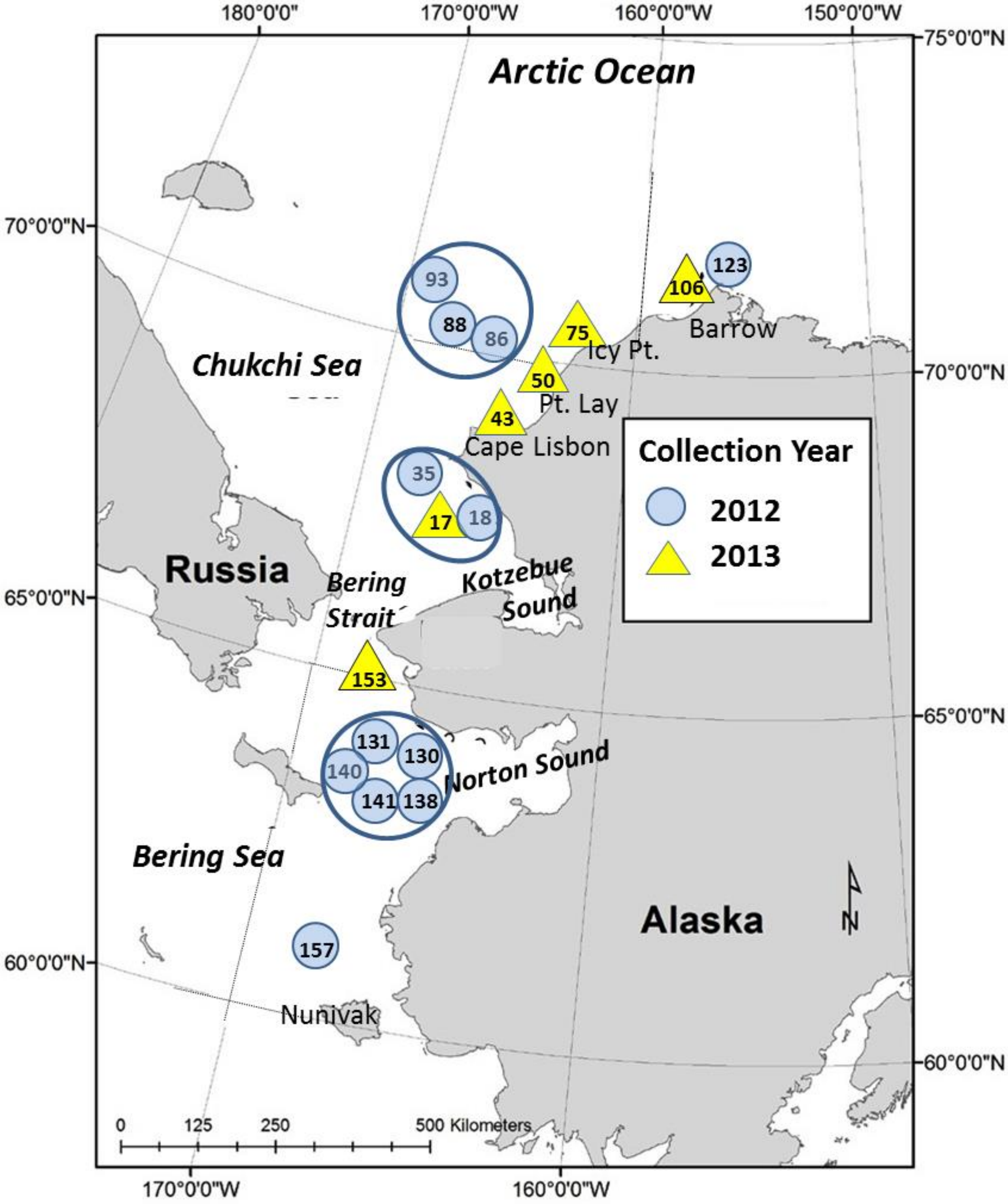

Figure 1. Locations of capelin collected in 2012 and 2013. Haul numbers are noted within circles and triangles, and correspond to information in Table 1. Several hauls were grouped as shown (circled) to provide a more robust sample size for some analyses.

Data collection

DNA was extracted from 1,610 tissue samples by using Qiagen DNeasy[9] Tissue kit protocols. Genetic data was obtained from 16 microsatellite loci and surveyed for signals of population structure in the 11 regional collections (Table 1). Individuals missing data from more than four loci were removed from analyses. Sequential Bonferroni correction was applied to analyses with multiple tests. Sequence data from the cyt-b mtDNA gene was used to confirm species identification and examine historic demography on a subset of samples (Table 1.) Genetic data (both Msat and MtDNA) of 192 Gulf of Alaska capelin from a previous unpublished study were added for comparison.

Microsatellite analysis

Microsatellite fragments data were obtained at 16 loci designed in previous capelin studies (Gordos et al., 2005; Roed et al., 2003; Table 2). Ten µl PCR reactions were made with 10 ng DNA, 0.2 µM unlabeled primer, 0.2 µM labeled primer, Master Mix 2x, and RNase free water (Qiagen). The PCR reactions were subjected to thermal cycling on a GeneAmp® 9700 (Applied Biosystems) under the following conditions: 95°C for 15 min, 28 cycles of amplification (94°C for 30 sec, annealing temperature (depends on the suite of loci) for 90 sec, and 72°C for 60 sec), final extension cycle of 60°C for 30 min, and a holding temperature of 15°C. Amplified microsatellite fragments were analyzed on a 16 capillary ABI 3130xl DNA Analyzer (Applied Biosystems (AB), and alleles were determined with Genemapper 5.0® (AB) software.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Capelin were not collected from a spawning event, thus, the data were analyzed in several ways: 1) All 1,610 individuals as one large group, and 2) samples grouped by haul or groups of hauls in a geographic region, and year of collection (Table 1, Fig. 1). A third set of analyses included samples from two capelin collections from Kodiak Island in the Gulf of Alaska, to serve as geographic and genetic outliers.

Table 2. Microsatellite loci examined in this study. Locus name, the number of alleles detected in the arctic collections, allele size range, the repeat type, source, and primer sequences. See Appendix for Gulf samples. Sources are: 1=Roed et al., 2003; 2=Gordos et al., 2005.

locus	# alleles	size range	repeat	source	5'-3' Forward Primer	5'-3' Reverse Primer
Mav9	40	172-252	2	1	ATGTGTGAGGCCAGAGCAGT	CCCACACCTGAGACAGACC
Mav17	15	198-232	2	1	GGGCAAAGCATTGTCTGA	ATCATTCCTGAGGGCTACAG
Mav38	16	127-157	2	1	GCAACATGACAGGACTCGTT	GGGCAAGGCTAAAGAAGAAA
Mav42	13	101-127	4	1	GCATAGTGTCCTGAATGATG	GTGACACTTTGCTTGGAG
Mav51	25	146-201	2	1	TGATAGTCTGGGAGGTTTGG	GGGTGGGCGTCGTTT
Mav56	53	83-194	2	1	CCCCAGCCTCCCTCAG	CCTTTACCCAGAGTCACCAT
Mav62	29	105-190	2	1	CAAGTGTGCTGGGATGAAGA	ACGCTGCAGGAGTCCAAC
Mav81	11	117-139	2	1	ATGTGAGACACGCATACACT	TGTGCAAACCAGAATGAAT
Mav135	18	81-121	2	1	GACGTCACTCCCGCAAGG	CAGCGTTACCAGGCAAATCC
Mvi1	56	100-228	2	2	CTGAGACTGTCTAGTATGCTG	CACTGCTATATCAAAAAGGCTCA
Mvi2	82	118-341	2	2	ATTCCTGACAAGAGTCTGTATCC	ATGTTGGAGGAGCTGTGAGG
Mvi3	20	139-221	4	2	CTTCCTATCAAGCGCATTAAGA	CCCCCAAAACTACTCTCTTCA
Mvi5	18	83-151	4	2	GTTTCAGAATGTTCCTCAAGAT	TTTGTCCTGAATTTCCCTACA
Mvi9	75	77-261	2	2	GACAGTCCTGCATTCGTCTG	GTCGTGTTTCTGTTTGCCTGT
Mvi16	110	137-419	2	2	CAAAGTAGGGGTGTATAACTGAAT	CTGATTGAAAGCCACAGGG
Mvi22	48	104-308	4	2	CATACCCTAACTATTAAGTGTGAACA	GCTGGAGCAACTTCATTCAG

Allele and genotype frequencies were estimated and expected Hardy-Weinberg (HW) proportions were calculated for each of the 16 microsatellite loci in GENEPOP 4.0 (Rousset, 2008) with Markov chain parameters of 10,000 dememorization, 200 batches and 50,000 iterations. Gene diversity was estimated by examining the expected level of heterozygosity in

GENEPOP 4.0. Allelic richness and number of private alleles (alleles unique to a group of samples) were calculated in HP-RARE 1.0 (Kalinowski, 2005). Allelic richness is the unbiased estimate of number of alleles per locus using rarefaction to account for uneven sample sizes (Hurlbert 1971; Smith and Grassle 1977; and Leberg 2002). Loci were also examined for linkage disequilibrium in both GENEPOP 4.0 and Genetix 4.05 (Belkhir, 2004). Graphs of the distribution of allele frequencies by locus were created in Excel®.

Population structure was explored in several ways. Genetic differentiation among pairwise temporal and spatial samples was analyzed with G-tests (GENPOP 4.0), F^{ST} (F-STAT 2.9.3, Goudet, 1995; 2001), and D^{est} (Jost, 2008) implemented in the software SMOGD vs. 2.6. (Crawford, 2010). Principal component analyses were computed from genotypes of Arctic capelin collections, Arctic individuals, Arctic and GOA collections, and Arctic and GOA individuals (1,604 arctic samples and 153 GOA samples) in Minitab 17 (Minitab Inc.). Because samples were collected from non-spawning fish, it is possible that sample collections are comprised of a mixture of spawning stocks, thus, samples were also partitioned into groups of genetic similarity independent of sampling location by using the model based clustering method in STRUCTURE (Pritchard et al., 2000). This software partitions individual fish to a pre-identified number of genetic groups based on a cluster algorithm to maximize estimations of both Hardy-Weinberg and linkage equilibrium. Clustering was performed with 1 to 10 populations to test overall population structure.

mtDNA

A subset of individuals (Table 1) were sequenced at the cyt-b region of the mtDNA with the primers: F: 5’ CATTTCAATCTGGTGAAACT and R: 5’ GGGTGTTCTACTGGCATTCC. Fragments were amplified by PCR in a 50-µL reaction volume containing 1X GoTaq Buffer (Promega Corp., Madison, WI), 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.2 µM each of forward and reverse primer, 1 unit of Flexi DNA polymerase (Promega), 10 ng sample DNA, and deionized water. Thermal cycling conditions were as follows: 95°C for 2 min; 30 cycles of amplification (95°C for 40 sec, 55°C for 40 sec, and 72°C for 1 min); 72°C for 7 min; and 4°C indefinitely. Forward sequences were obtained from the PCR product by the Sanger sequencing method. Sequences were aligned and edited with the software program CodonCode Aligner, vers. 3.7.1 (CodonCode Corp., Dedham, MA). Ambiguous end regions of cyt-b DNA sequences, particularly on the 3’ end, were trimmed to 650 bp in length to maximize the number of high-quality sequences. From the mtDNA sequences, the following genetic indices were calculated in Arlequin, vers. 3.5 (Excoffier and Lischer, 2010): the number of polymorphic sites (S), average nucleotide diversity (π), haplotype diversity (H), and Tajima’s (1989a and 1989b) test for neutrality (D).

The number of nucleotide differences between sequences was visually represented by a haplotype network (minimum spanning tree) created with the program Sneato, vers. 2 (Wooding, 2004; http://user.xmission.com/~wooding/Sneato/). Phylogenetic relationships among unique mtDNA haplotypes were evaluated with the program MEGA 6 (Tamura et al., 2013), wherein a tree was constructed with the neighbor-joining (NJ) method (Saitou and Nei, 1987) using the distance algorithm of Tamura and Nei, (1993). Support for nodes of the tree was evaluated with 1,000 bootstrap replicates (Felsenstein, 1985). The number of substitutions per site between all unique sequences was examined with the Tamura and Nei (1993) model.

Results

Arctic collections

The 16 microsatellite loci had different levels of polymorphism. The number of alleles per locus in the Arctic capelin ranged from 11 in *Mav81* to 110 in *Mvi16* (Table 2); the overall level of observed heterozygosity was 0.77 and ranged from 0.10 in *Mav81* to 0.95 in *Mav56* (Appendix 1). Significant departure from HW proportions was observed at 7 of the 16 loci after correction for multiple tests in the Arctic samples as a whole (Table 3). Of the 7 loci that departed from HW proportions, *Mvi16* and *Mvi9* exhibited high F_{IS} values (0.20 and 0.18), indicating excessive homozygosity; *Mav135*, *Mav81, Mav42* had moderately high F_{IS} values (0.04-0.06); and *Mav51* and *Mav56* had low and neutral F_{IS} values (0.01 and 0) (Appendix 1). An additional 6 loci also had an excess of homozygotes (*Mav 17, Mvi22*, *Mvi5, Mav9, Mvi2, and Mvi1*), although the departure from HW proportions was not significant.

Samples partitioned into the 11 geographic/temporal collections and analyzed at 16 loci revealed two loci that consistently departed from HW proportions: *Mvi9* (8 out of 11 collections) and *Mvi16* (10 of the 11 collections). This departure is indicative of the presence of null alleles caused by a variant at one of the primer sites. Thus, in the case of *Mvi16,* one allele is likely missing in more than half of the samples. *Mvi9* has a similar, but less severe pattern.

After correction for multiple tests, and omitting the two loci with possible null alleles, three tests by collection exhibited significant departure from HW proportions. Two of these departures occurred at *Mvi22* and *Mav51* in the Pt. Lay collection, and the third at *Mav81* in the Kotzebue 13 collection (Table 3).

Table 3. P-values for tests Hardy Weinberg equilibrium at 16 microsatellite loci for 11 capelin collections (Table 1), and all Arctic samples examined as one collection. Significant P-values after Bonferroni correction for multiple tests, P<0.0003, are denoted in bold.

Collection	*Mav135*	*Mav56*	*Mav17*	*Mvi22*	*Mvi5*	*Mvi16*	*Mav81*	*Mav9*	*Mvi9*	*Mav38*	*Mvi2*	*Mav51*	*Mav42*	*Mvi3*	*Mav62*	*Mvi1*
Nunavak12	0.1060	0.0137	0.2211	0.2897	0.3398	0.0042	0.0022	0.1323	**0.0000**	0.7808	0.1055	0.1187	0.1371	0.2065	0.5615	0.4866
Norton12	0.6119	0.1504	0.2683	0.8823	0.3679	**0.0000**	1.0000	0.0286	**0.0000**	0.4035	0.5829	0.2389	0.4539	0.4150	0.2311	0.4524
Kotzebue12	0.7872	0.0054	0.5623	0.2250	0.7537	**0.0000**	1.0000	0.4441	**0.0003**	0.0621	0.3183	0.3352	0.0219	0.2256	0.2393	0.5030
Chukchi12	0.0026	0.0817	0.1468	0.0124	0.1673	**0.0002**	0.6209	0.4578	**0.0000**	0.5161	0.2417	0.3303	0.0043	0.4868	0.8958	0.0799
Barrow12	0.6178	0.0396	0.0672	0.0653	0.1987	**0.0000**	0.1348	0.6307	0.0062	0.9359	0.0952	0.5196	0.2024	0.3851	0.7055	0.9482
Bering Strait13	0.7103	0.0871	0.3290	0.1539	0.1093	**0.0000**	1.0000	0.3867	**0.0000**	0.8687	0.6807	0.0373	0.0221	0.5099	0.7769	0.8365
Kotzebue13	0.6496	0.1203	0.4251	0.7413	0.2584	**0.0000**	**0.0002**	0.0690	0.0035	0.6106	0.2355	0.6701	0.2995	0.9171	0.8150	0.2237
CapeLibson13	0.3934	0.4780	0.4000	0.1480	0.4589	**0.0000**	1.0000	0.4577	**0.0001**	0.4102	0.4256	0.3005	0.0836	0.1402	0.9082	0.0328
Point Lay13	0.1098	0.0218	0.1753	**0.0000**	0.5633	**0.0000**	0.1493	0.1717	**0.0001**	0.0492	0.1809	**0.0002**	0.5181	0.0874	0.3511	0.1623
Icy Point13	0.7676	0.3420	0.2668	0.9463	0.4108	**0.0000**	1.0000	0.1213	**0.0000**	0.9545	0.0425	0.0769	0.1534	0.5186	0.2936	0.3912
Barrow13	0.0577	0.2146	0.4163	0.0831	0.0042	**0.0000**	0.3543	0.5949	0.0182	0.6670	0.0327	0.0810	0.6486	0.9689	0.5036	0.4767
All Arctic	**0.0007**	**0.0000**	0.0907	0.1665	0.0691	**0.0000**	**0.0000**	0.0223	**0.0000**	0.4255	0.1631	**0.0000**	**0.0002**	0.3756	0.5785	0.3933

Linkage disequilibrium was detected between eight of 240 locus pairs, each in a single, different collection, which suggests that the loci assort randomly. Allelic richness was similar across collections; after standardization for sample size, allelic richness over 16 loci ranged from 3.29 to 42.36 alleles with an average of 25.7 alleles (Appendix 1).

Genetic differentiation was not detected geographically or temporally among the collections of Arctic samples. None of the pairwise G-tests were significant after Bonferroni correction for multiple tests (Table 4). F_{ST} values, ranging from zero to 0.001, mirrored the G-test results (Table 4). D_{est} values, a divergence measure more suitable for highly allelic microsatellite loci, also indicated a low level of genetic differentiation among the Arctic collections (Table 5).

Table 4. Pairwise G-tests of 11 collections, 14 loci. P-values are above the diagonal. F_{ST} values are below the diagonal.

	Nunav 12	Norton 12	Kotzeb 12	Chuk 12	Barro 12	Bering 13	Kotzeb 13	Lisbon 13	P. Lay 13	Icy Pt. 13	Barrow 13
Nunavak12		0.018	0.318	0.209	0.107	0.464	0.509	0.338	0.421	0.302	0.418
Norton12	0.0010		0.089	0.002	0.045	0.172	0.135	0.117	0.091	0.030	0.045
Kotzebue12	0	0.0007		0.135	0.097	0.599	0.196	0.376	0.542	0.300	0.817
Chukchi12	0.0003	0.0010	0.0008		0.046	0.033	0.035	0.102	0.305	0.042	0.129
Barrow12	0.0002	0	0.0001	0.0004		0.015	0.193	0.246	0.032	0.150	0.016
Bering Str. 13	0.0001	0.0008	0	0.0009	0.0006		0.216	0.703	0.443	0.528	0.790
Kotzebue13	0.0009	0.0004	0.0012	0.0011	0.0002	0.0004		0.563	0.305	0.422	0.059
C. Libson13	0.0001	0	0	0.0007	0	0	0.0004		0.087	0.839	0.648
Point Lay13	0.0001	0.0001	0	0.0005	0.0001	0	0.0003	0.0001		0.685	0.638
Icy Point13	0	0.0004	0.0004	0.0005	0.0001	0	0	0	0		0.820
Barrow13	0	0.0005	0	0.0004	0.0004	0	0.0008	0	0	0	

Table 5. Pairwise D_{est} of 11 collections, 16 loci above the diagonal/14 loci (minus null alleles) below the diagonal.

	Nunav 12	Norton 12	Kotzeb 12	Chuk 12	Barro 12	Bering 13	Kotzeb 13	Lisbon 13	P. Lay 13	Icy Pt. 13	Barrow 13
Nunavak12		0.001	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000
Norton12	0.002		0.002	0.006	0.003	0.003	0.000	0.000	0.001	0.001	0.003
Kotzebue12	0.000	0.003		0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Chukchi12	0.000	0.005	0.002		0.000	0.002	0.001	0.002	0.000	0.003	0.002
Barrow12	0.000	0.002	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000
Bering Str. 13	0.000	0.002	0.000	0.001	0.000		0.000	0.000	0.000	0.000	0.000
Kotzebue13	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.002
C. Lisbon13	0.001	0.000	0.000	0.001	0.000	0.000	0.000		0.000	0.000	0.000
Point Lay13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000
Icy Point13	0.000	0.001	0.001	0.002	0.000	0.000	0.000	0.000	0.000		0.000
Barrow13	0.000	0.003	0.000	0.001	0.001	0.000	0.001	0.000	0.000	0.000	

Principle component analyses of the Arctic fish by collection and by individual did not exhibit a geographic or temporal pattern of divergence (Fig. 2 and 3). Dispersal of Arctic individuals illustrated a broad range of variation (Fig. 3).

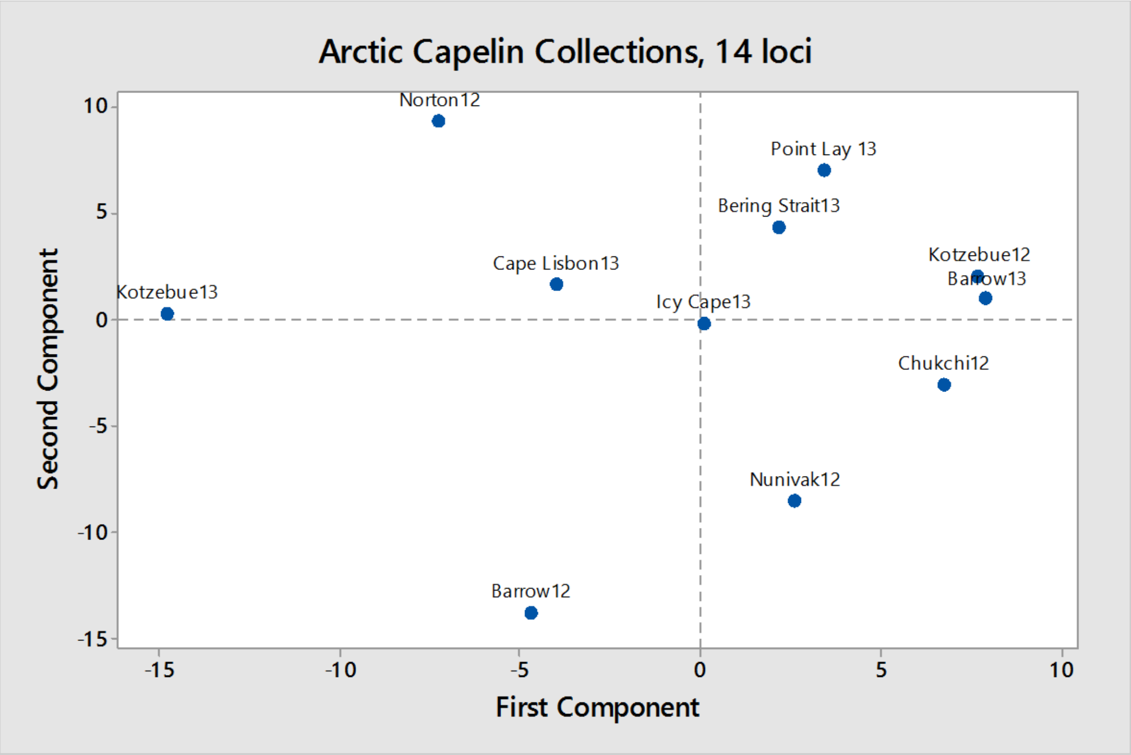

Figure 2. Principal component analysis of Arctic capelin collections based on 14 loci.

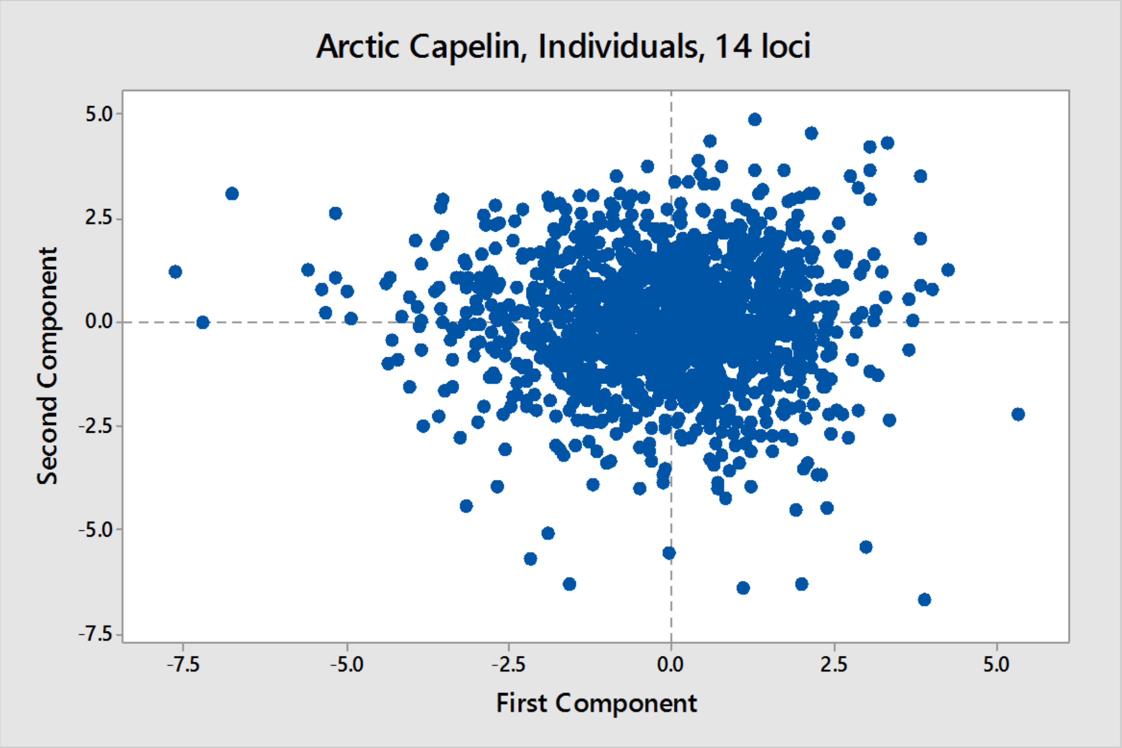

Figure 3. Principal component analysis of Arctic capelin individuals based on 14 loci.

To ascertain if the broad range of variation of individuals in the PCA was due to a mix of individuals from multiple populations, we examined the microsatellite data with the program STRUCTURE. The estimated likelihood of the samples partitioned into 1-10 populations was inconclusive (Table 5). The estimates are similar across all K values. Fig. 4 illustrates the samples partitioned into 2 populations (K=2), with most individuals associated in varying proportions of each population from 50% to 95%.

Table 6. STRUCTURE output of 1567 Arctic capelin based on 14 loci. K= the number of populations, probability of the estimated Ln, mean value of ln, and variance of the estimate.

K	est. Ln prob	mean value of ln likelihood	var of ln likelihood
1	-98,732	-98,622	220
2	-99,162	-98,432	1460
3	-99,923	-98,252	3372
4	-99,727	-98,161	3130
5	-99,677	-98,178	2998
6	-99,727	-98,152	2334
7	-101,148	-98,232	5831
8	-101,923	-98,280	7284
9	-98,828	-98,212	1231
10	-99,559	-98,307	2503

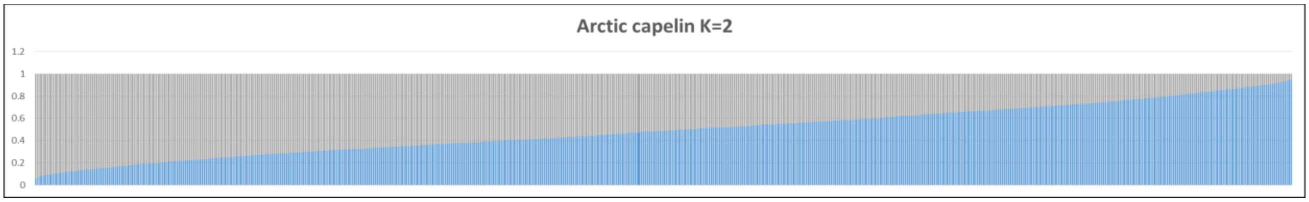

Figure 4. Proportional assignment of 1,567 individual Arctic capelin based on the clustering method implemented in STRUCTURE when two populations are postulated (k=2). Individual samples (x-axis) sorted by partitioning to 2 populations (relative proportion in gray and blue on the y-axis).

Gulf of Alaska collections

The 16 microsatellite loci surveyed exhibited a greater level of polymorphism in the capelin from the GOA than from the Arctic. The number of alleles per locus in the GOA capelin ranged from 4 alleles in *Mav81* to 76 alleles in *Mvi9* (Appendix 1) and the overall level of observed heterozygosity was 0.79, ranging from 0.02 in *Mav81* to 0.98 in *Mvi2, Mvi9,* and *Mvi16.* Significant departure from HW proportions was observed at both *Mvi16* and *Mvi9* which exhibited high F_{IS} values likely due to null alleles (Table 6). After correcting for multiple tests, and omitting the two loci with likely null alleles, five tests departed significantly from HW proportions. Four of these departures occurred in the Kodiak st. 26 collection, a number greater than expected by chance. *Mvi2* departed from HWE at both collections.

Table 7. P-values for Hardy Weinberg equilibrium tests for microsatellite data at 16 loci for 2 collections of Gulf of Alaska capelin as outlined in Table 1. Significant P-values (after Bonferroni correction for multiple tests, P<0.0015) are denoted in bold.

Collection	*Mav135*	*Mav56*	*Mav17*	*Mvi22*	*Mvi5*	*Mvi16*	*Mav81*	*Mav9*	*Mvi9*	*Mav38*	*Mvi2*	*Mav51*	*Mav42*	*Mvi3*	*Mav62*	*Mvi1*
Kodiak07 (52)	0.4509	0.1808	0.0123	0.0037	0.0153	**0.0005**	1.0000	0.9589	**0.0000**	0.2582	**0.0007**	0.0706	0.0227	0.7520	0.3746	0.0092
Kodiak07 (26)	**0.0011**	0.0116	0.2469	**0.0000**	0.0149	**0.0000**	1.0000	0.4479	**0.0000**	0.8125	**0.0000**	**0.0000**	0.0172	0.2773	0.0180	0.1668

Table 8. Pairwise G-tests of 13 collections, 14 loci. P-values are above the diagonal. F^{ST} values are below the diagonal. Significant values after correction for multiple testing is in bold.

	Nunav 12	Norton 12	Kotzeb 12	Chuk 12	Barro 12	Bering 13	Kotzeb 13	Lisbon 13	P. Lay 13	Icy Pt. 13	Barrow 13	Kodi07 st. 52	Kodi 07 st. 26
Nunavak12		0.018	0.318	0.209	0.107	0.464	0.509	0.338	0.421	0.302	0.418	**HS**	**HS**
Norton12	0.001		0.089	0.002	0.045	0.172	0.135	0.117	0.091	0.030	0.045	**HS**	**HS**
Kotzebue12	0.000	0.001		0.135	0.097	0.599	0.196	0.376	0.542	0.300	0.817	**HS**	**HS**
Chukchi12	0.000	0.001	0.001		0.046	0.033	0.035	0.102	0.305	0.042	0.129	**HS**	**HS**
Barrow12	0.000	0.000	0.000	0.000		0.015	0.193	0.246	0.032	0.150	0.016	**HS**	**HS**
Bering Str. 13	0.000	0.001	0.000	0.001	0.001		0.216	0.703	0.443	0.528	0.790	**HS**	**HS**
Kotzebue13	0.001	0.000	0.001	0.001	0.000	0.000		0.563	0.305	0.422	0.059	**HS**	**HS**
C. Libson13	0.000	0.000	0.000	0.001	0.000	0.000	0.000		0.087	0.839	0.648	**HS**	**HS**
Point Lay13	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000		0.685	0.638	**HS**	**HS**
Icy Point13	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000		0.820	**HS**	**HS**
Barrow13	0.000	0.001	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000		**HS**	**HS**
Kodiak07 (52)	**0.049**	**0.047**	**0.043**	**0.047**	**0.045**	**0.044**	**0.049**	**0.046**	**0.044**	**0.048**	**0.043**		0.024
Kodiak07 (26)	**0.052**	**0.049**	**0.045**	**0.049**	**0.047**	**0.047**	**0.051**	**0.048**	**0.045**	**0.051**	**0.046**	0.002	

Table 9. Pairwise D^{est} of 13 collections, 16 loci above the diagonal/14 loci (minus null alleles) below the diagonal.

	Nunav 12	Norton 12	Kotzeb 12	Chuk 12	Barro 12	Bering 13	Kotzeb 13	Lisbon 13	P. Lay 13	Icy Pt. 13	Barrow 13	Kodi07 st. 52	Kodi 07 st. 26
Nunavak12		0.001	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	**0.168**	**0.195**
Norton12	0.002		0.002	0.006	0.003	0.003	0.000	0.000	0.001	0.001	0.003	**0.150**	**0.177**
Kotzebue12	0.000	0.003		0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.168**	**0.191**
Chukchi12	0.000	0.005	0.002		0.000	0.002	0.001	0.002	0.000	0.003	0.002	**0.165**	**0.198**
Barrow12	0.000	0.002	0.000	0.000		0.000	0.000	0.000	0.000	0.000	0.000	**0.165**	**0.195**
Bering Str. 13	0.000	0.002	0.000	0.001	0.000		0.000	0.000	0.000	0.000	0.000	**0.157**	**0.179**
Kotzebue13	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	0.000	0.002	**0.167**	**0.177**
C. Lisbon13	0.001	0.000	0.000	0.001	0.000	0.000	0.000		0.000	0.000	0.000	**0.153**	**0.179**
Point Lay13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000		0.000	0.000	**0.161**	**0.180**
Icy Point13	0.000	0.001	0.001	0.002	0.000	0.000	0.000	0.000	0.000		0.000	**0.163**	**0.189**
Barrow13	0.000	0.003	0.000	0.001	0.001	0.000	0.001	0.000	0.000	0.000		**0.145**	**0.179**
Kodiak07 (52)	**0.131**	**0.113**	**0.132**	**0.132**	**0.129**	**0.121**	**0.133**	**0.078**	**0.126**	**0.126**	**0.109**		0.006
Kodiak07 (26)	**0.160**	**0.144**	**0.158**	**0.168**	**0.162**	**0.147**	**0.145**	**0.090**	**0.147**	**0.157**	**0.146**	0.005	

All G-tests that compared the Arctic and GOA pairs of capelin collections had highly significant P-values (Table 8). Comparison of F_{ST} and D_{est} values resulted in similar findings (Table 8 and 9), although most pairwise D_{est} values were higher than the F_{ST} values. Given the high level of heterozygosity of the microsatellite markers, it is not surprising that D_{est} is a better measure of divergence. The amount of genetic diversity was greater in the GOA samples, based on the increase in allelic richness at 12 of the 16 loci examined (Fig. 5). Allelic richness of the GOA samples, after standardization for sample size, ranged from 3.0 to 60.22 alleles with an average of 30.0 alleles. Private alleles were detected between the Arctic and GOA collections at every locus (Appendix 2.)

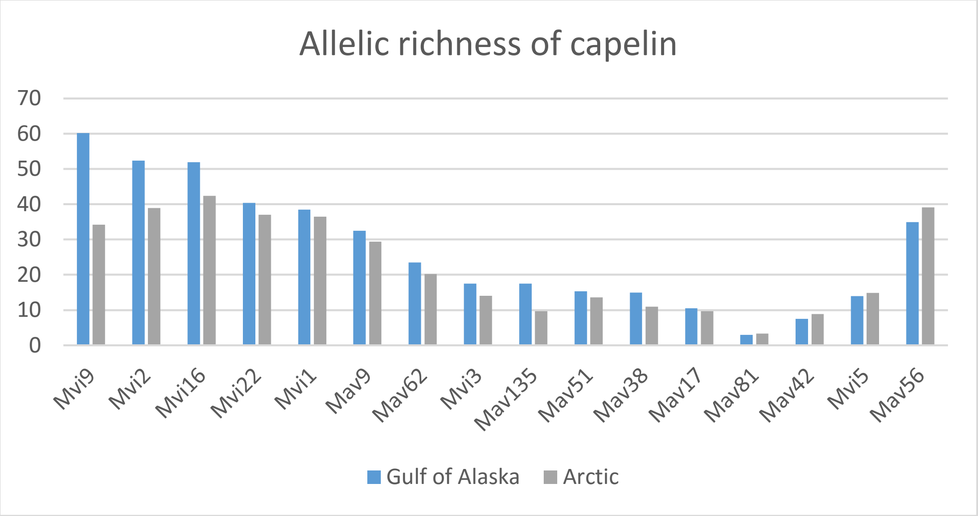

Figure 5. Allelic richness of 16 Msat markers for Gulf of Alaska and Arctic capelin.

Principal component analysis of individuals illustrates the nearly complete lack of introgression between GOA and Arctic capelin (Fig. 6). When examined by collection, the Arctic samples are highly distinct from the GOA samples by component 1, and appear distinct from each other by component 2 (Fig. 7). No geographic or temporal structure was noted within the Arctic.

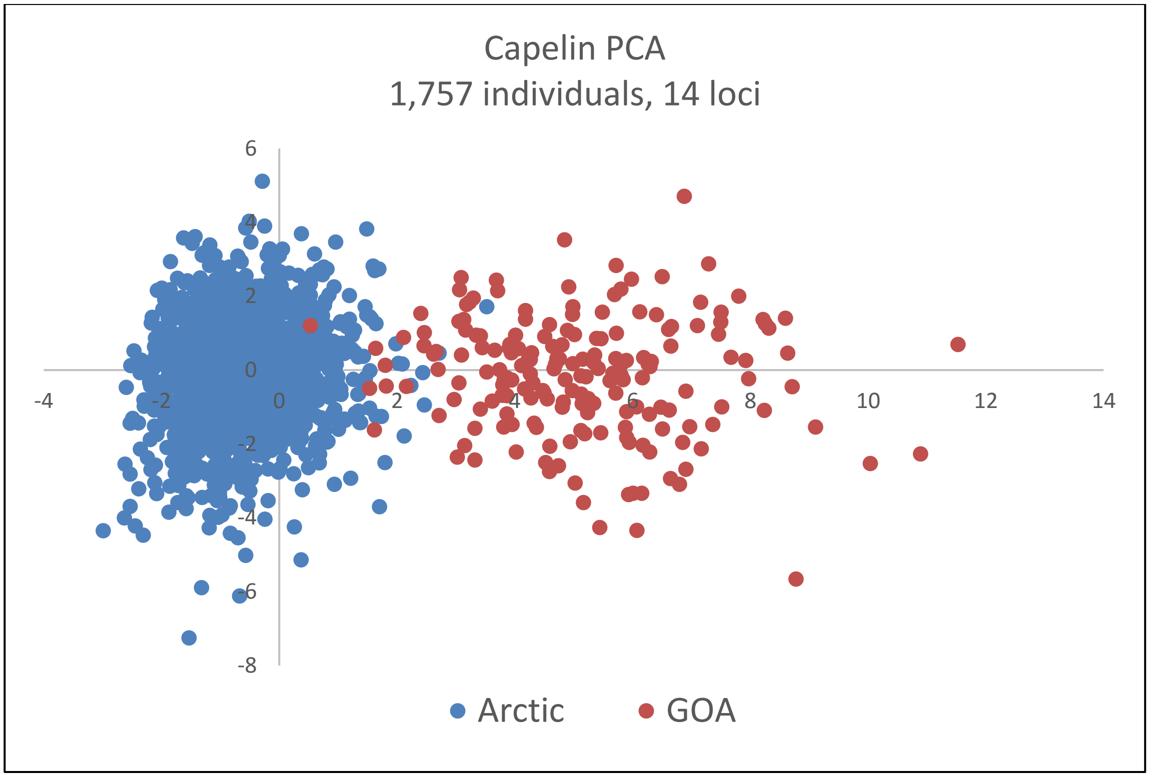

Figure 6. Principal Component analysis of capelin individuals. Arctic samples displayed as blue and Gulf of Alaska samples are in red.

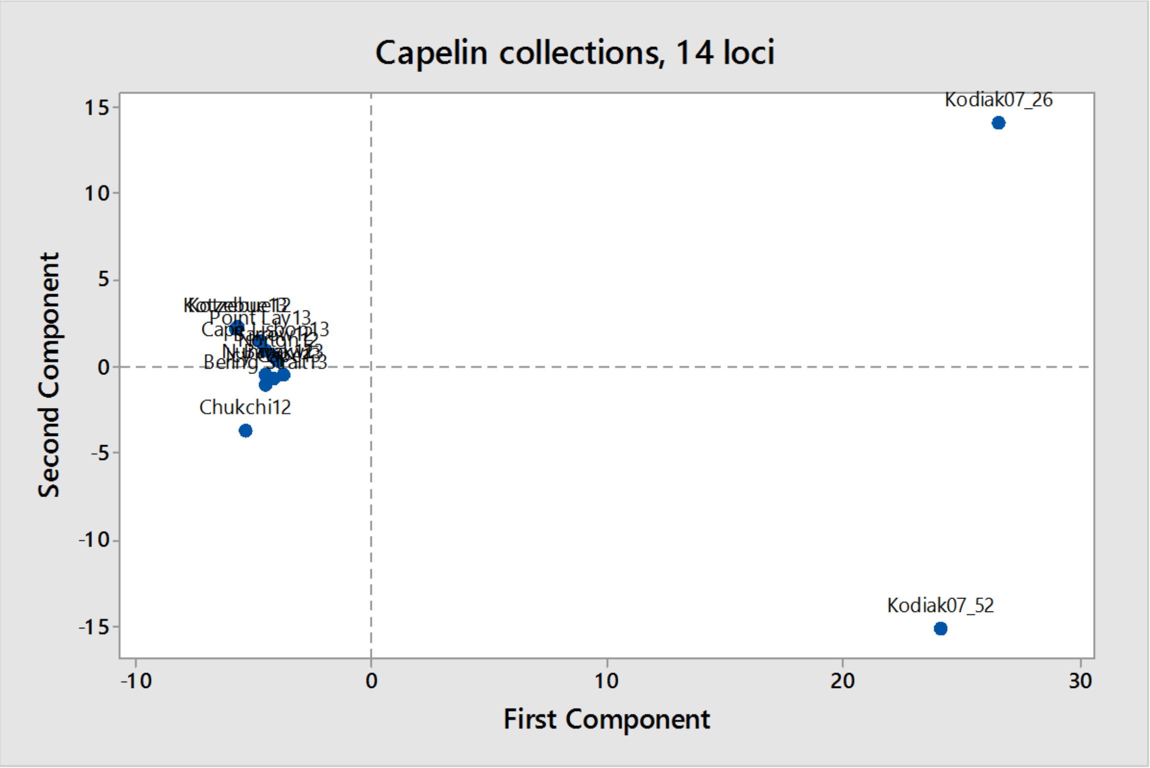

Figure 7. Principal Component analysis of Arctic and GOA (Kodiak) capelin collections.

STRUCTURE identified the GOA capelin as distinct from the Arctic capelin (Fig. 8). As before (Fig. 4), the program separated half of the Arctic fish into one of two populations with an individual assignment of 75% or greater accuracy, but was not able to clearly distinguish two Arctic populations.

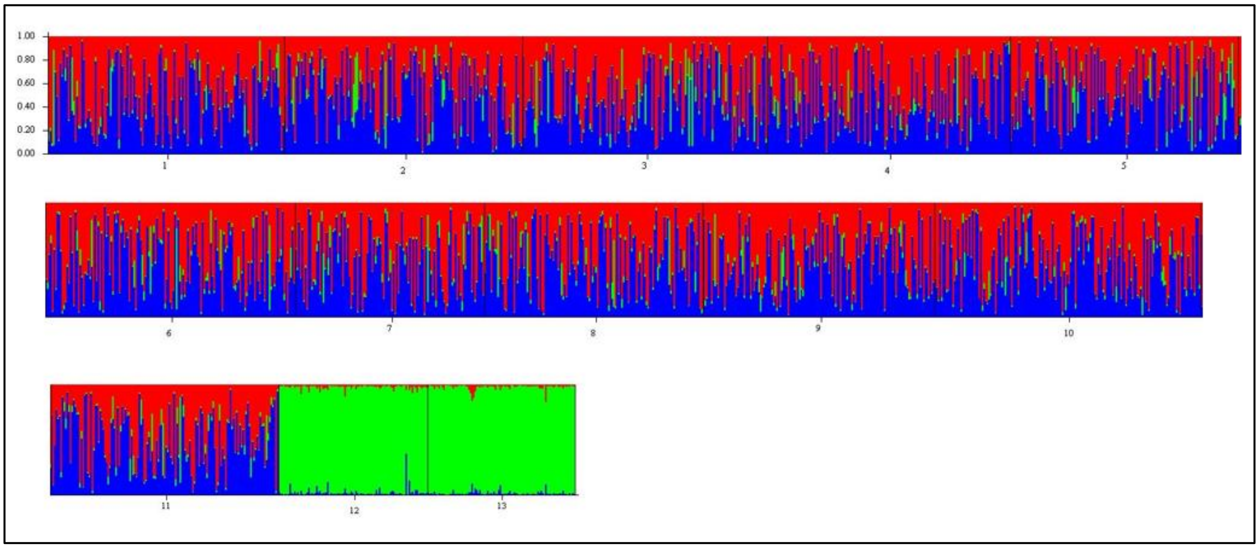

Figure 8. Proportional assignment of Arctic and GOA individuals (x-axis) based on the clustering method implemented in STRUCTURE with K=3 stock groups. The block of green samples at the end are individuals from the GOA. The Red and Blue are Arctic samples.

mtDNA analyses

Sequence information from the mtDNA cyt-b gene revealed a large divergence (12 bp or 1.8%) between the Arctic and GOA capelin (Table 10, Fig. 9, Appendix 3). As with the microsatellite data, the sequence data from the GOA samples were more variable than from the Arctic samples. The GOA samples had two times higher haplotypic diversity than the Arctic samples, H = 0.68 and 0.32, respectively (Table 10). The nucleotide diversity (π) of the GOA samples was nearly three times higher than of the Arctic samples. Less than 20% of the GOA individuals had the common haplotype; the rest of the GOA samples had haplotypes that diverged from the common haplotype by 1 to 18 base pairs. More than 40% of the Arctic samples had the same haplotype, whereas the rest of the Arctic samples had haplotypes that radiated from the common haplotype by 1 to 8 base pairs. Both areas indicated non-neutrality of samples: D = -2.661 Arctic and -1.674 GOA (Table 10). Consensus of sequences from three areas (Barrow, eastern Bering Sea, and Gulf of Alaska) are provided in Appendix 2.

Table 10. N = sample size (650 nucleotides each sample), S= # polymorhic sites (unique haplotypes), H = average haplotype diversity (S/N), π = average nucleotide diversity, and D = Tajima test for neutrality.

	N	S	H	π	D
Barrow	145	59	0.41	0.00238	-2.646
Nunivak Island	144	67	0.47	0.00281	-2.651
Arctic total	289	93	0.32	0.00260	-2.661
Kodiak Island	44	36	0.68	0.00653	-1.674

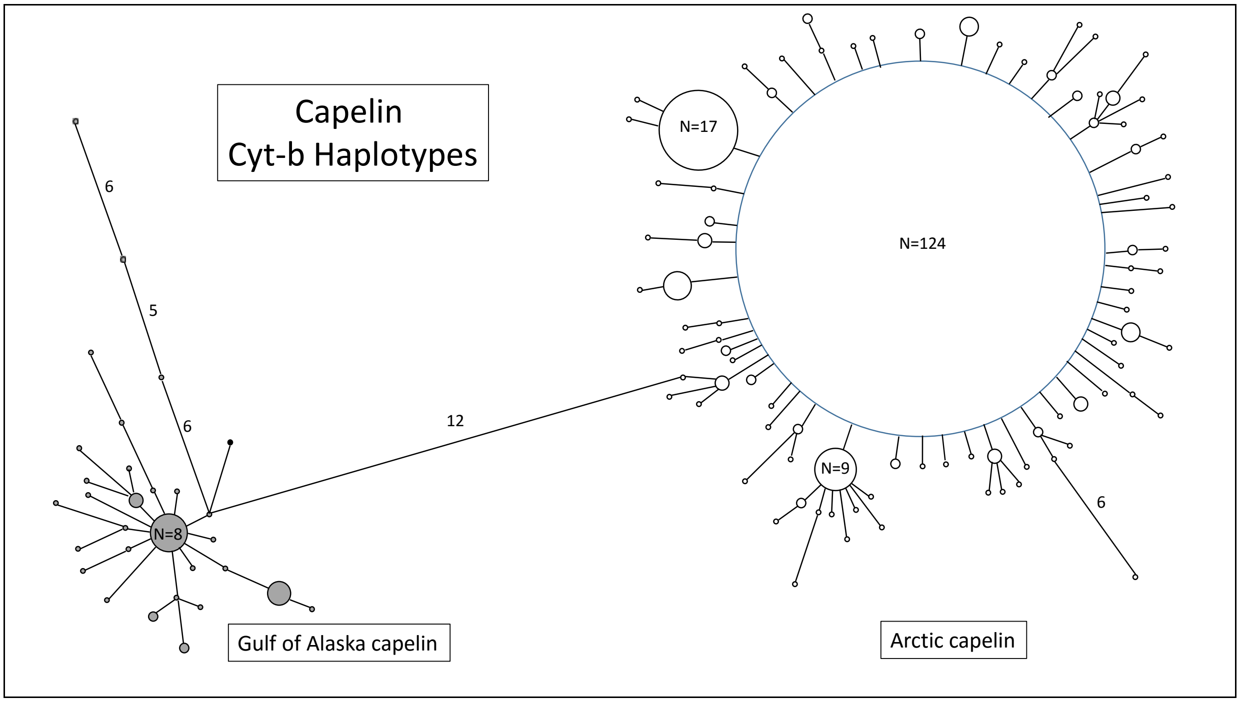

Figure 9. Network of Gulf of Alaska (N=44) and Arctic capelin (N=289) mtDNA cyt-b haplotypes. Circles size is proportional to the number of individuals (N) with the same haplotype. Lines represent a divergence of 1-3 base pairs, or more where numerically noted.

A neighbor–joining tree illustrates the large divergence between Arctic and GOA capelin that has 100% bootstrap support (Fig. 10). Several branches within the GOA area of the tree have over 80% bootstrap support (not shown), whereas the Arctic area of the tree revealed one nearly homogeneous branch.

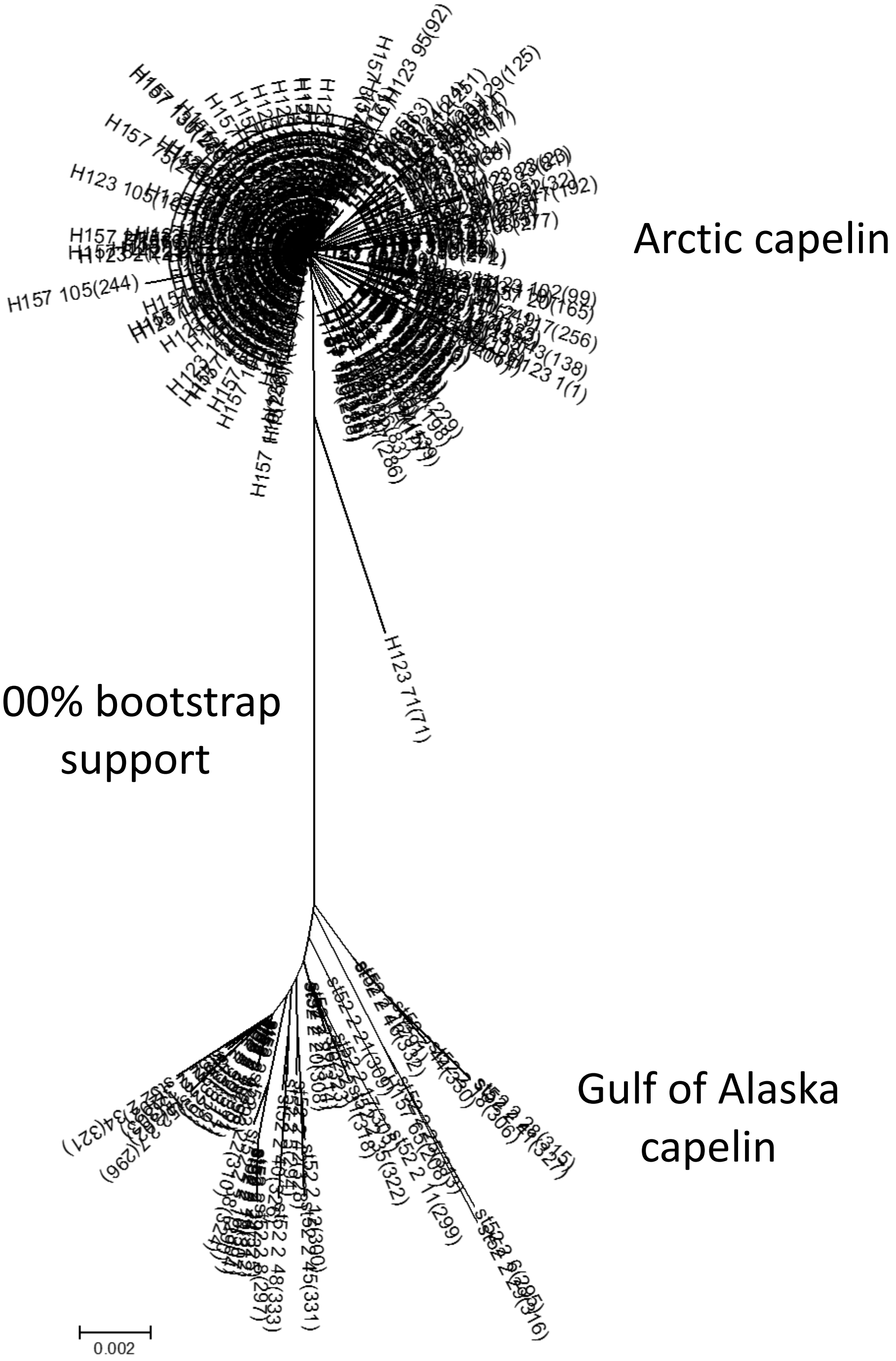

Figure 10. Neighbor–joining tree of mtDNA cyt-b sequence information of Arctic (N=289) and GOA (N=44) capelin. Each branch represents and individual.

Discussion

This is the first comprehensive population genetic study done of capelin in Alaska. The conclusions of this study are based on a survey of microsatellite loci and mtDNA cyt-b sequences of non-spawning capelin collected across the Chukchi Sea, Bering Sea, and Gulf of Alaska. The challenges in detecting population structure in pelagic species are multi-fold. In forage species, the effective population size is typically large enough that even reproductively isolated populations can be difficult to detect because the effect of genetic drift is insignificant, except on very long time scales (Kliman et al., 2008). In the Arctic, genetic variation is often reduced by bottlenecks produced during previous ice ages and after subsequent rapid expansion of population size, there can be little apparent population structure. Furthermore, spawning cohorts of capelin have rarely been collected in the vast expanse of the Alaskan Arctic, and only non-spawning fish were available for our study. Another potential obstacle to detecting population structure is the choice of genetic markers. Structure may not be detected with some genetic markers, which does not necessarily imply that structure does not exist; only that structure was not detected with the genetic markers examined.

Several pieces of evidence allow us to speculate that more than one spawning population of capelin exists in Alaskan Arctic waters. First, half of the microsatellite loci in the Arctic samples were out of HW equilibrium when samples were examined as a single collection, and the majority of loci (13/16), while not all significantly out of equilibrium, had an excess of homozygotes, which is indicative of a mixture of populations. Second, the results from the program STRUCTURE (Pritchard, 2000) produced similar outcomes among simulated populations of 1-10. Simulated clusters of the Arctic samples of K=2 included individuals with

95% assignment to a single population. When two simulated populations were inferred (K=2), individuals with an assignment of at least 75% to one population or the other were highly differentiated. Genotypes at all loci (except the two with null alleles) in each of the two groups were in HWE. A G-test of the two groups revealed highly significant differences in allele frequencies at each of the 16 loci, and over all loci combined (P=HS). Arctic cod (*Boreogadus saida*), in comparison, had a maximum assignment of < 70%, for samples to one of two simulated populations; and samples at each end of the sorted distribution were homogeneous (Wildes et al. BOEM report 2016). Third, graphs of allele frequencies illustrate that half of the loci do not have smooth or unimodal distributions (Appendix 2). If several stocks of capelin exist in Alaskan Arctic waters, the genetic evidence suggests that they disperse after spawning to forage throughout the Arctic and Bering Sea.

An alternate hypothesis is that population structure was greater in the past, and that recent fluctuating ocean temperatures have caused increased dispersal of capelin, which in turn has caused mixing of spawning stocks. If enough time has not passed for genetic equilibrium to occur after population mixing, then the broad range of variation and excess of homozygotes observed across the Alaskan Arctic region would be expected. A confounding factor is the lack of knowledge about the location and mode of spawning in Alaskan waters (beach or ocean). Research on Atlantic capelin showed genetic divergence between these two spawning modes (Dodson et al., 1991).

With much larger sample sizes and six microsatellite loci, five of which were used in our study, Ketchington (et al., 2015) found genetic divergence among NW Atlantic capelin. In their study, loci *Mvi16* and *Mvi9* had expected HW proportions; the presence of null alleles at these two loci in our study, but not in the Atlantic fish is likely due to mutation in the primer sequence. This difference indicates that the capelin in the Pacific Arctic are genetically distinct from those in the Atlantic Arctic.

Both maternally inherited mtDNA and parent–based nuclear DNA confirm that Arctic capelin are genetically divergent from Gulf of Alaska capelin (Fig. 8-10). Two geographic regions sequenced within the Arctic: Barrow in the Arctic Ocean and Nunivak in the eastern Bering Sea do not illustrate a biogeographical divergence in the mtDNA, while Kodiak in the GOA is divergent from these two Arctic collections by 12 bp, with no shared haplotypes. The deep division of the cyt-b region of the mtDNA as reported by Dodson (et al., 2007), reflects historic ice–age isolation, while examination of generationally assorting nuclear markers confirm the division is contemporary. Tajima's test for neutrality ($D = -2.661$) of the Arctic region suggests rapid population size expansion after a bottleneck. Many Arctic species exhibit evidence of a genetic bottleneck after multiple ice age isolations, followed by a rapid post-glacial population expansion. Analyses of both mtDNA and microsatellite data indicate that Arctic capelin are more genetically homogeneous than the GOA capelin. Arctic capelin had less than half of the mtDNA haplotype diversity (0.32) of the GOA capelin (0.68), and lower allelic richness of the microsatellite loci, 25.7 versus 30.0 alleles.

No mtDNA haplotypes in the GOA collections examined from around Kodiak Island were detected in the Arctic samples collected for our study or vice versa. Of high interest would be to determine if areas of sympatry of the GOA/Arctic capelin exist. Perhaps in the southern Bering Sea? Or is there biogeographical isolation between the two types? Even though the Arctic and GOA capelin share many of the same microsatellite alleles, are the two types reproductively compatible? Are they two species? Because capelin are so temperature sensitive, it is unknown whether ocean temperature changes would drive GOA capelin into the Arctic or would these individuals die off?

We conclude that genetic evidence supports weak population structure of capelin in the Arctic. A continued effort to understand stock structure of capelin, such as genetic examination of spawning cohorts, would provide valuable information of future stock shifts, and associated predator movement, as documented in the Atlantic. We also confirm that Arctic capelin are highly divergent from capelin in the Gulf of Alaska, and as such, conclude that Arctic capelin are a unique resource in Alaska.

Acknowledgements

A huge thank-you to the many collectors of samples on the BOEM crews, and to Ingrid Spies, Mike Canino (NPFSC/AFSC), Dan O'Neill (engineer FV Seastorm), and Mayumi Arimitsu (U.S. Geological Survey) for additional samples. Appreciation and thanks to Dr. Chris Kondzela (AFSC) for reviews of the manuscript. A special gratitude to Franz Mueter and Jared Weems (UAF) for coordinating this collection of studies.

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Appendix 1. Capelin (*Mallotus villosus*) information by loci, including name of locus, GENEBANK accession number, allele size range of Arctic collections (Gulf size range) and number of bp repeats. Collections: 1=Nunivak12, 2=Norton12, 3=Kotzebue12, 4=Chukchi12, 5=Barrow12, 6=Bering St.13, 7=Kotzebue13, 8=Cape Lisbon13, 9=Pt. Lay13, 10=Icy Point13, 11=Barrow13, 12=Kodiak07 St. 52, and 13=Kodiak07 St. 26. Collection sizes (N), number of alleles (NA), allele richness (NS) corrected to the smallest sample size, observed heterozygosity (Ho), Gene Diversity (expected heterozygosity) (D), and estimated inbreeding coefficient (F^{is}). Total is N across all populations. All other values in the total column are an average across all populations.

Mav9		AY291351, 2 bp repeat (CA), allele size range 172-252 (168-240)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	132	141	144	141	130	152	108	133	137	157	142	1517	95	95	190
N_A	30	31	34	30	31	28	32	32	30	32	32	40	33	32	35
N_S	28.81	29.04	31.44	28.88	30.09	26.81	31.29	30.16	27.98	29.32	29.61	29.40	33.00	32.00	32.5
H_o	0.95	0.95	0.95	0.95	0.95	0.94	0.94	0.94	0.95	0.94	0.95	0.92	0.95	0.96	0.96
D	0.950	0.946	0.946	0.949	0.948	0.940	0.942	0.942	0.948	0.944	0.947	0.946	0.952	0.958	0.955
F_{is}	0.051	0.025	0.009	0.014	0.059	0.000	0.027	0.042	0.006	0.028	0.040	0.027	-0.007	0.022	0.008

Mav17		AY291353, 2 bp repeat (GT), allele size range 198-232(170-236)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	135	140	145	141	134	152	116	134	143	164	144	1548	95	95	190
N_A	12	11	9	9	11	9	12	10	10	11	10	15	10	11	13
N_S	10.70	10.30	8.49	8.66	10.04	8.60	11.35	9.33	9.57	9.87	9.60	9.68	10.00	11.00	10.5
H_o	0.76	0.76	0.75	0.74	0.78	0.76	0.75	0.74	0.77	0.75	0.78	0.735	0.72	0.75	0.735
D	0.759	0.758	0.748	0.737	0.783	0.763	0.755	0.740	0.770	0.751	0.776	0.759	0.724	0.753	0.739
F_{is}	-0.047	0.067	0.004	0.124	0.037	-0.026	-0.005	0.042	0.037	0.099	0.016	0.032	0.142	0.091	0.117

Mav38		AY291355, 2 bp repeat (CA), allele size range 127-157 (125-161)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	139	143	145	145	127	153	116	132	143	162	146	1551	95	94	189
N_A	13	12	13	13	10	10	11	12	11	14	14	16	14	16	18
N_S	11.24	10.85	11.38	11.42	9.84	9.55	10.39	11.12	10.04	12.33	12.29	10.95	13.97	16.00	14.95
H_o	0.69	0.68	0.72	0.69	0.67	0.73	0.66	0.68	0.69	0.67	0.72	0.703	0.81	0.80	0.81
D	0.687	0.678	0.717	0.687	0.671	0.729	0.663	0.678	0.690	0.675	0.716	0.682	0.808	0.797	1.605
F_{is}	0.078	-0.021	0.029	0.026	-0.033	0.005	-0.067	-0.105	0.006	-0.061	-0.071	-0.017	0.114	0.026	0.803

Mav42		AY291356, 4 bp repeat (GT)(TA), allele size range 101-127 (105-121)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	138	141	144	146	133	151	116	132	141	162	140	1544	95	95	190
N_A	9	11	10	9	9	10	10	10	9	9	10	13	8	7	8
N_S	8.56	9.48	8.89	7.94	8.58	9.10	9.84	9.07	8.74	8.50	9.29	8.91	8.00	7.00	7.50
H_o	0.60	0.61	0.59	0.60	0.62	0.63	0.66	0.60	0.62	0.63	0.61	0.581	0.48	0.43	0.45
D	0.602	0.609	0.589	0.600	0.622	0.635	0.664	0.603	0.622	0.628	0.614	0.617	0.481	0.432	0.457
F_{is}	0.085	-0.014	-0.03	0.098	0.01	0.061	0.027	0.058	0.087	0.155	0.104	0.062	0.147	0.073	0.11

Mav51		AY291357, 2 bp repeat (CA)(TGTC)(CA), allele size range 146-201 (146-192)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	136	135	145	145	133	151	116	133	140	164	143	1541	94	87	181
N_A	14	12	17	13	15	17	15	13	15	17	17	25	16	15	17
N_S	13.21	11.61	15.33	11.86	13.15	14.66	14.34	12.18	13.89	14.39	15.18	13.62	15.62	15.00	15.31
H_o	0.83	0.81	0.85	0.81	0.81	0.83	0.82	0.83	0.84	0.84	0.84	0.759	0.83	0.83	0.83
D	0.832	0.811	0.848	0.811	0.809	0.833	0.817	0.832	0.836	0.838	0.836	0.828	0.832	0.833	0.833
F_{is}	0.099	0.069	0.08	0.099	0.071	0.157	-0.024	0.033	0.154	0.097	0.071	0.085	0.041	0.241	0.141

Mav56		AY291359, 2 bp repeat (CA), allele size range 83-194 (85-194)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	140	141	143	141	128	153	115	134	143	164	144	1546	95	94	189
N_A	44	41	47	41	42	43	39	41	41	45	40	53	36	34	41
N_S	40.38	37.87	42.80	37.27	39.21	40.37	38.07	38.75	37.42	41.04	36.86	39.09	35.89	34.00	34.95
H_o	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.94	0.96	0.94	0.954	0.96	0.96	0.96
D	0.949	0.951	0.952	0.948	0.952	0.955	0.948	0.954	0.944	0.955	0.945	0.950	0.956	0.96	0.958
F_{is}	0.029	0.016	-0.006	-0.002	-0.026	-0.020	-0.019	-0.002	0.000	-0.021	0.008	-0.004	0.02	0.058	0.039

Mav62		AY291360, 2 bp repeat (CA), allele size range 105-190 (109-136)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	135	142	144	145	132	152	111	134	140	160	144	1539	95	94	189
N_A	23	25	20	20	19	23	22	20	24	21	22	29	26	21	28
N_S	20.87	23.02	19.22	19.17	17.76	20.82	21.03	19.27	22.23	18.70	20.81	20.26	25.93	21.00	23.47
H_o	0.89	0.90	0.88	0.88	0.88	0.87	0.88	0.87	0.90	0.88	0.90	0.896	0.93	0.93	0.93
D	0.894	0.896	0.877	0.881	0.881	0.869	0.885	0.874	0.898	0.882	0.896	0.885	0.929	0.931	0.93
F_{is}	-0.019	-0.014	-0.037	-0.009	-0.058	-0.038	0.032	-0.025	0.021	-0.006	0.008	-0.013	0.026	-0.005	0.011

Mav81		AY291361, 2 bp repeat (GT), allele size range 117-139 (127-137)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	139	143	144	141	130	153	112	134	140	161	145	1542	95	95	190
N_A	5	3	3	5	6	3	5	2	5	2	2	11	3	3	4
N_S	4.05	2.66	2.66	4.56	4.92	2.62	4.70	2.00	4.04	2.00	2.00	3.29	3.00	3.00	3
H_o	0.08	0.11	0.11	0.15	0.15	0.08	0.14	0.09	0.10	0.08	0.10	0.103	0.02	0.02	0.02
D	0.084	0.113	0.106	0.154	0.151	0.082	0.144	0.086	0.103	0.078	0.105	0.110	0.021	0.021	0.021
F_{is}	0.227	-0.056	-0.052	0.030	0.085	-0.038	0.318	-0.043	0.027	-0.039	0.077	0.051	-0.003	-0.003	-0.003

Mav135		AY291365, 2 bp repeat (CA), allele size range 81-121 (85-123)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	142	143	139	145	130	153	116	134	143	164	146	1555	95	94	189
N_A	11	10	10	11	11	10	10	10	11	13	9	18	17	18	19
N_S	10.02	8.96	9.33	9.78	10.43	9.21	9.7	9.7	10.02	11.41	8.64	9.72	16.97	18	17.49
H_o	0.58	0.68	0.64	0.68	0.68	0.66	0.65	0.63	0.66	0.63	0.64	0.624	0.77	0.85	0.81
D	0.576	0.682	0.643	0.685	0.685	0.661	0.650	0.630	0.665	0.633	0.638	0.650	0.771	0.854	0.813
F_{is}	0.046	0.016	0.016	0.154	0.079	-0.047	-0.008	0.052	0.096	0.085	-0.052	0.041	0.03	0.116	0.073

Mvi1		AY686620, 2 bp repeat (GTCTCT), allele size range 100-228 (102-200)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	136	143	141	145	130	148	112	132	141	163	143	1534	95	94	189
N_A	38	44	43	42	41	40	37	41	39	40	36	56	39	38	42
N_S	34.14	39.59	37.59	37.53	37.30	36.01	35.75	37.17	36.07	36.11	33.72	36.45	38.93	38.00	38.47
H_o	0.95	0.96	0.95	0.95	0.95	0.95	0.96	0.96	0.95	0.96	0.96	0.949	0.96	0.97	0.965
D	0.949	0.961	0.948	0.955	0.953	0.954	0.955	0.960	0.954	0.956	0.957	0.955	0.963	0.967	0.965
F_{is}	-0.007	0.003	-0.018	0.025	-0.001	0.037	-0.019	0.029	0.019	0.006	-0.008	0.006	0.039	0.010	0.045

Mvi2	AY686621, 2 bp repeat (GATA)(CACA)(GATA), allele size range 118-341 (118-339)											Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	136	141	144	140	122	153	115	133	143	163	145	1535	94	95	189
N_A	47	42	42	48	44	47	40	41	44	45	48	82	50	55	70
N_S	40.58	36.89	36.73	42.00	40.41	40.64	37.23	37.22	37.65	38.09	40.67	38.91	50.00	54.79	52.40
H_o	0.95	0.95	0.95	0.95	0.95	0.96	0.95	0.95	0.95	0.95	0.95	0.922	0.97	0.98	0.98
D	0.951	0.949	0.946	0.953	0.953	0.956	0.951	0.953	0.949	0.951	0.951	0.951	0.973	0.976	0.975
F_{is}	-0.005	-0.001	0.02	0.048	0.028	0.022	0.067	-0.002	0.05	0.032	0.072	0.030	0.049	0.105	0.154

Mvi3	AY686622, 4 bp repeat (GATA)(GATG)(GATA), allele size range 139-221 (147-229)											Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	139	142	143	143	130	153	116	134	143	164	144	1551	95	95	190
N_A	15	14	17	14	15	17	14	15	14	16	15	20	15	20	21
N_S	14.42	13.16	15.71	12.99	14.33	15.19	13.45	13.82	12.94	14.09	14.08	14.07	15.00	20.00	17.50
H_o	0.83	0.80	0.85	0.83	0.84	0.85	0.82	0.81	0.82	0.82	0.83	0.847	0.58	0.64	0.32
D	0.834	0.804	0.850	0.831	0.839	0.849	0.818	0.815	0.825	0.823	0.833	0.829	0.585	0.643	0.321
F_{is}	-0.044	-0.042	0.013	-0.043	-0.037	-0.008	0.010	-0.026	-0.035	-0.030	0.000	-0.022	-0.008	0.083	0.038
F_{is}	0.022	-0.014	0.014	0.051	0.018	0.022	0.023	-0.012	0.047	-0.005	0.050	0.020	0.111	0.144	0.128

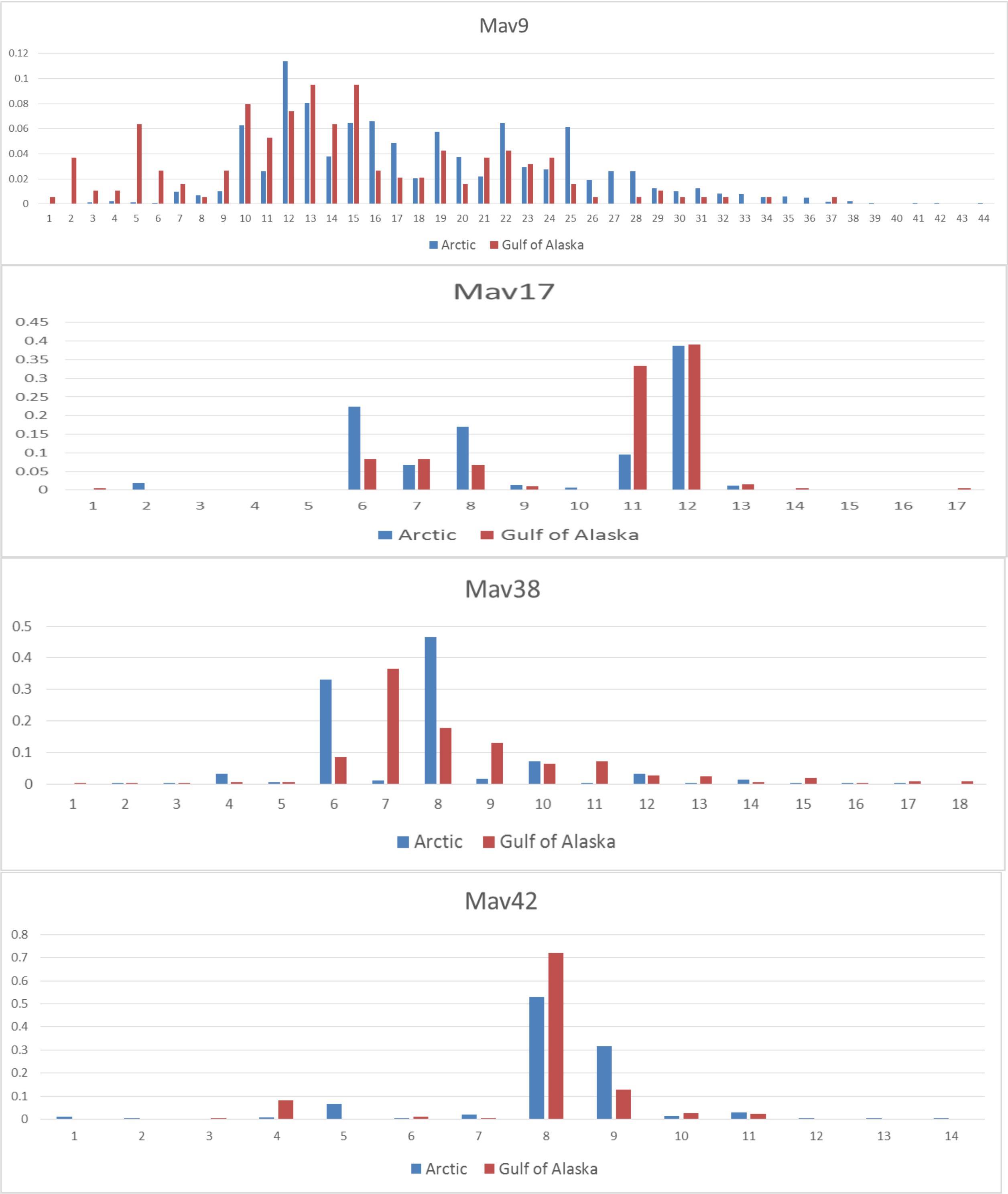
Mvi5		AY686623, 4 bp repeat (GATA), allele size range 83-151 (87-147)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	136	139	145	125	123	152	116	134	143	164	143	1520	95	94	189
N_A	16	15	15	16	16	15	16	16	16	16	14	18	15	13	16
N_S	15.04	14.55	14.38	15.18	15.81	14.17	15.58	15.1	14.85	14.71	13.86	14.84	14.97	13	13.99
H_o	0.89	0.89	0.89	0.88	0.91	0.89	0.90	0.90	0.88	0.89	0.90	0.876	0.85	0.86	0.86
D	0.891	0.891	0.891	0.882	0.910	0.892	0.896	0.901	0.884	0.893	0.898	0.894	0.850	0.860	0.855
F_{is}	0.042	-0.001	0.017	0.002	-0.001	0.056	0.067	-0.019	0.034	0.010	0.003	0.020	-0.102	-0.115	-0.109

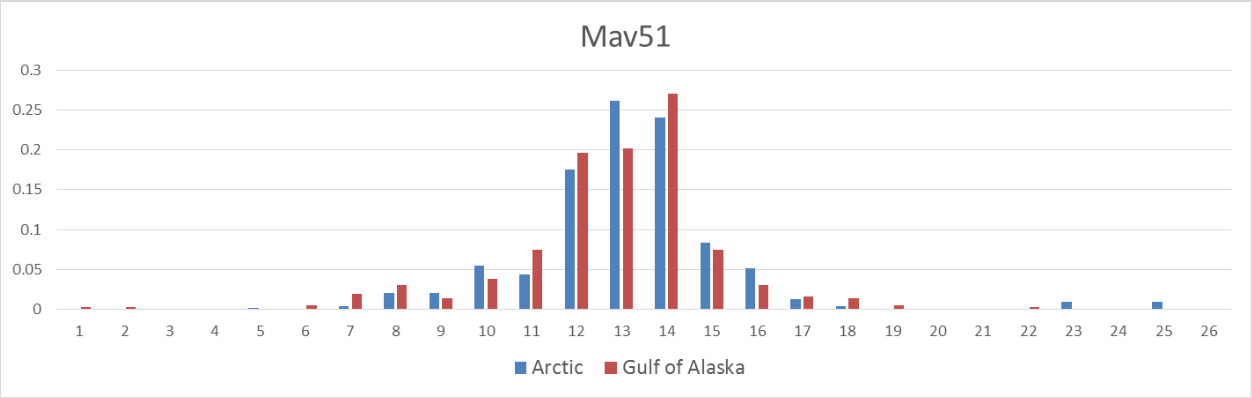
Mvi9		AY686624, 2 bp repeat (GACA), allele size range 77-261 (77-261)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	135	140	143	145	131	152	111	133	139	164	144	1537	94	91	185
N_A	30	45	42	43	35	46	39	40	41	39	42	75	62	59	76
N_S	27.28	37.80	34.54	35.09	30.98	38.22	35.77	34.61	35.12	32.24	34.91	34.23	61.44	59	60.22
H_o	0.90	0.92	0.91	0.92	0.92	0.92	0.92	0.91	0.90	0.91	0.91	0.745	0.98	0.97	0.98
D	0.904	0.917	0.909	0.917	0.916	0.921	0.922	0.912	0.902	0.906	0.908	0.913	0.982	0.972	0.977
F_{is}	0.328	0.190	0.131	0.218	0.117	0.186	0.150	0.184	0.162	0.226	0.120	0.184	0.491	0.322	0.415

Mvi16		AY686628, 2 bp repeat (GTAT), allele size range 137-419 (143-423)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	132	141	138	142	127	150	110	131	142	162	144	1519	66	75	141
N_A	55	59	57	54	43	56	45	55	59	62	63	110	56	50	66
N_S	42.4	44.38	45.11	40.66	36.43	40.96	38.6	42.98	43.09	45.71	45.69	42.36	56	47.8	51.9
H_o	0.97	0.97	0.97	0.97	0.96	0.97	0.96	0.96	0.96	0.97	0.97	0.97	0.98	0.98	0.98
D	0.967	0.973	0.972	0.968	0.965	0.966	0.964	0.964	0.964	0.970	0.972	0.968	0.984	0.977	0.981
F_{is}	0.115	0.205	0.247	0.185	0.282	0.179	0.208	0.200	0.153	0.230	0.200	0.200	0.091	0.249	0.17

Mvi22		AY686629, 4 bp repeat (GTAT), allele size range 104-308 (108-298)									Total			Total
Collection	1	2	3	4	5	6	7	8	9	10	11	Arctic	12	13	Kodiak
N	130	141	141	143	130	153	112	132	141	162	145	1530	95	93	188
N_A	42	40	37	40	37	41	39	39	37	39	39	48	45	36	47
N_S	39.87	38.09	35.31	37.32	36.03	38.91	38.26	36.88	35.06	35.51	36.67	37.02	44.70	36.00	40.35
H_o	0.97	0.97	0.96	0.97	0.96	0.97	0.97	0.97	0.97	0.96	0.97	0.967	0.97	0.97	0.97
D	0.967	0.965	0.963	0.965	0.964	0.969	0.969	0.966	0.967	0.964	0.966	0.966	0.971	0.967	0.969
F_{is}	0.022	-0.014	0.014	0.051	0.018	0.022	0.023	-0.012	0.047	-0.005	0.050	0.020	0.111	0.144	0.128

Appendix 2. Frequency of alleles by locus for Arctic and Gulf capelin.




Mav51
0.3
0.25
0.2
0.15
0.1
0.05
0
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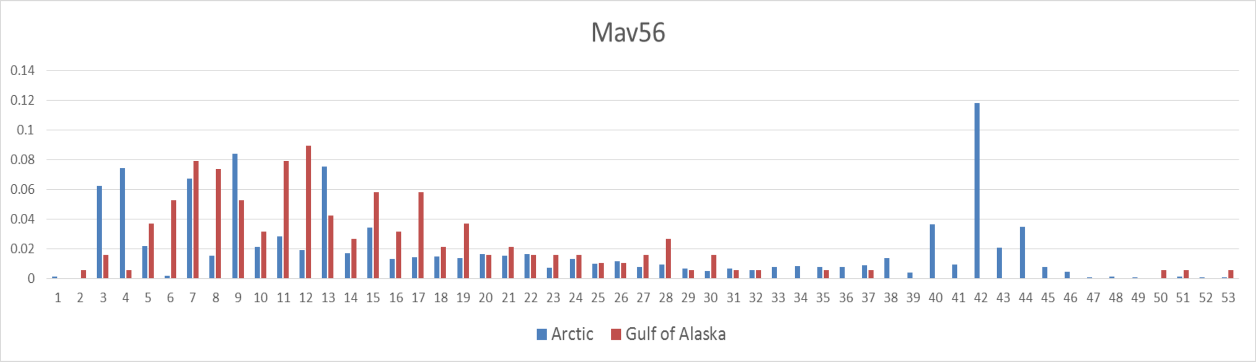
Arctic
Gulf of Alaska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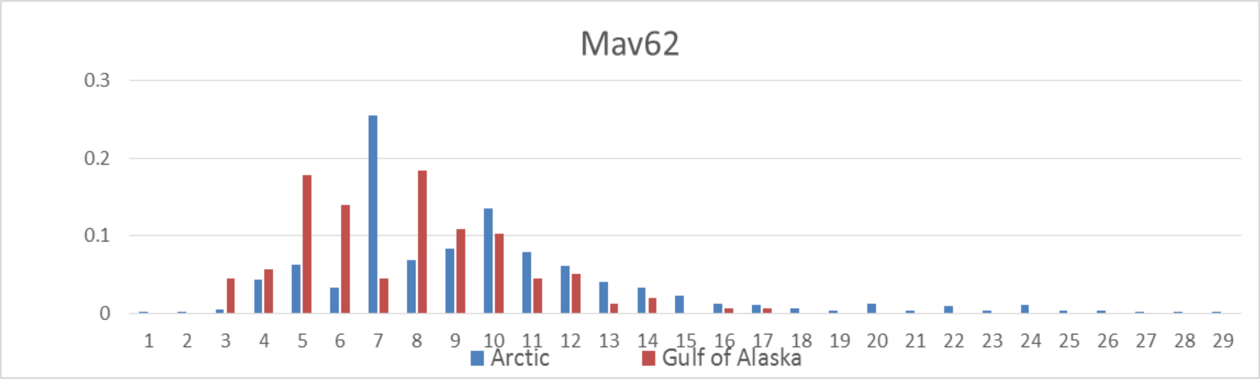
0.12
0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53
Arctic
Gulf of Alaska


Mav62
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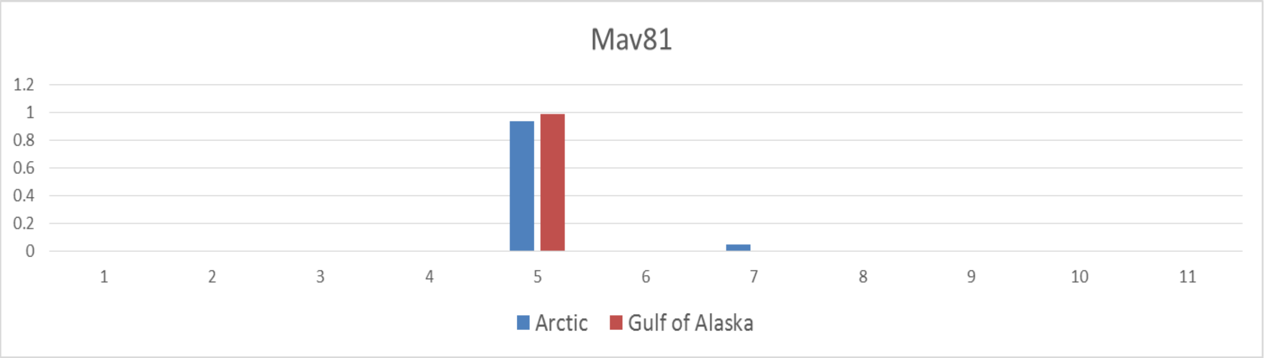
0.1
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29
Arctic
Gulf of Alaska


Mav81
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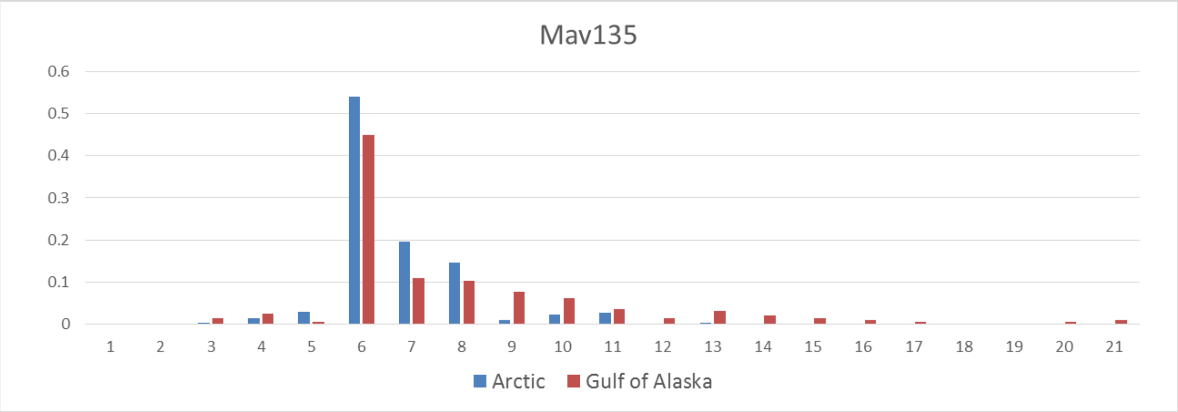
1
0.8
0.6
0.4
0.2
0
1 2 3 4 5 6 7 8 9 10 11
Arctic
Gulf of Alaska


Mav135
0.6
0.5
0.4
0.3
0.2
0.1
0
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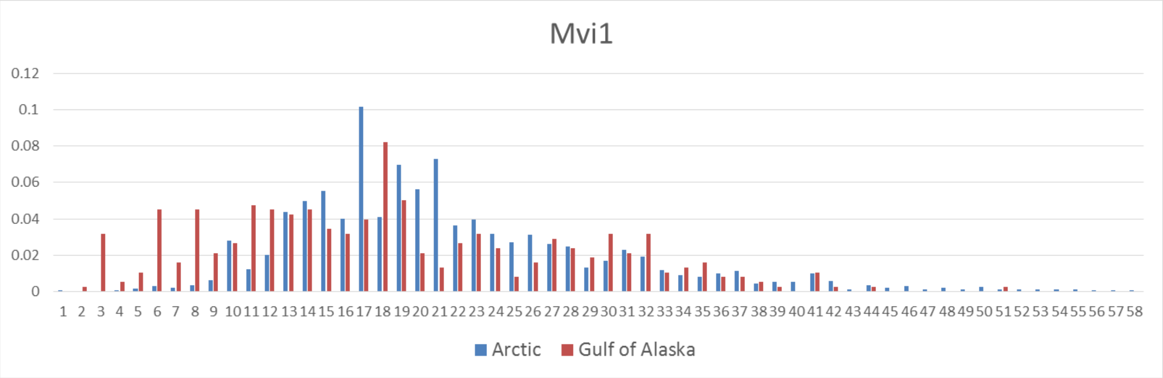
Arctic
Gulf of Alaska


Mvi1
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0.08
0.06
0.04
0.02
0
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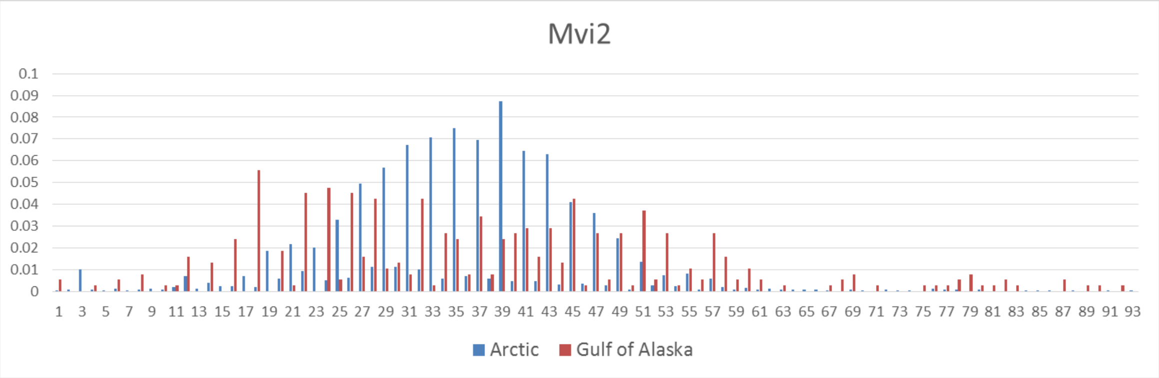
Arctic
Gulf of Alaska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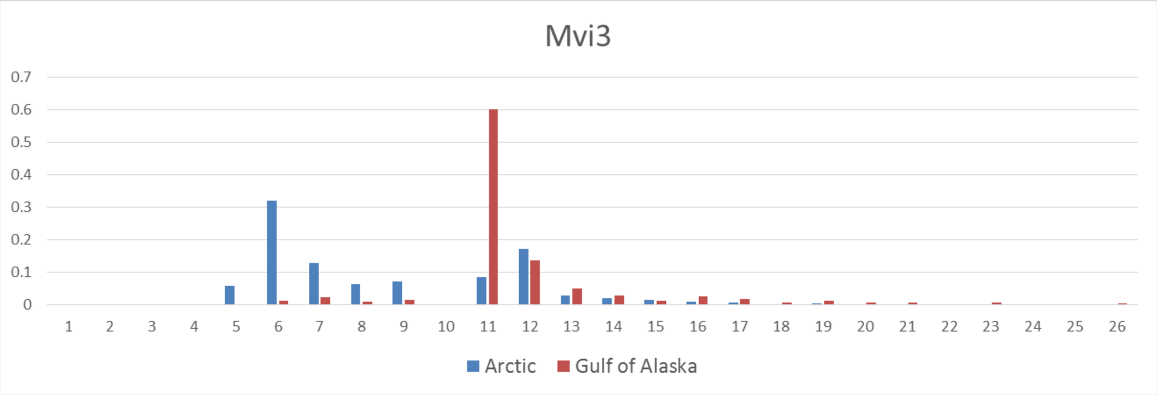
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45 47 49 51 53 55 57 59 61 63 65 67 69 71 73 75 77 79 81 83 85 87 89 91 93
Arctic
Gulf of Alaska


Mvi3
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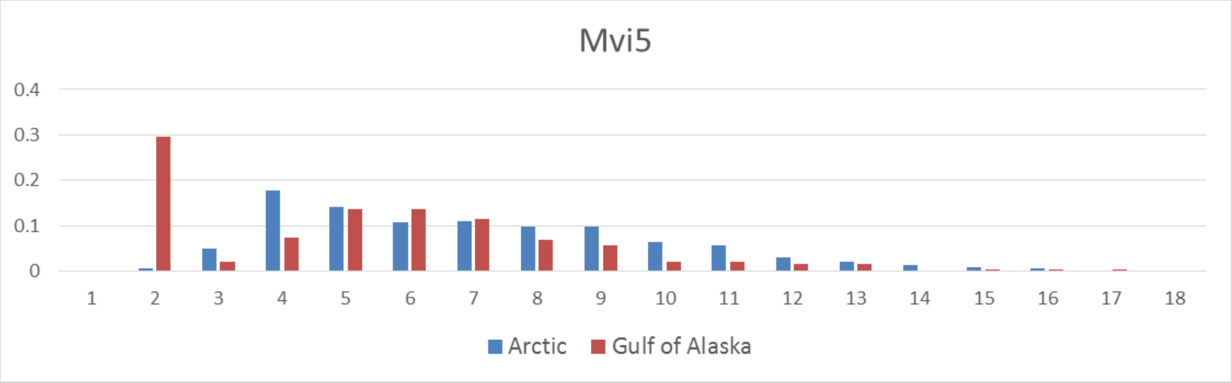
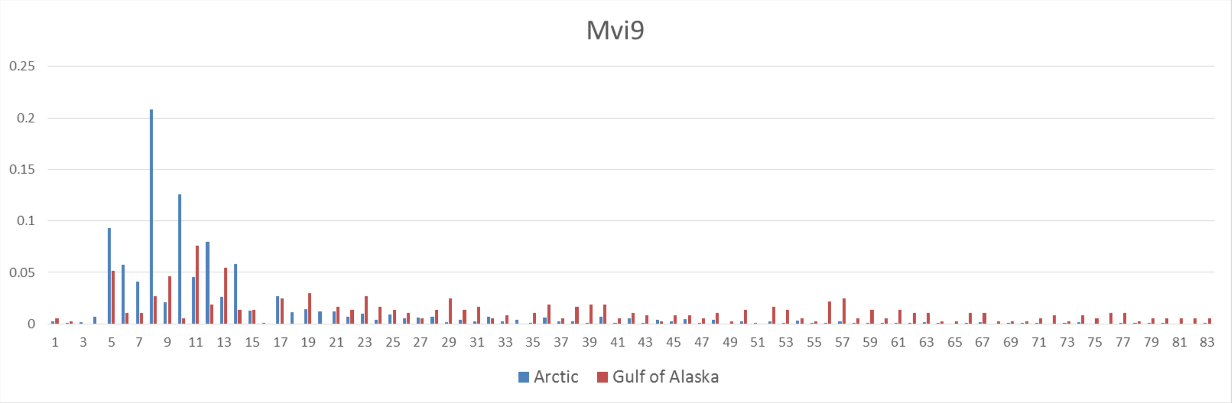
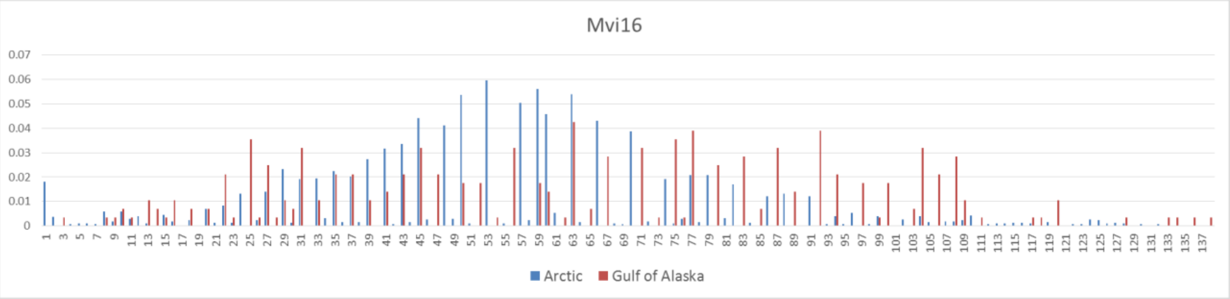
0.6
0.5
0.4
0.3
0.2
0.1
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
Arctic
Gulf of Alaska


Mvi5
0.4
0.3
0.2
0.1
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
■ Arctic ■ Gulf of Alaska


Mvi9
0.25
0.2
0.15
0.1
0.05
0
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45 47 49 51 53 55 57 59 61 63 65 67 69 71 73 75 77 79 81 83
■ Arctic ■ Gulf of Alaska


Mvi16
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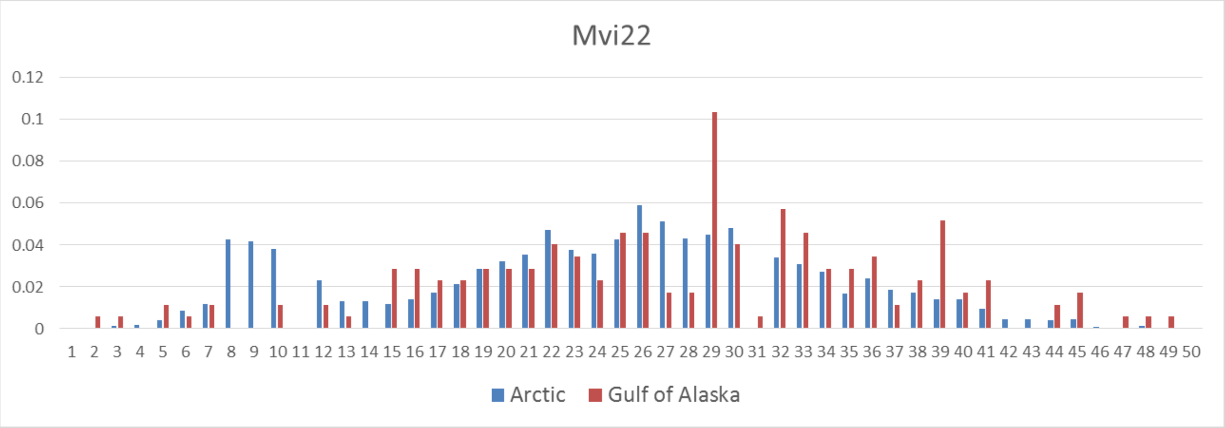
0.06
0.05
0.04
0.03
0.02
0.01
0
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45 47 49 51 53 55 57 59 61 63 65 67 69 71 73 75 77 79 81 83 85 87 89 91 93 95 97 99 101 103 105 107 109 111 113 115 117 119 121 123 125 127 129 131 133 135 137
■ Arctic ■ Gulf of Alaska


Mvi22
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0.1
0.08
0.06
0.04
0.02
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50
■ Arctic ■ Gulf of Alaska

Appendix 3. Mitochondrial cyt-b consensus sequences of (1.) Arctic –near Barrow, AK capelin and (2.) Arctic-near Nunivak Island, Bering Sea capelin, and (3.) Gulf of Alaska capelin near Kodiak Island.

1. Arctic – near Barrow, Arctic Ocean, AK (N=145)

ATTCTTACAGG(T/C)CT(A/G)TT(T/C)CTGGCCAT(A/G)CATTACACTGCCGA(A/G)ACTGC(T/C)ACAGCATTCTCCT
CCGTAGT(A/G)CACCTATGCCGTGACGT(A/G)AATTA(T/C)GG(A/G)TGACTAATCCG(A/G)AACATGCA(T/C)GCT
AACGGAGCATCTTTCTTCTTTATTTGCATTTA(T/C)CTCCA(T/C)ATCGGCCGAGGCCTTTACTATGGCTCTTTCCTTT
ATAAAGAGACTTGAAACGTCGGCGT(A/G)GTCCTTCT(A/C)CTACTAGT(T/C)AT(A/G)AT(A/G)ACTGCCTT(T/C)G
T(A/G)GGCTATGT(T/C)CT(G/C)CCTTGAGG(A/G)CAAAT(A/G)TCTTT(T/C)TG(A/G)GG(A/G)GCAACAGTAATT
ACAAACCTCCT(A/C)TCGGCCGTCCC(T/C)TACATGGGT(T/C)T(A/G)GA(T/C)CTCGT(T/C)(T/C)T(A/G)TG(A/G)(
T/C)TGTGGGG(A/G)GG(T/C)TTTTCAGT(T/C)GACAGCGCCAC(A/C)TTAACCCG(T/C)TTCTTCGCTTTCCACTT(T/
C)AT(T/C)CTTCCTTTCATTATCGCTGC(A/G)GCAACCGTTGT(A/G)CACCTACTTTTCCTTCATCAAAC(A/G)GGCTC
TAA(T/C)AACCCTGTCGGCCTGAACTCGGACGC(A/G)GACAA(A/G)AT(T/C)CCCTTTCACTCTTACTTTATTGTCAA
(A/G)GATCTGGT(A/C)GGCTTCAT(A/G)GCCCT(A/G)TTCCTGGCCCTAGT(A/G)TCCTT(A/G)GCCCTATTTGCCCC
(T/C)AACTTGTTAGGAGACCCCGACAACTTCACGGCGGCCAACCC

2. Arctic – near Nunivak Is., Bering Sea, AK (N=144)

ATTCTTAC(A/G)GGCCT(A/C)TTTCTGGCCAT(A/G)CATTACACTGC(T/C)GAGACTGCCAC(A/G)GCATTCTCCTCC
GT(A/G)GTACACCT(A/C)TGCCGTGACGTAAATTA(T/C)GGGTGACTAATCCGAAACATGCA(T/C)GCTAACGG(A/
G)GCATC(T/C)TTCTTCTTTATTTGCATTTA(T/C)CT(A/C)CA(T/C)ATCGG(T/C)CGAGGCCTTTACTATGGCTCTTTC
CTTTATAAAGAGACTTGAAACGTCGGCGT(A/G)(A/G)T(T/C)CTTCT(A/T/C)CT(A/T)CTAGT(C/G/T)ATGAT(A/G)
ACTGC(C/G)TTTGT(A/G)GGCTATGT(A/C)CTCCCTTG(A/G)GG(A/G)CA(A/G)ATGTCTTTTTG(A/G)GG(A/G)GC(
A/G)AC(A/G)GTAATTACAAACCTCCTCTCGGCCGTCCC(T/C)TA(T/C)ATGGGT(T/C)T(A/G)GACCT(A/C)GTC(T/C
)T(A/G)TGA(T/C)T(A/G)TGGGGAGGTTTTTC(A/G)GTTGACAGCGCCAC(A/C)TT(A/G)ACCCGCTTCTTCGCTTTC
CACTTCAT(T/C)CTTCCTTTCATTATCGCTGC(A/G)GCAACCGTTGT(A/G)CAC(T/C)TACTTTTCCTTCATCAAAC(A/
G)GGCTCTAA(T/C)AACCCTGTCGGCCT(C/G)AACTCGGACGC(A/G)GACAAAAT(T/C)CCCTTTCACTCTTACTTTA
T(T/C)GTCAA(A/G)GA(T/C)CTGGTCGGCTTCATG(A/G)CCCT(A/G)TTCCTGGCCCT(A/C)GTATC(T/C)TT(AG)GC
CCTATTTGCCCC(T/C)AACTT(A/G)TTAGG(A/G)GACCC(A/C)GACAACTTCACGGC(A/G)GCCAACCC

3. Gulf of Alaska near Kodiak Island (N=44)

ATTCTTACAGGCCT(A/G)TTTCT(A/G)GCCAT(A/G)CATTACAC(T/G)GCTGA(A/G)ACTGCCACAGCATTCTCCTCC
GT(A/G)GTACACCTATGCCGTGACGTAAATTATGGGTG(A/G)CTAATCCGAAACATGCATGC(T/C)AACGGAGCAT
CTTTCTTCTTTATTTGCATTTACCTCCATATCGGCCGAGGCCTTTACTATGGCTCTTTCCTTTATAAAGAGACTTGAAA
(T/C)GTCGGCGT(A/G)GT(T/C)CTTCTCCTACTAGTTATGAT(A/G)ACTGC(T/C)TTTGTAGGCTATGT(T/C)CTCCCT
TGAGG(A/G)CA(A/G)ATGTCTTTTTGAGG(A/G)GCAACAGTAATTACAAACCTCCTCTCGGCCGTCCCTTATAT(A/G
)GG(T/C)TT(A/G)GACCTCGTCCT(A/G/C)TG(A/G)TT(A/G)TGGGG(A/C)GGTTTTTCGGTTGACAGCGCCACCTTA
ACCCGCTTCTTCGCTTTCCACTTCATCCTTCCTTT(T/C)ATTATCGCTGCAGCAACCGTTGTACACTT(A/G)CTTTTCCT
TCATCAAACAGGCTCTAACAACCCTGT(T/C)GGCCT(A/G)AACTCGGACGCGGACAAAAT(T/C)CCCTTTCACTCTT
ACTTTAT(T/C)GTCAAAGATCT(A/G)GTCGGCTTCATGGCCCTATTCCTGGCCCTCGTATCCTT(A/G)GCCCTATTTG
CCCCCAACTTGTTAGGAGA(T/C)CC(CG)GACAACTTCACGGC(A/G)GC(T/C)AACCC

Appendix Z.

Boreogadus saida Genetics in the Alaskan Arctic

Authors

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August 31, 2016

Prepared under BOEM Awards
M12AC00009 (UAF), M12PG00018 (AFSC) and M10PG00050 (USF&WS)

Prepared under CIAP Award Number
F12AF00188 (UAF)

US Department of the Interior
Bureau of Ocean Energy Management
Alaska OCS Region
Environmental Studies Program

US Department of the Interior
US Fish and Wildlife Service
Alaska Department of Natural Resources
Coastal Impact Assistance Program

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Abbreviations, Acronyms, and Symbols

Arctic Eis	Arctic Ecosystem Integrated Survey
BOEM	Bureau of Ocean Energy Management
CIAP	Coastal Impact Assistance Program
UAF	University of Alaska Fairbanks
SFOS	School of Fisheries and Ocean Sciences
NOAA	National Oceanic and Atmospheric Administration
AFSC	Alaska Fisheries Science Center
PMEL	Pacific Marine Environmental Laboratory
USFWS	US Fish and Wildlife Service
ADFG	Alaska Department of Fish and Game

List of Oral and Poster Presentations

None to report.

Proposed Objectives and Study Chronology

This project examines the genetic structure of Arctic cod (*Boreogadus saida*) in the waters surrounding northern Alaska (Chukchi Sea and Arctic Ocean). The samples will be used to monitor stock structure over time and these samples will form the initial genetic baseline of the region.

In 2011, we began development of microsatellite (Msat) markers for *B. saida*. After submitting the proposal to BOEM, we were contacted by John Nelson of SeaStar biotech. Nelson advised he had been working on *B. saida*, and a collaboration was developed. *B. saida* samples were received September 2012. Samples were processed late 2012. Additional genetic tissue was retained and shipped to J. Nelson for potential future standardization of markers. J. Nelson kindly provided his Msat marker information for our project. Additional tissue was extracted (paired with genetic samples) and provided to Jen Marsh for isotope studies.

Primer testing of the newly developed markers and optimization of markers (both new and J. Nelson markers) was completed by mid-2013. DNA was isolated and data for the 2012 samples was generated late 2013. Samples for the 2013 midwater trawl were received Oct. 2013. Tissue samples were processed, DNA was isolated and Msat data was generated in 2014. All 2012 samples were shipped to Tom Helser for aging studies.

Msat data was analyzed and report writing began in 2015. An opportunity to obtain mtDNA information on the samples arose and a subset was sequenced, and data added to the emerging report. The report is finalized June 2016. Raw data for both Msat and mtDNA accompany this report.

Boreogadus saida genetics in the Alaskan Arctic

Abstract

Population structure of *Boreogadus saida* (*B. saida*) (Arctic cod) was examined with nuclear and mitochondrial DNA (mtDNA) loci. Non-spawning *B. saida* were collected from the Chukchi Sea and Arctic Ocean adjacent to Alaska, in 2012 and 2013. Genetic data was obtained (n=1493) from 15 microsatellite markers, including two loci developed for this study. Newly developed microsatellite locus *Sai25* clearly distinguishes morphologically similar *B. saida* from juvenile *Gadus chalcogrammus* (pollock). Two microsatellite loci, *Sai13* and *Bsa60*, departed significantly from Hardy- Weinberg equilibrium (HWE) expectations in nearly every collection, P > 0.0001, likely indicating the presence of null alleles. Sequence information of the mtDNA cytochrome oxidase I gene from a subset of these samples (n=351), resulted in one main haplotype and 4 smaller clades. Data from 13 nuclear loci in HWE suggest *B. saida* is a single panmictic population in the Chukchi Sea and Arctic Ocean adjacent to Alaska. While the suite of genetic markers in this study did not detect population structure in this species with low genetic diversity, it does not preclude that structure may exist.

Introduction

Boreogadus saida is a little known, mostly cryopelagic resident of the circumpolar Arctic. This small cod feeds on plankton, and because it is lipid rich (Elliot and Gaston 2008), is the primary food source for Arctic marine life, including mammals, birds and fish. While able to tolerate temperatures below 0°C, this fish prefers a temperature of 3-5°C (Drost et al. 2014). These petite cold water fish mature at a size of 60-160 mm, which corresponds to 1-3 years of age (Craig 1982, Nahrgang et al. 2014), and reach a maximum size of 300-400 mm.

The Arctic habitat of *B. saida* is warming (NOAA, National Climatic data center). While benefitting some species, a restructuring of the ecosystem may be detrimental to others. Distribution shifts or decline of *B. saida* with increased temperatures is likely (Renaud et al. 2012; Cheung 2013). Seabirds and marine mammals depend on *B. saida* as a primary food source (Bradstreet 1980) and regional stability of seabird populations is contingent on this species (Springer et al. 1984).

Increased access to the Arctic region opens the potential for increased resource exploitation (Christiansen et al., 2014). Additional pressures are expected to follow sea ice loss, such as development of potential fisheries, the introduction of shipping routes, and oil and gas exploration. *B. saida* has been suggested as a monitoring species of oil pollution in cold waters (Nahrgang et al. 2010; Jonsson et al. 2010; Anderson et al. 2015). As the Arctic region experiences increased exploration, it is important to obtain baseline information to compare against future changes. Genetic information provides an inherent baseline with which to assess future changes such as population bottlenecks, mutations, and movement of stocks in this vast area.

Recent genomic studies have begun to uncover the phylogenetic relationships of species. Genetic studies of species related to *B. saida* suggest *Arctogadus glacialis* (Polar cod) is a closely related, but distinct taxa (Coulson et al. 2006; Breines et al. 2008; Owen et al. 2015). Indeed, the common names, Arctic cod and Polar cod, are used interchangeably for *Boreogadus saida* and *Arctogadus glacialis* in the literature. Other studies indicate that Pacific cod (*Gadus macrocephalus*) and Greenland cod (*Gadus ogac*) are closely related sibling species and that Atlantic cod (*Gadus morhua*) and walleye pollock (*Gadus chalcogrammus*) are closely related to these four cod species (Moller et al. 2002, Coulson et al. 2006; Breines 2008, Owen 2015). One study suggests that *G. chalcogrammus* may be a recent hybrid of *B. saida* and *G. morhua* (Halldorsdottir and Arnason 2015).

Despite few barriers and high levels of gene flow in pelagic fish species, a large body of genetic research has detected varying degrees of population structure in Atlantic cod (40 papers summarized in O'Leary 2007; Sarvas and Fevolden, 2005; Fevolden et al., 2012; Pampoulie et al, 2006; 2008; 2015; Jorde et al, 2007; Karlsen et al, 2013; Hemmer-Hansen et al, 2013; Therkildsen et al, 2013, and Bradbury et al, 2014). Although less studied, structure has also been detected in *G. macrocephalus* (Cunningham et al., 2009; Canino et al., 2010), *G. chalcogrammus* (Grant et al., 2010) and *B. saida* in the N. Atlantic (Madsen et al., 2015) and across its circumpolar range (Nelson and Bouchard, 2013). Our study examined stock structure with microsatellite loci and mtDNA sequence data of *B. saida* in the marine waters around the northwest part of Alaska, including the northern Bering Sea, and Arctic waters between the eastern Chukchi and the western Beaufort Seas.

Methods

Sample Collection

Non-spawning *B. saida* were collected from the eastern Chukchi Sea in 2012 and 2013 (Table 1, Fig. 1). Collections were obtained by bottom trawl in 2012. Between 5 and 36 fish were retained from each haul. Conversely, in 2013, *B. saida* were collected by mid-water/surface trawl and larger samples sizes (150+) were retained from a single haul. Whole fish were frozen at sea. Lengths and weights were obtained in the laboratory, and a fin clip and piece of heart tissue were extracted for genetic research. Tissue was preserved in 95% ethanol. An additional sample of *B. saida* from N. Bering Sea, collected in 2010 by surface/mid-water trawl prior to this study, was added to all analyses. This is the southernmost collection available and collectors state it was unusual to catch *B. saida* in the northern Bering Sea (pers. Comm. Jim Murphy, NOAA). A small sample of *G. chalcogrammus* collected from the Bering Sea in 2012 (n=20) was also examined as a standard to rule out mis-identified fish, because of morphological similarities to *B. saida* in the juvenile phase.

Table 1. Collections of *B. saida* including year, latitude and longitude, number of samples examined for microsatellites and mtDNA (total number from specified region in bold), average length (mm) of fish in the collection (mean by region in bold).

Area of Collection	Year	Latitude (N)	Longitude (W)	Number Msats	Number mtDNA	Mean length (mm)
Northern Bering Sea	**2010**			**89**	**54**	**121.4**
Station 8		*60.10*	*171.00*	*3*	*1*	*108.3*
Station 9		*60.30*	*171.85*	*20*	*15*	*110.4*
Station 33		*62.00*	*168.00*	*20*	*14*	*129.06*
Station 52		*63.49*	*164.32*	*6*	*1*	*110.5*
Station 53		*63.51*	*163.18*	*5*	*5*	*128.4*
Station 55		*64.40*	*162.43*	*10*	*5*	*128.6*
Station 57		*64.41*	*164.33*	*10*	*7*	*122.2*

Station 58		*64.20*	*165.10*	*10*	*4*	*112.8*
Station 65		*64.59*	*168.59*	*5*	*2*	*142.4*
Kotzebue	**2012**			**144**	**70**	**111.8**
Haul 1		*66.51*	*168.50*	*31*	*19*	*111.9*
Haul 2		*66.03*	*168.49*	*30*	*20*	*119.3*
Haul 5		*66.48*	*167.25*	*30*	*24*	*114.7*
Haul 8		*66.99*	*165.92*	*30*	*7*	*105.4*
Haul 14		*66.99*	*164.69*	*23*	*0*	*116.0*
N. of Point Hope	**2012**			**144**	**37**	**100.8**
Haul 54		*70.00*	*165.56*	*30*	*0*	*106.6*
Haul 56		*69.50*	*165.65*	*11*	*0*	*89.8*
Haul 57		*69.50*	*165.73*	*30*	*17*	*109.6*
Haul 59		*69.50*	*167.12*	*31*	*20*	*92.8*
Haul 67		*70.01*	*167.02*	*34*	*0*	*98.5*
Haul 120		*70.00*	*168.47*	*8*	*0*	*99.7*
N. Chukchi Sea	**2012**			**144**	**46**	**113.3**
Haul 89		*72.50*	*168.46*	*36*	*35*	*112.7*
Haul 92		*72.51*	*166.84*	*30*	*11*	*118.8*
Haul 109		*71.50*	*166.95*	*32*	*0*	*105.8*
Haul 111		*72.01*	*166.90*	*31*	*0*	*119.2*
Haul 112		*72.00*	*168.50*	*15*	*0*	*108.5*
Barrow, Arctic Ocean	**2012**			**144**	**22**	**107.4**
Haul 43		*71.00*	*159.04*	*30*	*6*	*114.9*
Haul 44		*71.00*	*157.75*	*32*	*12*	*111.1*
Haul 48		*71.52*	*157.39*	*30*	*1*	*104.6*
Haul 74		*71.50*	*158.42*	*5*	*0*	*86.5*
Haul 76		*72.00*	*157.19*	*13*	*2*	*99.1*
Haul 77		*72.01*	*158.82*	*18*	*0*	*92.0*
Haul 78		*72.48*	*158.44*	*16*	*1*	*102.3*
N. of Point Hope - st. 69	**2013**	70.02	165.58	**163**	**37**	**47.3**
Icy Cape-coastal - st. 75	**2013**	70.52	161.04	**150**	**0**	**53.4**
Barrow, Arctic Ocean	**2013**			**300**	**21**	**47.05**
station 111		*71.50*	*157.53*	*150*	*6*	44.7
station 115		*71.49*	*158.97*	*150*	*15*	49.4
Beaufort Sea1 - st. 150	**2013**	71.82	154.97	**98**	**31**	**52.8**
Beaufort Sea2 - st. 151	**2013**	71.82	155.18	**149**	**33**	**36.7**

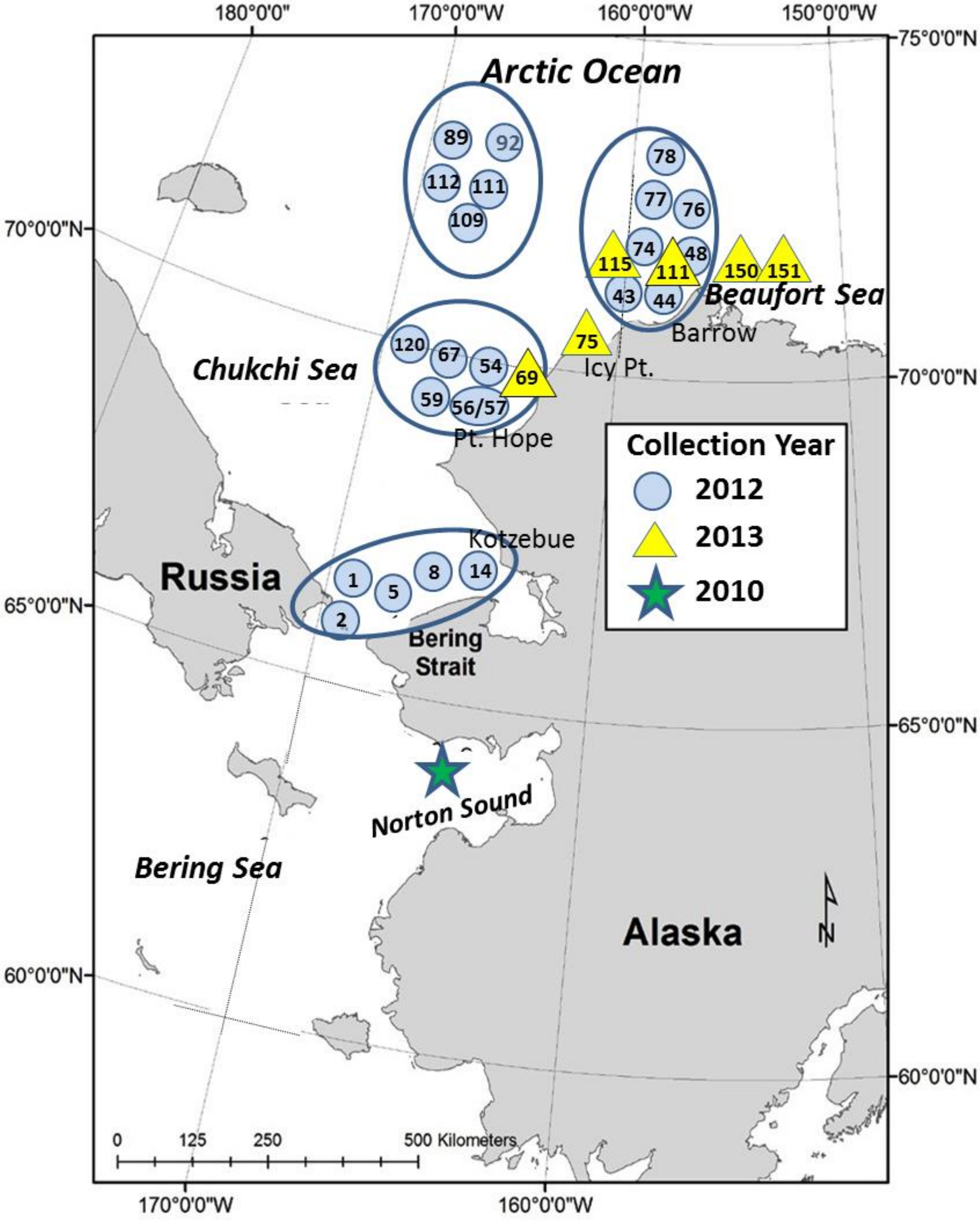

Figure 1. *B. saida* collected in 2010, 2012, and 2013. Haul and station numbers are noted within circles and triangles, and correspond to information in Table 1. Several hauls were grouped as shown (circled) to provide a more robust sample size for some analyses.

Data collection

DNA was extracted from 1,525 tissue samples using Qiagen DNeasy[10] Tissue kit protocols. Genetic data was obtained from microsatellite loci to assess current population structure. Sequence data from the cytochrome oxidase subunit I (COI) mtDNA gene was used to confirm species identification and examine historic demography.

Microsatellites

At the project onset, microsatellite markers had not been developed specifically for *B. saida*, however, several marker sets for Atlantic cod and Pacific cod were screened for potential use in *B. saida*. In addition, we embarked on marker development specifically in *B. saida*. During our study, it was ascertained that John Nelson (SeaStar BioTech Inc., Canada), was doing an Arctic wide population genetic study of *B. saida*. He kindly shared primer information from markers he was currently developing for *B. saida*, and optimization information about marker sets from related species.

Marker development

A microsatellite enriched library was constructed from the DNA of *B. saida* collected in the Chukchi Sea, with the help of Dr. Christopher Saski at Clemson University Genomics Institute, using modified methods of Glenn and Schable (2005). DNA was digested with restriction enzyme *RsaI*, resulting in approximately 500 base pair (bp) fragments. Double-stranded linkers were ligated to the resulting fragments providing primer-binding sites for polymerase chain reaction (PCR) amplification. Microsatellite containing DNA fragments were

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[10] Mention of trade names or commercial companies is for identification only.

enriched by an in-tube hybridization with biotinylated oligos containing a mix of common SSR repeat motifs. These selected fragments were amplified by PCR and products were carried into E. coli (DH10b electrocompetent) via a cloning vector. Transformants were placed in carbenicillin LB plates and colonies were robotically chosen using the Genetix Q-bot and stored as glycerol stocks at -80°C.

Clonal DNA was purified and sequenced using BigDye® chemistry (Applied Biosystems). Microsatellite repeats were identified with MSATCOMMANDER software (Faircloth 2008) and primers were designed. Promising primer sets were identified in 34 of 624 sequences. These 34 loci were screened for variability in 8 individuals (Kotzebue 2012, Haul 1, #1-8; Table 1) of *B. saida*. 10 µl PCR reactions were made using 10 ng DNA, 1X GoTaq® buffer and 1 unit of GoTaq® Flexi DNA Polymerase (Promega), 0.2 mM of each dNTP (Fermentas), 2.5 mM $MgCl_2$, 0.2 µM unlabeled primer, 0.2 µM labeled primer, and deionized water. Thermal cycling was performed on a GeneAmp® 9700 (Applied Biosystems) under the following conditions: 95° C for 15 min., 28 cycles of amplification (94°C for 30 sec., annealing temperature (depends on the suite of markers) for 90 sec., and 72°C for 60 sec.), final extension cycle of 72°C for 30 min., and a holding temperature of 15°C. Fragments were analyzed on a 16 capillary ABI 3130xl DNA Analyzer (Applied Biosystems (AB)), and alleles were determined with Genemapper 5.0® (AB) software.

Microsatellite Data

In addition to the new markers developed for this study, 27 markers developed previously were also explored. Thirteen previously developed markers and two of the newly developed markers were optimized, for a total of 15 markers utilized in our study (Table 2). The entire collection of *B. saida* (1,525) and the 20 *G. chalcogrammus* individuals were examined at these 15 loci. Individuals with data missing at 4 or more loci, or individuals suspected to be a species other than *B. saida* based on allelic banding patterns, were removed from analyses.

Table 2. Microsatellite loci examined in this study. Locus name, the number of alleles detected in this study, allele size range, the repeat type, source, and primer sequences. Sources are: 1=Nelson et al., 2013; 2=Miller et al., 2000; 3=Jakobsdottir et al., 2006; 4=Skirnisdottir et al., 2008; 5= O'Reilly et al., 2000; and 6=Wildes (this report).

locus	# alleles	size range	repeat	source	5'-3' Forward Primer	5'-3' Reverse Primer
Bsa6	19	180-216	2	1	CTCTAGAGCGTTTTGTCTCC	AACCATTTGTTTTGGTACAGG
Bsa7	11	177-200	2	1	TCTTGGAGAAAAGGAATCGG	AAAAGGTACACGACAAACCG
Bsa14	15	178-224	4	1	CGATACTATAGCTGCAAACGC	ATGAAATGCTATCCGACTCC
Bsa15	8	171-199	4	1	GAAGACACCTCGTCACGC	CTCCTTCATCTGTGGTCAGC
Bsa60	13	171-248	4	1	AAAGGGTTCATTCAAAAGGG	GCTTTCATCTCAAAACACCC
Bsa101	15	125-158	4	1	GTGCTTGTGTGTGTTTCAGC	TGTTAATGCTGCTTCTTTGC
Gmo8	13	101-138	4	2	GCAAAACGAGATGCACAGACACC	TGGGGGAGGCATCTGTCATTCA
Gmo32	7	100-118	3	3	CAATCGCCGTCCAACCAAC	GGCGGCAGCAACGATTCTC
Gmo127	13	259-315	4	4	TCTGGTGCAGATCCTCGATG	TCAGAGGTTCCGGTCGTAAG
Sai13	24	194-304	4	6	CAGTTGACCACATCCCACCA	ATTTCACGTCCCATACCCCG
Sai25	4	280-289	3	6	ACCATCAGGGCCAATGAGTG	GTCCGCCGTCAAGGTAAGAA
Tch5	73	174-264	4	5	GCCTTAATATCACGCACA	TCGCATTGAGCCTAGTTT
Tch6	33	77-177	2	5	AGACGGCCACTCATACAGAC	CAATCACTTCTGATGTGGTC
Tch11	58	122-374	4	5	ATCCATTGGTGTTTCAAC	TCGAGTTCAGGTGGACAA
Tch20	48	160-366	4	5	ACATTGTAAACGGCGATTC	TGGTTAGTCTGAGACCCAG

Microsatellite analyses

The *B. saida* were not collected from a spawning event, and therefore the data were pooled in several ways (Table 1, Fig. 1). First, the data were examined as a single collection (n=1493). Second, to examine potential temporal differences, the data were analyzed by year-545 individuals collected in 2012, 859 individuals collected in 2013, and 80 northern Bering Sea individuals in 2010. Third, to examine potential spatial differences, the data were examined by partitioning the samples by geographically proximate collections, resulting in 7 groupings: N.

Bering Sea, Kotzebue Sound, Point Hope, N. Chukchi Sea, Icy Cape, Barrow, and W. Beaufort Sea. Finally, each collection was analyzed separately: six 2013 collections, four 2012 groups of collections and N. Bering Sea for a total of 11 groups.

Allele and genotype frequencies were estimated and expected Hardy-Weinberg proportions were calculated for each of 15 microsatellite loci, for each of the four partitioned sample groups in GENPOP 4.0 (Rousset, 2007, based on Guo & Thompson, 1992), using Markov chain parameters of 10,000, 200 batches and 50,000 iterations. Gene diversity (heterozygosity) was estimated in GENPOP 4.0, and allelic richness - number of alleles per locus using rarefaction to account for unbiased estimates of uneven sample size- (Hurlbert 1971, Smith and Grassle 1977, and Leberg 2002), was estimated by using the software program HP-Rare 1.0 (Kalinowski 2005). Loci were examined for linkage disequilibrium in Genetix 4.05 (Belkhir, 2004).

Population structure was explored in several ways. Genetic differentiation among pairwise temporal and spatial samples was determined in GENPOP 4.0 (G-test) and F-STAT (F_{ST}) (Goudet, 1995). Graphs of the distribution of alleles by locus were created in Excel®. Principal component analyses were run for each of the 4 groups in Minitab 17 (Minitab Inc.). Because samples were collected from non-spawning fish, it is possible that sample collections were comprised of a mixture of individual spawning stocks, so fish were also partitioned into groups of genetic similarity independent of sampling location by using the model based clustering method in STRUCTURE (Pritchard et al., 2000). This software partitions individual fish to a pre-identified number of genetic groups based on a cluster algorithm to maximize estimations of both Hardy-Weinberg and linkage equilibrium (15 microsatellite loci and 349 alleles). Clustering was performed where the number of populations ranged from 1 to 3 (to test overall structure) and 11 (to see if fish from one location were different from the next). To ascertain whether genetic differences exist between sample collections at different locations, 100% simulation tests were used to investigate whether samples from one location assign to the same or different sample locations. Simulated mixtures of fish with genotypes from one location were re-assigned back to the baseline of collections. Mixtures from a highly diverged sample set will re-assign with a higher degree of accuracy. For this test, the software program ONCOR (Kalinowski, 2008), was used because it employs a "leave one out cross validation" approach that better accounts for statistical sampling issues (Anderson et al, 2007). If an individual's multilocus genotype is incomplete (i.e. there is missing data), it will be dropped from analysis, but will remain in the baseline in order to estimate the origin of other fish. 1,256 individuals were analyzed using ONCOR software.

mtDNA

Individuals with microsatellite alleles outside the typical allele size range were identified as being potentially a species other than *B. saida*. These individuals, along with a sub-set of *B. saida* from each geographic region (a total of 351 samples), were sequenced at the cytochrome oxidase I (COI) region of the mtDNA. Two sets of (COI) primers reported by Ward (et al., 2005) and used by McCusker (et al., 2013) for use in *B. saida* and *A. glacialis* (GenBank accession numbers KC015250, and KC015200) were tested in this study. A plate of 20 individuals was sequenced for each set of COI primers. The latter primer set provided slightly better results, and was therefore used in all subsequent amplifications. The COI fragment was amplified by PCR in a 50-µL reaction volume containing 1X GoTaq Buffer (Promega Corp., Madison, WI), 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.2 µM each of forward and reverse primer, 1 unit of Flexi DNA polymerase (Promega), 10 ng DNA, and deionized water. Thermal cycling conditions were as follows: 95°C for 2 min; 30 cycles of amplification (95°C for 40 s, 55°C for 40 s, and 72°C for 1 min); 72°C for 7 min; and 4°C indefinitely. Forward sequences were obtained from the PCR product by the Sanger sequencing method. Sequences were aligned and edited with the software program CodonCode Aligner, vers. 3.7.1 (CodonCode Corp., Dedham, MA). Ambiguous end regions, particularly on the 3′ end of the sequences, were trimmed to 591 bp in length to achieve the maximum number of high-quality sequences.

The following genetic indices were calculated in Arlequin, vers. 3.5 (Excoffier and Lischer, 2010): number of haplotypes (*H*), number of polymorphic sites (*S*), average nucleotide diversity (π) and haplotype diversity (*h*).

For the purpose of examining phylogenetic relationships, the data were supplemented with COI sequences from Genbank of *G. morhua* (KJ204885, KF929905, and KC015385), *A. glacialis* (HM421732, HM421733, and KC015200), *G. chalcogrammus*, (KP975591 and JQ354518) and *B. saida* (JQ354017, JQ354016, and KC015250).

The number of nucleotide differences between sequences was visually represented by a haplotype network (minimum spanning tree) created with the program Sneato, vers. 2 (Wooding, 2004; http://user.xmission.com/~wooding/Sneato/). Phylogenetic relationships among unique mtDNA haplotypes were evaluated with the program MEGA 6 (Tamura et al., 2013), wherein a tree was constructed with the neighbor-joining (NJ) method (Saitou and Nei, 1987) using the distance algorithm of Tamura and Nei, (1993). Support for nodes of the tree was evaluated with 1000 bootstrap replicates (Felsenstein, 1985). The number of substitutions per site between all unique sequences were examined with the Tamura and Nei (1993) model and analyses included mean divergence and range of divergence between each species pair.

Results

Microsatellite marker development

Most of the newly designed *B. saida* markers exhibited low heterozygosity. Twelve of the 34 primer sets tested on a set of 8 *B. saida* samples, produced readable results. Five markers were invariant (*Sai1, Sai14, Sai20, Sai23* and *Sai32*), three had an excess of PCR artifacts and were difficult to genotype (*Sai2, Sai3*, and *Sai31*), and two markers were nearly invariant, having 2 and 3 rare alleles respectively (*Sai21* and *Sai33*). The remaining 2 new markers (*Sai13* and *Sai25*) were used in subsequent analyses. *Sai13* is a variable 2 base pair (bp) repeating microsatellite, with 23 alleles in this data set, ranging in size from 194-304 bp. *Sai25* is a 3 bp repeat with 4 alleles ranging in size from 280-289 bp.

Species

Sai25 unequivocally distinguishes *G. chalcogrammus* from *B. saida* (Fig. 2). Only four alleles were detected at this locus in the *B.saida* samples; however, *G. chalcogrammus* is highly variable at this locus. In the 20 individuals examined, 15 alleles were detected, ranging from 337 – 391 bp. Whereas *Sai25* is the clearest microsatellite marker, other microsatellite loci also exhibited allele differences between *G. chalcogrammus* and *B. saida*. *Bsa101* produced a mutally exclusive set of alleles. Alleles *125 and *129 in *G. chalcogrammus*, and *130-*158 in *B. saida*, although allele *129 could be confounded with allele *130. Six other loci contained alleles found only in *G. chalcogrammus*: *Gmo32*- *112, *115, *118; *Tch5*- *200, *213, *216, *225, *241, *253; *Bsa14*- *252; *Gmo8*-*199, *214, *227; *Tch6*- *181; and *Bsa60*-*171. In addition, these two species can be distinguished with mtDNA fragment of the COI gene (23 bp difference).

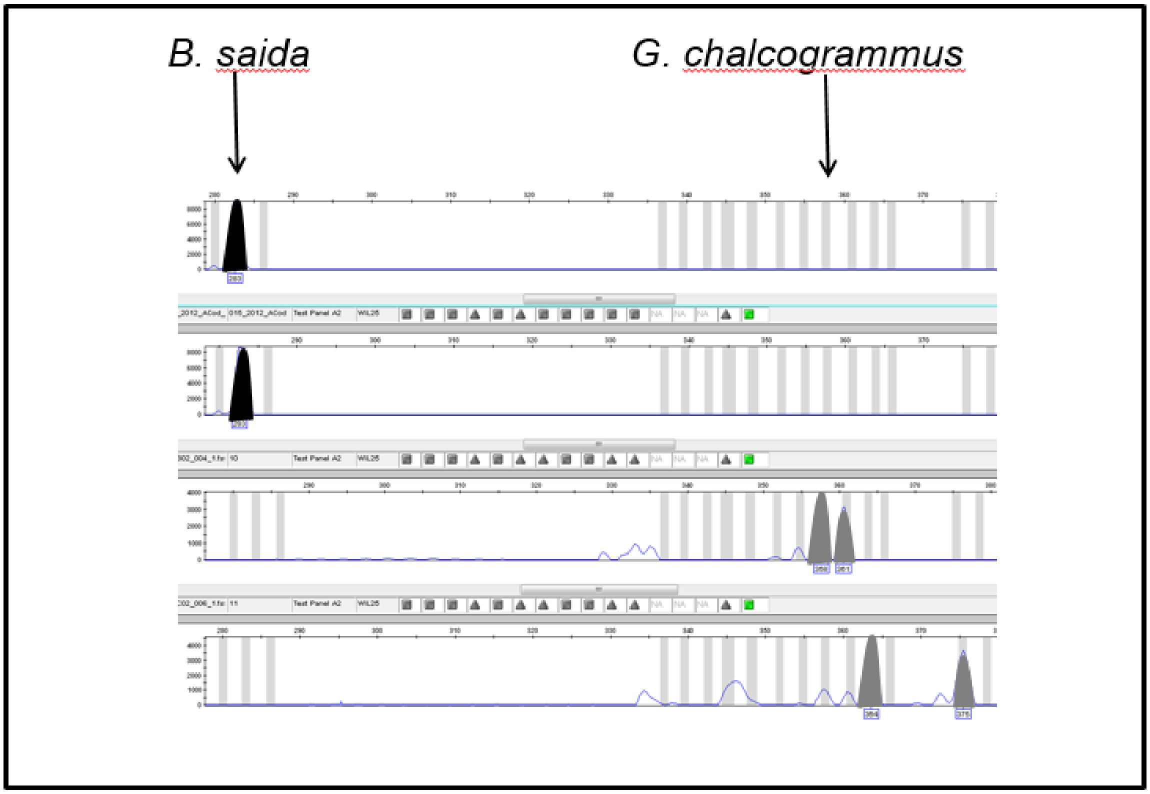


Figure 2. *Sai25* genotype output from Genemapper® software, showing discrete alleles for *B. saida* and *G. chalcogrammus*. Each horizontal bar represents an individual; the dark ‘peak’ designates the size of the amplified fragment: one peak indicates parents shared the same allele, two peaks indicate parents had different alleles. Individuals 1 and 2 are *B. saida* and individuals 3 and 4 are *G. chalcogrammus*.

Both methods confirmed that four individuals were *G. chalcogrammus*, three from the 2012 collections (#551, 782, 809) and one from the 2013 midwater trawl (st69, #126). Another potentially confounding species screened for in the data set was *A. glacialis*, genetically discernable by *Gmo8* alleles larger than 134 (Madsen et al., 2009). By this criteria, *A. glacialis* was not detected in our samples. Samples identified as *G. chalcogrammus*, and individuals missing 4 or more loci (n=24) were dropped from further analyses. The total number of *B. saida* used in subsequent analyses was 1,493 representing 98% of the sample set.

Marker specifics

The four *Tch* markers developed by O'Reilly (et al., 2000) were highly variable with 30 or more alleles, and heterozygosity ranged from 0.90 - 0.96. Three of the four markers exhibited a smooth frequency distribution of alleles in the *B. saida* samples (Fig. 3).

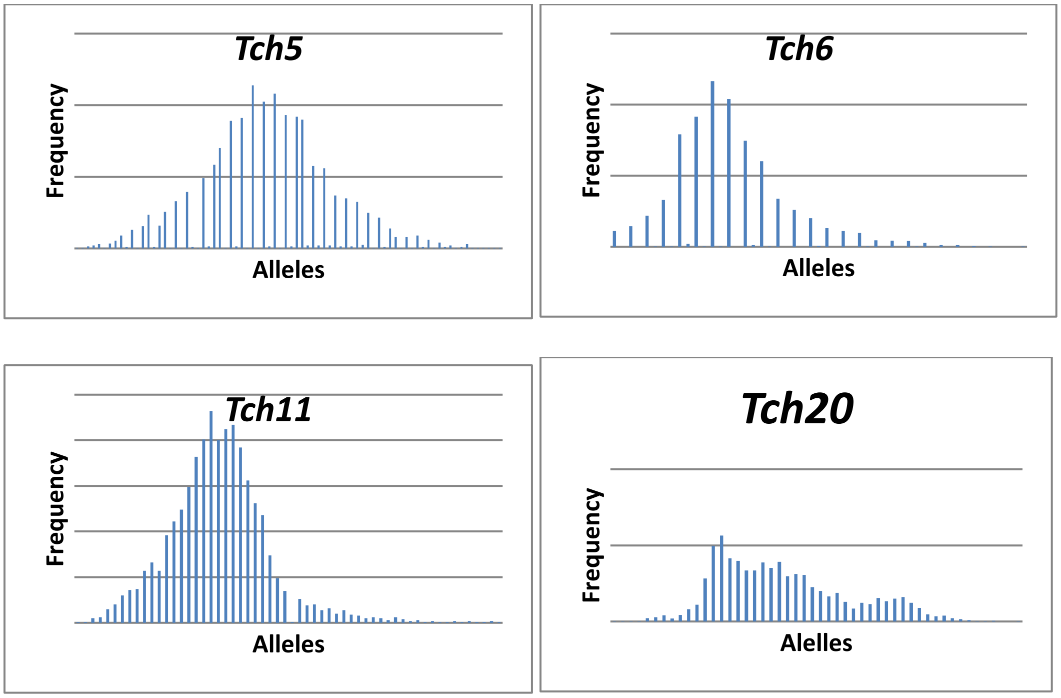


Figure 3. Frequency of alleles in highly variable *Tch* markers.

In contrast, the other 11 loci had fewer alleles (mean = 13), and a range of homozygosity of 0.11 at *Gmo8* to 0.80 at *Sai13*. Many of these loci exhibited a 'ragged' or disrupted pattern of allele frequency distribution. For example, Figure 4.

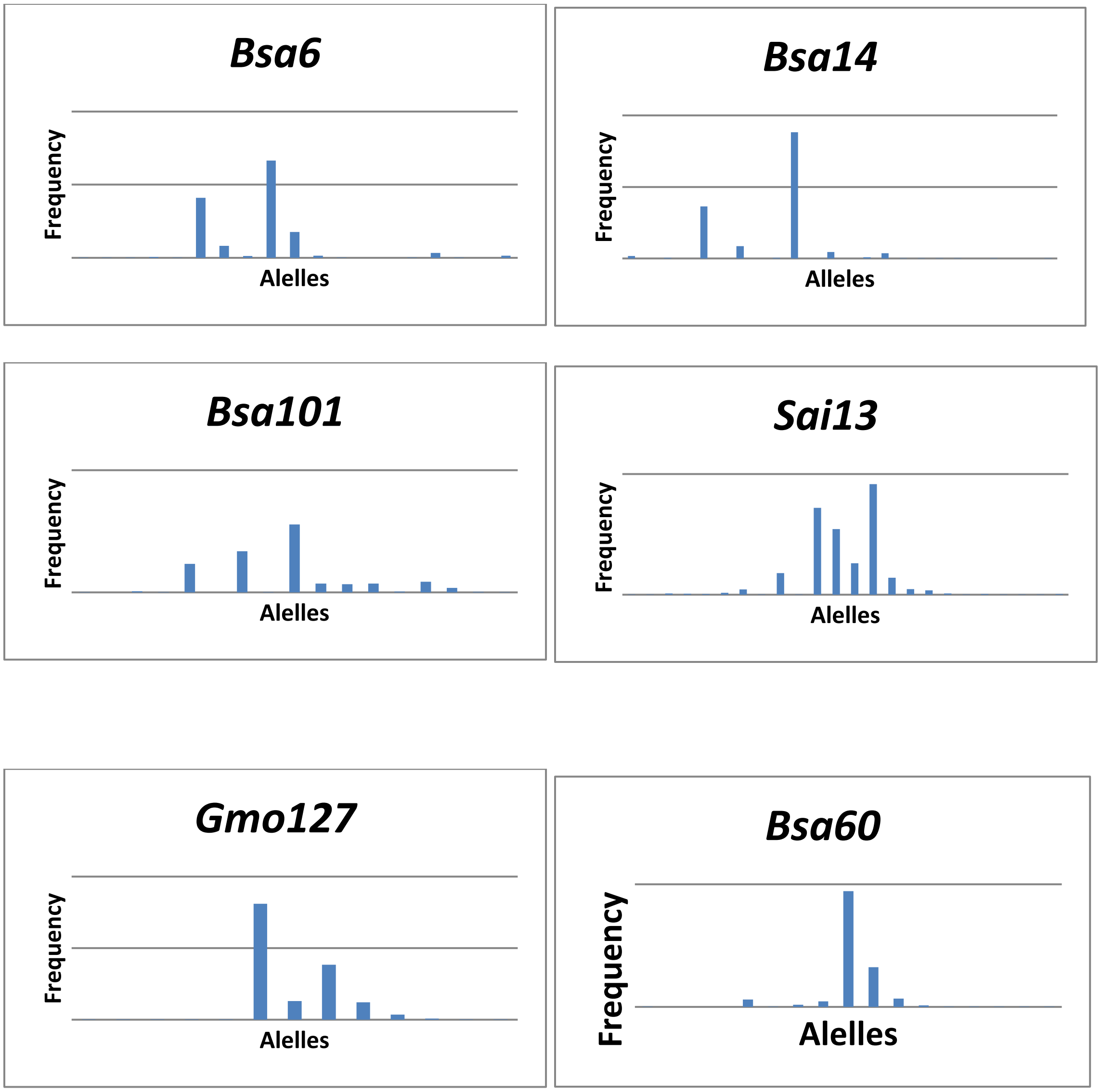


Figure. 4. ‘Ragged’ frequency distribution of 6 loci.

Microsatellite heterozygosity ranged from 0.10 (*Gmo8*) to 0.96 (*Tch20*) over all samples, and averaged 0.58 over loci. Allelic richness was low, and similar across collections, averaged over all loci for both the 7 group and 11 group data sets was between 12.5 and 13.5. Private alleles were detected at most of the loci and throughout the collections. Marker specifics are listed in Appendix 1.

Data analyses-microsatellite markers

The 15 microsatellite markers examined with the program Genetix (Belkhir et al., 2004), showed non-random association of alleles. When the entire collection of 1,493 fish was examined for HWE proportions, 3 of the 15 loci departed significantly ($P<0.0001$) from equilibrium: *Sai13, Bsa*60 and *Gmo8* (all individuals, Table 3). Departures from HWE proportions were due to a greater than expected number of homozygotes. *Sai13* was significantly out of equilibrium for every collection and grouping ($P=0$). This locus presented a higher than expected number of homozygotes for all alleles, which is a strong indication of the presence of null alleles. *Bsa60* departed from HWE proportions at 5 collections, caused primarily by excess homozygosity at the two most abundant alleles, *203 and *207, and a lack of *203/*207 heterozygotes. *Gmo8* equilibrium may be skewed by the presence of one high frequency allele, a second allele of low frequency, and a couple of rare alleles.

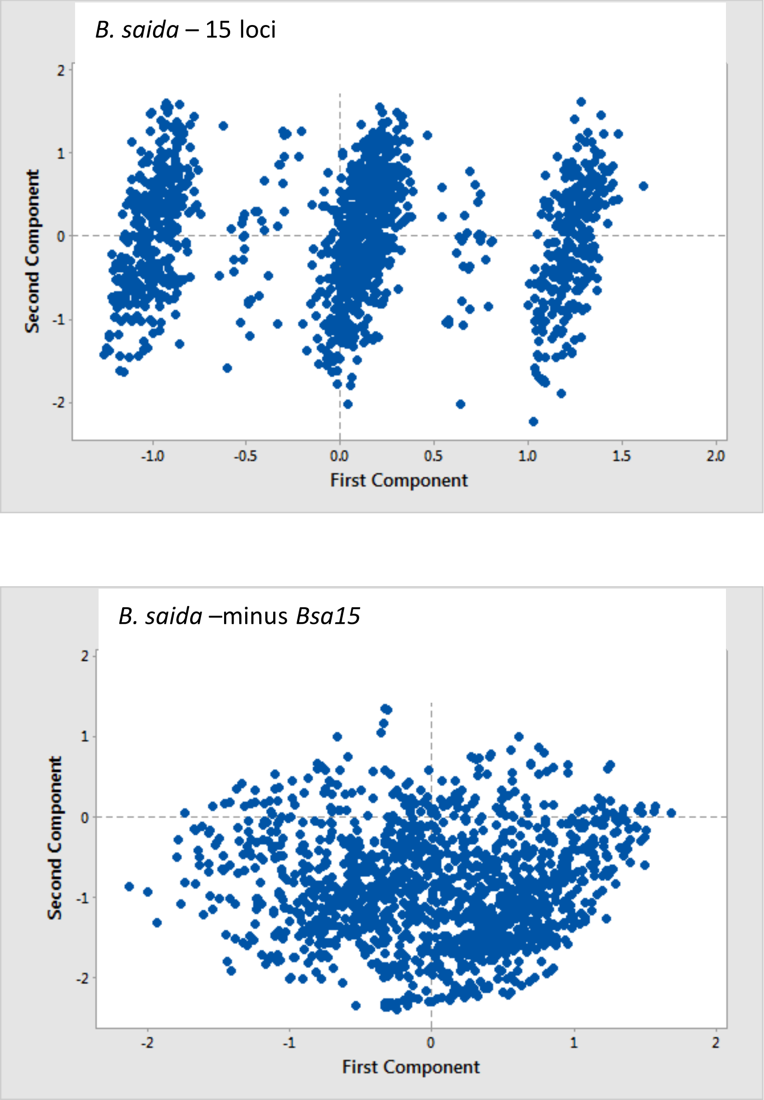
By partitioning the data by collection year (2 groups), the same departures were observed, except the 2012 collection was in equilibrium at locus *Gmo8* ($P=0.51$). Spatial partitioning (7 groups, Fig. 1) revealed Barrow (2 years) out of HWE, despite dropping *Sai13*. Further partitioning analyses into 11 groups (separating out both collection year and geographic region) indicated no groups were out of HWE after removal of *Sai13,* and corrected for multiple tests (Table 3).

Table 3. P-values for Hardy-Weinberg equilibrium tests for 4 partitions of *B. saida* data at 15 loci. The first data set represents the total collection, across all individuals. The second set is the 11 collections outlined in Table 1. The third data set groups the collections by geographic region (Fig. 1). The last data set partitions the data by year. Significant P-values (after Bonferonni correction for multiple tests) are denoted in bold, and HS is highly significant. The total is the P-value of Hardy-Weinberg departures across 14 loci (*Sai13* excluded).

	BSA14	*BSA7*	*Sai13*	*Sai25*	*Bsa60*	*Gmo8*	*Bsa6*	*Bsa101*	*Tch6*	*Tch20*	*Gmo32*	*Bsa15*	*Tch5*	*Tch11*	*Gmo127*	total
All individuals	0.07	0.80	**0**	0.49	**0**	**0**	0.43	0.50	0.38	0.50	0.36	0.89	0.26	0.11	0.82	**HS**
Kotzebue12	0.08	0.74	**0**	0.35	0.05	0.54	0.44	0.42	0.85	0.72	1.00	0.37	0.69	0.49	0.02	0.30
P. Hope12	0.23	0.51	**0**	0.59	**0**	1.00	0.26	0.24	0.37	0.15	1.00	0.27	0.01	0.37	0.90	0.01
Chukchi12	0.80	0.70	**0**	0.18	0.58	1.00	0.78	0.68	0.30	0.80	1.00	0.93	0.13	0.67	0.97	0.98
Barrow12	0.94	0.24	**0**	0.58	0.01	0.40	0.01	0.65	0.66	0.45	1.00	0.61	0.82	0.54	0.98	0.30
N. Bering Sea 10	0.01	0.55	**0**	0.35	0.56	1.00	0.30	0.25	0.76	0.02	0.50	0.67	0.51	0.35	0.58	0.30
St.69 (P. Hope13)	0.25	0.82	**0**	0.14	0.45	1.00	0.61	0.05	0.01	0.34	0.42	0.63	0.02	0.77	0.58	0.18
St75 (Icy Pt. 13)	0.82	0.06	**0**	0.77	0.30	0.13	0.75	0.43	0.86	0.54	1.00	0.40	0.43	0.26	0.58	0.13
St.111 (Barrow 13)	0.36	0.55	**0**	1.00	0.15	**0**	0.21	0.27	0.40	0.59	1.00	0.29	0.40	0.86	0.37	0.20
St.115 (Barrow13)	0.38	0.60	**0**	0.42	0.01	1.00	0.40	0.94	0.23	0.79	0.22	0.93	0.07	0.50	0.06	0.66
St. 150 (Beau13)	0.24	1.00	**0**	0.42	**0**	.44	0.86	0.52	0.16	0.12	0.60	0.15	0.97	0.02	0.96	0.06
St. 151 (Beau13)	0.03	0.71	**0**	1.00	0.02	.04	0.20	0.86	0.27	0.22	1.00	0.66	0.05	0.12	0.90	0.04
All pops (11)	0.04	0.83	**HS**	0.73	**0**	0.20	0.21	0.51	0.20	0.21	0.99	0.78	0.01	0.32	0.63	**HS**
Kotzebue12	0.08	0.74	**0**	0.35	0.05	0.54	0.44	0.42	0.86	0.71	1.00	0.37	0.69	0.49	0.02	0.30
PHope12/13	0.09	0.79	**0**	0.52	**0**	1.00	0.77	0.21	0.24	0.41	0.65	0.36	0.03	0.48	0.83	0.01
Chukchi12	0.80	0.70	**0**	0.18	0.58	1.00	0.78	0.69	0.30	0.82	1.00	0.93	0.15	0.66	0.97	0.98
Barrow12/13	0.54	0.71	**0**	0.89	**0**	**0**	0.1	0.58	0.32	0.87	0.23	0.93	0.11	0.60	0.67	**0**
N. Bering Sea 10	0.01	0.55	**0**	0.35	0.56	1.00	0.30	0.25	0.76	0.02	0.50	0.67	0.52	0.37	0.58	0.21
Icy Pt. 13	0.82	0.06	**0**	0.77	0.30	0.13	0.75	0.43	0.86	0.54	1.00	0.40	0.40	0.26	0.58	0.67
Beaufort13	0.01	0.73	**0**	1.00	**0**	0.01	0.22	0.92	0.12	0.40	0.61	0.99	0.69	0.02	0.98	0.01
All pops (7)	0.01	0.77	**HS**	0.79	**0**	0.05	0.51	0.66	0.52	0.41	0.96	0.93	0.13	0.26	0.68	**HS**
2012	0.59	0.58	**0**	0.35	**0**	0.51	0.14	0.74	0.41	0.08	1.00	0.50	0.35	0.38	0.63	**HS**
2013	0.09	0.84	**0**	0.35	**0**	**0**	0.53	0.28	0.14	0.63	0.05	0.97	0.16	0.36	0.86	**HS**
All pops (year)	0.02	0.83	**HS**	0.38	**0**	**0**	0.28	0.54	0.21	0.22	0.21	0.84	0.26	0.39	0.88	**HS**

Data analyses-genic differentiation

Principal component analysis initially revealed three groups, although, the analysis, was likely driven by an artifact of a single locus, *Bsa15*, with primarily two equally frequent alleles (and heterozygotes). When *Bsa15* was removed, the remaining 14 loci yielded one large genetically panmictic group (Fig. 5).


a.

b.

Figure 5. Principal component analyses of *B. saida* individuals at (a) 15 loci and (b) 14 loci after dropping *Bsa15*.

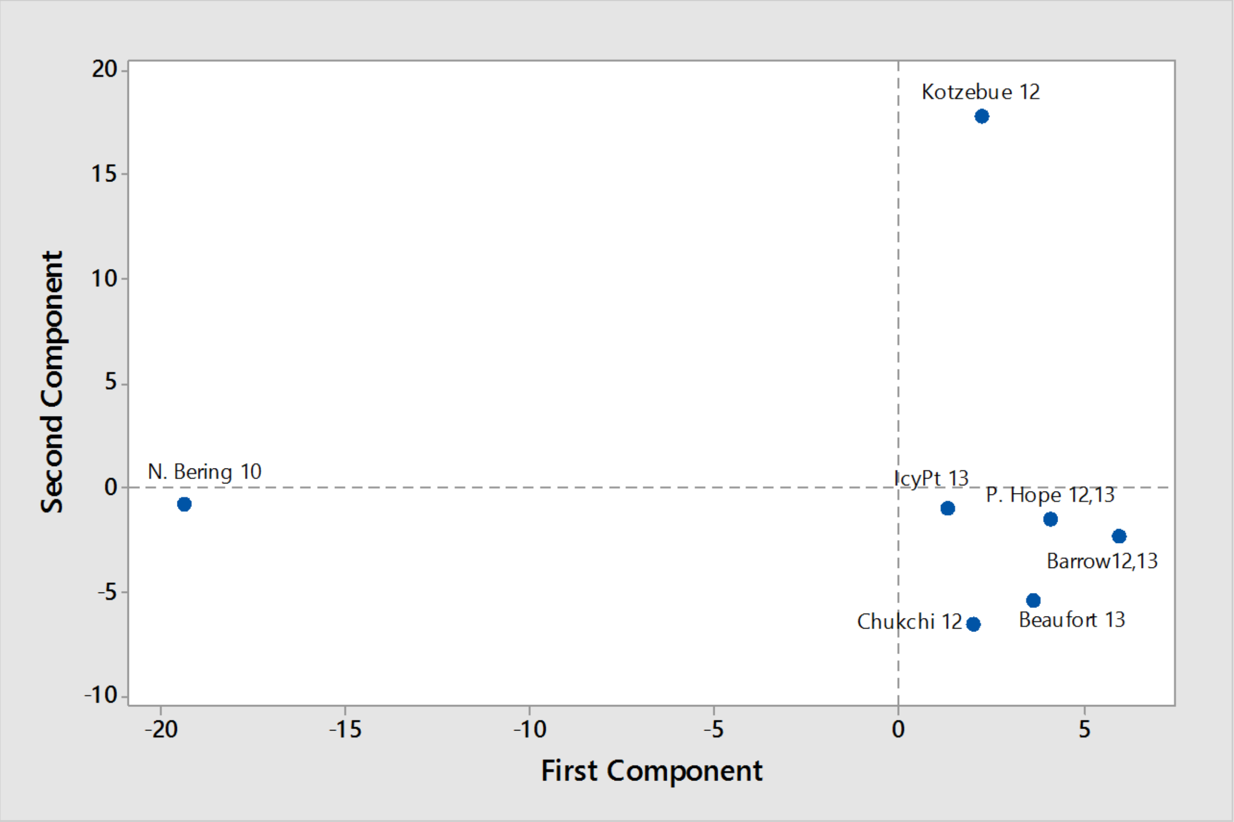


Figure 6. Principal component analyses of 7 collection groups with 15 loci.

The top 5 alleles influencing the first principal component (N. Bering divergence) for 7 groups and 15 loci were: *Tch5* *218, *Tch11* *146, *Bsa101* *142, *Bsa6* *216, and *Tch20* *316. The top 5 alleles driving the second component (Kotzebue divergence) were: *Tch6* *101, *Tch20* *325, *Tch11* *242, *Gmo8* *103, and *Tch20* *276.

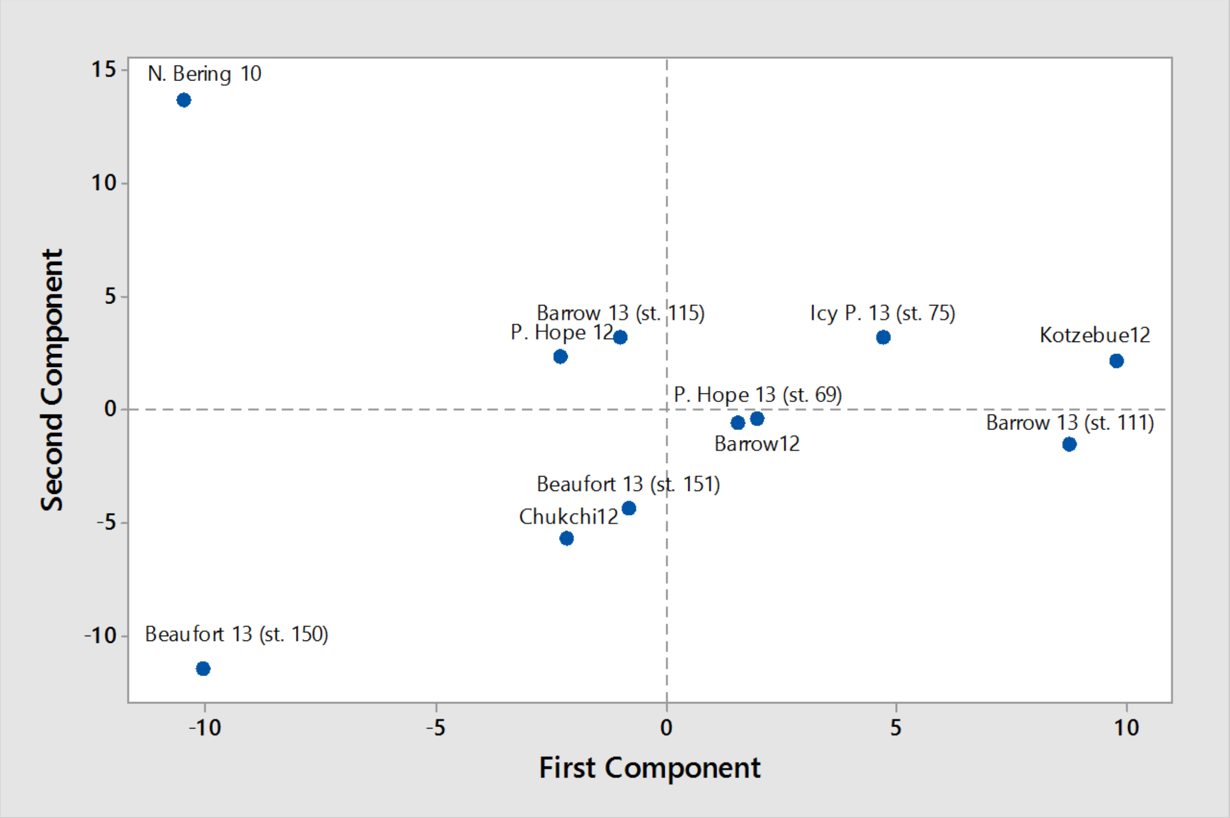


Figure 7. Principal component analysis of 11 collection groups with 15 loci.

The top 5 alleles influencing the first principal component (N. Bering and Beaufort) divergence for 11 groups, 15 loci: *Tch6* *149, *Bsa6* *216, *Tch11* *154 and *248, *Tch20* *316, and the top 5 alleles driving the second principal component divergence (Beaufort1 2013): *Bsa7* *187, *Tch11* *195 and *264, *Bsa15* *187, and *Sai13* *230.

The lack of structure over all individuals was verified by the results from the program STRUCTURE (Fig. 8). In no instance was there a preponderance of samples from one genetic grouping in one of the geographic locations. Data portioning all the samples into 1 to 3 genetic stock groups yielded similar results (not shown). The correct reassignment of simulated samples (in ONCOR) back to the baseline was less than 20%, further verifying a lack of structure (Table 4).

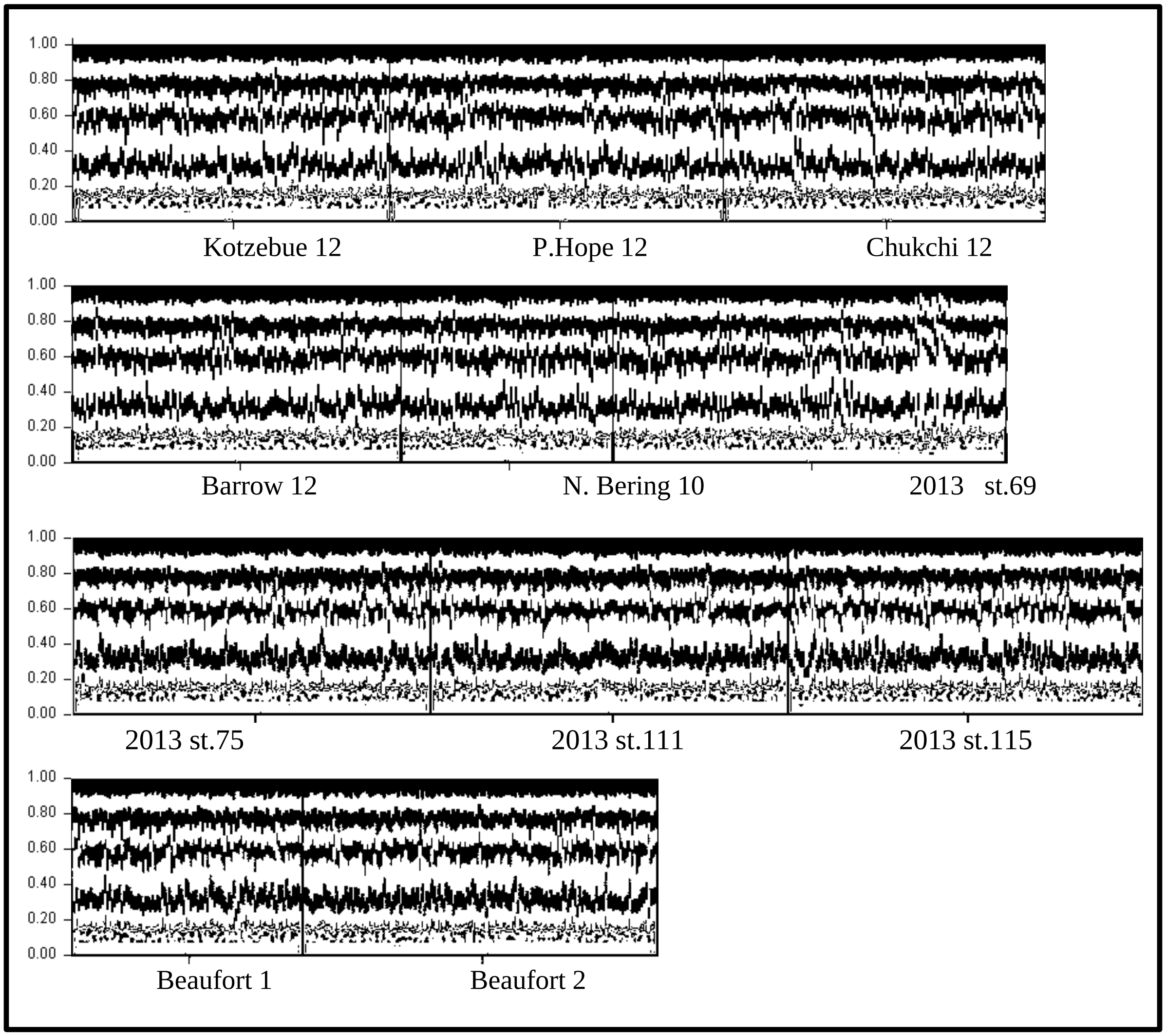


Figure 8. Samples from each of 11 collection groups partitioned based on the clustering method implemented in STRUCTURE. Each box for each of the identified locations contains individual sample information (along the x axis) partitioned into 11 different stock groups (k=11) (colors identified on the y axis).

Table 4. Geographic location evaluation - individual assignment as implemented in ONCOR. Simulated samples were selected from a genetic baseline developed from samples collected at each of the 11 collection groups identified in Fig. 1/Table 1. Shown are the percent re-assignment to the correct collection and assignment to the largest mis-identified collection

Collection	N	% Correct	Largest Mis - ID	
Kotzebue 12	101	12.9	Point Hope 12	12.9
Point Hope 12	98	10.2	Beaufort 13 (st. 151)	13.3
Chukchi 12	92	4.3	Beaufort 13 (st. 150)	16.3
Barrow 12	82	14.6	Point Hope 13 (st. 69)	13.4
Norton 10	81	12.3	Point Hope 13 (st. 69)	14.8
Point Hope 13 (st. 69)	153	5.9	Chukchi 12	13.1
Icy Point (st. 75)	140	6.4	Norton 10	14.3
Barrow 13 (st. 111)	144	11.1	Point Hope 13 (st. 69)	13.9
Barrow 13 (st. 115)	139	12.9	Norton 10	14.4
Beaufort 13 (st. 150)	91	6.6	Chukchi 12	13.2
Beaufort 13 (st. 151)	135	18.5	Point Hope 12	11.1

A comparison of allele frequencies between collection years 2012 and 2013 with a pseudo-exact G-test showed no overall differences (P=0.132) except at locus *Bsa60* (P=0.0001). Pairwise tests of the 11 collections (Table 5) resulted in significant G-test values (after correction) between Icy Cape 13 and P. Hope 12; and at half of the tests involving Beaufort13 st.151. F statistics for these same comparisons were non-significant.

To create the 7 group analyses, the two Pt. Hope collections were combined as they were not significantly different from each other. The three Barrow collections and the two Beaufort collections were also combined. (Table 6). Elaborate binning schemes of alleles with a frequency of 3 or fewer individuals, provided similar results (not shown).

Table 5. Pairwise G-tests of 11 collections, 15 loci, P values above the diagonal, F^{ST} values below the diagonal. Significant values in bold.

	Kotz 2012	Hope 2012	Chuk 2012	Barrow 2012	N. Ber 2010	P.Hope 13, st.69	I.Cape 13, st.75	Barrow 13, st.111	Barrow 13, st.115	Bea13 st.150	Bea13 st.151
Kotzebue 12		0.012	0.194	0.174	0.082	0.327	0.253	0.118	0.013	0.379	**0.008**
P. Hope 12	0.0026		0.061	0.121	0.049	0.042	**0**	0.027	0.038	0.265	0.138
Chukchi 12	0	0.0070		0.494	0.501	0.921	0.792	0.466	0.307	0.742	0.076
Barrow 12	0.0007	0.0013	0		0.240	0.461	0.642	0.100	0.020	0.775	**0**
N. Bering Sea 10	0.0023	0	0.0004	0.0001		0.509	0.677	0.041	0.420	0.271	**0**
P.Hope 13 st. 69	0.0002	0.0011	0	0	0		0.594	0.815	0.434	0.296	0.033
Icy Cape 13 st.75	0.0007	0.0012	0	0	0	0		0.256	0.307	0.272	**0.008**
Barrow 13 st.111	0.0003	0.0004	0	0	0	0	0		0.121	0.089	0.115
Barrow 13 st.115	0.0005	0.0003	0	0	0	0	0	0		0.156	**0.006**
Beau13 st.150	0.0023	0.0005	0	0.0002	0.0010	0.0011	0.0017	0.0014	0.0002		0.321
Beau13 st.151	0.0022	0	0.0002	0.0014	0.0005	0.0006	0.0004	0.0003	0.0006	0.0008	

Table 6. Pairwise G-test of 7 collections, 15 loci, P values above the diagonal, F^{ST} values below the diagonal. Significant values in bold.

	Kotz12	PHope12/13	Chukchi12	Barrow12/13	N. Bering 10	Icy Pt.13	Beaufort13
Kotzebue12		0.143	0.192	0.152	0.081	0.253	0.029
PHope12/13	0.0010		0.625	0.868	0.232	0.066	0.170
Chukchi 12	0	0		0.856	0.500	0.791	0.383
Barrow12/13	0.0060	0	0		0.215	0.547	**0.009**
N. Bering 10	0.0023	0	0.0004	0		0.656	0.010
Icy pt.13	0.0007	0.0001	0	0	0		0.023
Beaufort13	0.0021	0	0	0.0006	0.0005	0.0007	

mtDNA

Sequence information was obtained from 351 *B. saida* samples at 591 bp of the COI gene. Analysis in Arlequin v.3.5 indicated 37 haplotypes (*H*) at 30 polymorphic sites (*S*) with no insertions or deletions. Five clades emerged: one main clade and 4 subclades radiating from it by one or two base pair differences, with singleton haplotypes radiating from four of the five clades (Fig. 9). Both the Neighbor-Joining tree and haplotype network revealed shallow structure in the *B. saida* data set (Fig. 10). Nucleotide diversity (π) averaged over all loci was

0.002162 (+/- 0.001507) and haplotypic diversity (*h*) averaged 0.11. Haplotype sequences are listed in Appendix 2.

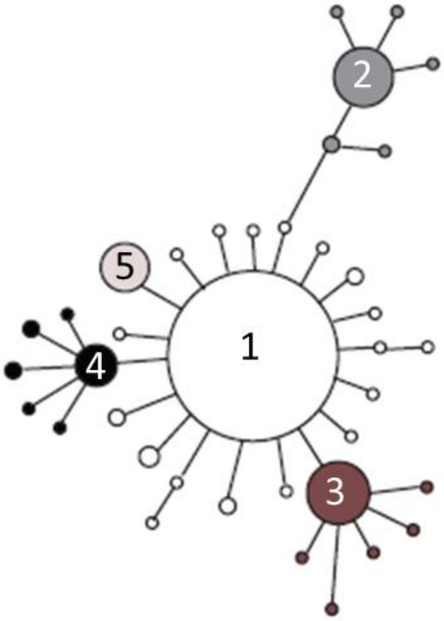


Figure 9. Haplotype network of *B. saida* in the Chukchi Sea. Clades are numbered to correspond with individuals designated in Appendix 3.

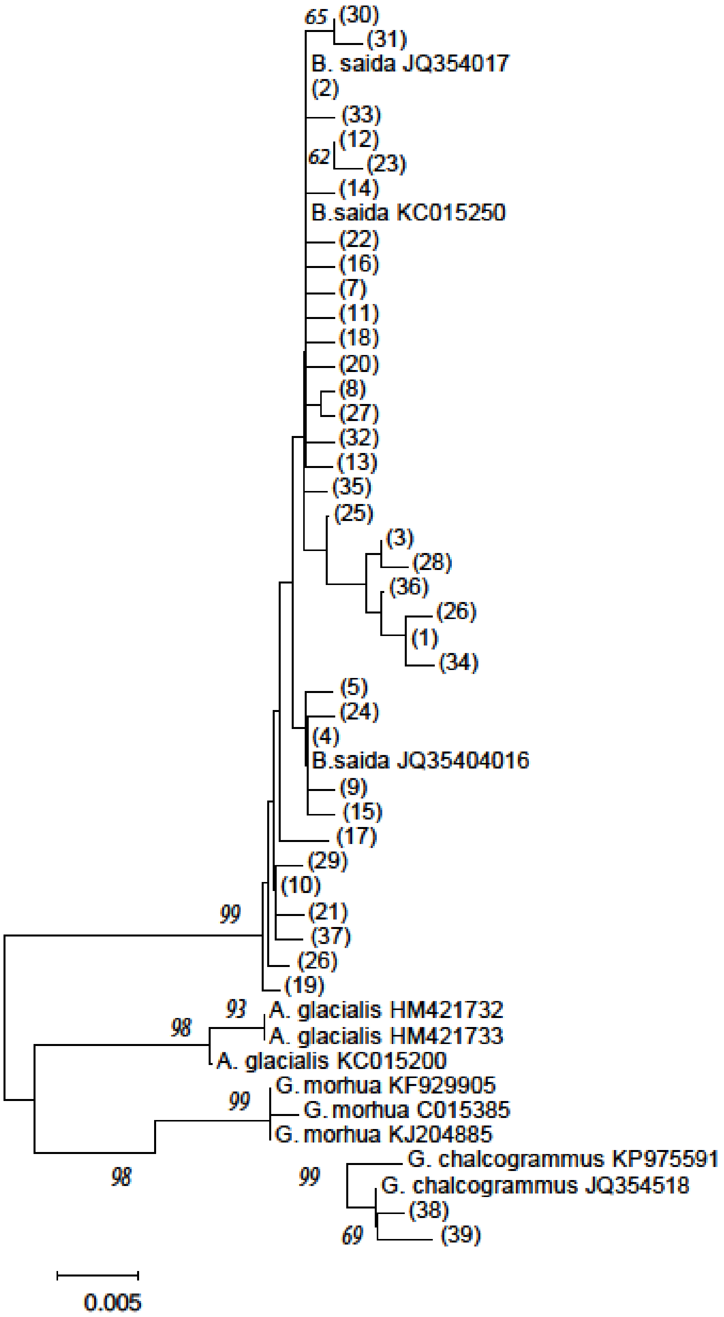


Figure 10. Neighbor-Joining tree created in MEGA 6.0, consensus of 39 COI haplotypes. GenBank sequences of *A. glacialis* (3), *G. morhua* (3), *G. chalcogrammus* (2), and *B. saida* (3) were added to root the tree with known sequences. Nodes with bootstrap support (1000 replicates) greater than 50% are noted with italic numbers.

Microsatellite markers were examined for individuals in each of the five clades (Fig. 9), and compared. G-test did not detect differentiation among the mtDNA clades. Interestingly, *BSA60* was in HWE for all groups, and *Sai13* was in HWE (after correction) for all but the main clade (previously out of HWE at all partitions P=0), although the 4 subclades had only 18-35 individuals in each group.

Table 7. P-values for Hardy Weinberg equilibrium tests of microsatellite markers for the 5 mtDNA haplotype clades (Fig. 9). Significant P values (after correction) are noted in bold.

	Bsa14	*Bsa7*	*Sai13*	*Sai25*	*Bsa60*	*Gmo8*	*Bsa6*	*Bsa101*	*Tch6*	*Tch20*	*Gmo32*	*Bsa15*	*Tch5*	*Tch11*	*Gmo127*	Total
Main clade	0.13	0.67	**0**	0.37	0.04	1	0.49	0.96	0.47	0.45	0.70	0.27	0.98	0.63	0.85	**HS**
Subclade 2	0.85	1	0.50	1	0.06	0.16	0.61	0.34	0.45	0.08	0.32	0.72	0.49	0.78	0.24	0.54
Subclade 3	0.36	1	0.60	1	0.33	0.15	0.35	0.98	0.01	0.94	1	0.73	0.07	0.38	0.19	0.40
Subclade 4	0.85	0.18	0.33	1	0.07	1	0.47	0.14	0.65	0.52	1	0.57	0.03	1	0.80	0.49
Subclade 5	0.31	1	0.01	1	0.06	1	0.31	1	0.08	0.49	1	0.14	0.49	0.24	0.10	0.15

Discussion

Contemporary structure among pelagic species is often difficult to discern, particularly in the absence of basic life history information. This is especially true with pelagic species in the Arctic. These populations likely contracted with glacial advance, resulting in bottleneck and low genetic diversity. It is therefore important to note that while the suite of genetic markers in our study did not detect population structure, it does not preclude that structure may exist. Data from both nuclear and mitochondrial markers in this study suggest *B. saida* in the Chukchi and Alaskan Arctic Ocean are from a single panmictic population. The principal component analysis by individual resulted in a shotgun blast pattern with no apparent geographic structuring. Both STRUCTURE and ONCOR programs identified *G. chalcogrammus* samples (not shown), but indicated that the *B. saida* samples were from one population. G-test's resulted in several significant P values, mostly station 151- the farthest NE collection. F_{st} values indicated no significant population structure. Microsatellite frequencies were highly similar to those reported for the Chukchi collection by Nelson et al. (2013), allowing for future standardization with other *B. saida* data in a larger geographic context.

Low nucleotide and haplotypic diversity identified at the COI gene of the mitochondria suggest a recent population bottleneck or founder event (Grant & Bowman 1998), and clades indicate either successful mutations that have spread in the population or historic distributions of *B. saida* that may have resided in pockets of isolation during periods of glacial fluctuation, and are currently re-connected. These subgroups each contain individuals from all regions sampled, from the N. Bering Sea to the western Beaufort Sea, which indicates a lack of geographic structure in the region.

A few oddities in the study provide food for thought. To re-iterate: individuals were not collected from a known spawning population. The length of individuals from the 2010 and 2012 collections ranged from 86mm to 142mm, indicating they are likely 2-3 year olds. [As a side bar it was noted that some of the 2012 hauls were saturated in a thick white material, resembling milt- possibly an anti-freeze substance seeping from the fish]. In contrast, the 2013 collections, averaged 47mm in length, were young of the year, and genetic information may reflect familial lineages. This may be true for Beaufort13- st.151, which appeared differentiated in several tests (PC analysis for 11 groups, G-tests and HW). St.151 were the smallest fish examined (avg. 36.7mm). Other oddities, such as allelic frequency raggedness at many of the loci (skewness from the stepwise mutation model), and the unexpected random alleles distributed throughout the microsatellite data, remain unexplained. For example, at locus *Sai13*, four individuals were homozygous for private alleles 300 or 304. The overall allelic richness was low, and may be masking divergence. Finally, HWE tests indicated all 11 collections at locus *Sai13* were significantly out of equilibrium (P=0), but when grouped by mtDNA identified sub-groups, 4 of the 5 groups were found to be in HWE. *Bsa60* is also in HWE in all 5 COI groups (previously departed in 6 of 11 collections). In fact, after correction for multiple tests, only one HWE test was significant when individuals were grouped by COI haplotype. Two tests out of 75 is an expected number of significant tests given the number of tests conducted.

Hardy-Weinberg departures may be indicative of selection (or null alleles) or signal a mixture of stocks (the Wahlund Effect). Because more significant departures occurred with geographic groupings of collections than by groupings by mtDNA clades, perhaps future study should focus on sequencing additional samples, effectively increasing the size of the mtDNA subgroups and review HWE and G-test results of samples grouped by mtDNA clades, especially at *Sai13*. G-test results between all sub-clade pairs for all loci were insignificant, however sample sizes of the sub-groups were small (n=18-35).

The dearth of life history knowledge made this a challenging genetic study. Are stocks mixing throughout the area, and if collected during spawning, would subtle structure be more detectable? Changing conditions may drive increased movement and mixing, or may have done so already.

Acknowledgements

A huge thank-you to the many collectors of samples and to Chase Page for processing them. Appreciation and thanks to Dr. Chris Kondzela and Dr. David Tallmon for reviews of the manuscript, and Dr. Christopher Saski of Clemson University for Msat library development. We are grateful to Dr. R. John Nelson of Seastarbiotech for his assistance with marker information and general collaboration.

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Appendix 1. Arctic cod (*Boreogadus saida*) information by loci, including name of locus, GENEBANK ascession number, allele size range and number of bp repeats. Collection: 1 = Norton Sound10, 2 = Kotzebue12, 3 = Pt. Hope12, 4 = Pt. Hope13 (st69), 5 = Icy Pt. 13 (st75), 6 = Open Chukchi12, 7 =Barrow12, 8 = Barrow13 (st111), 9 = Barrow13 (st115), 10 = Beaufort13 (st150), and 11 = Beaufort13 (st151). Collection sizes (N), number of alleles (N_A), allele richness (N_S) corrected to the smallest # of genes-170, observed heterozygosity (H_o), expected heterozygosity (H_e), and estimated inbreeding coefficient (Fis). Total is N across all populations. All other values in the total column are an average across all populations.

Bsa6 HO070596, allele size range 180–216, # alleles-16, 2 bp repeat (CA)

Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	116	137	163	148	107	121	149	149	97	148	1424
N_A	9	11	11	11	11	11	8	9	11	8	11	10.1
N_S	8.91	10.05	9.52	9.74	10.29	7.75	8.29	9.40	9.43	7.74	9.09	9.11
H_o	0.64	0.64	0.62	0.67	0.72	0.69	0.58	0.68	0.73	0.68	0.72	0.67
H_e	0.67	0.67	0.67	0.71	0.70	0.70	0.68	0.67	0.68	0.68	0.68	0.68
F_{is}	0.04	0.05	0.07	0.05	-0.02	0.01	0.15	-0.02	-0.07	0.00	-0.07	0.02

Bsa7 HO070778, allele size range 177-200 , # alleles-11 , 2 bp repeat (CA)

Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	133	138	164	150	135	138	148	149	96	148	1488
N_A	6	8	7	6	7	9	5	7	6	6	7	6.7
N_S	5.95	6.82	6.17	5.35	5.97	7.74	4.23	6.04	5.06	5.77	6.29	5.95
H_o	0.33	0.33	0.28	0.28	0.27	0.27	0.20	0.31	0.30	0.17	0.25	0.27
H_e	0.3	0.30	0.27	0.29	0.28	0.26	0.21	0.32	0.29	0.16	0.24	0.27
F_{is}	-0.09	-0.11	0.00	0.04	0.03	-0.01	0.02	0.04	-0.06	-0.05	-0.03	-0.02

Bsa14 HO071740, allele size range 178–224, # alleles-15, 4 bp repeat (GATA)

Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	132	137	164	149	134	136	148	149	96	148	1482
N_A	10	10	9	11	12	11	9	9	11	10	8	10
N_S	9.86	9.04	8.21	9.52	9.41	9.85	8.05	7.94	9.48	9.63	7.14	8.94
H_o	0.54	0.55	0.63	0.57	0.53	0.63	0.54	0.57	0.65	0.58	0.53	0.57
H_e	0.60	0.57	0.59	0.59	0.54	0.60	0.56	0.58	0.61	0.57	0.56	0.58
F_{is}	0.11	0.04	-0.07	0.03	0.02	-0.05	0.02	0.03	-0.06	-0.02	0.06	0.01

Bsa15 HO071607, allele size range 171-199, # alleles-8, 4 bp repeat (GATT)

Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	132	140	165	146	135	137	147	148	97	149	1485
N_A	3	4	4	6	4	6	4	5	5	3	5	4.5
N_S	2.96	3.86	3.55	4.68	3.55	5.10	3.48	4.08	4.38	3.00	4.39	3.91
H_o	0.52	0.54	0.44	0.51	0.47	0.50	0.47	0.54	0.53	0.49	0.55	0.46
H_e	0.51	0.52	0.50	0.52	0.52	0.53	0.51	0.52	0.53	0.50	0.53	0.52
F_{is}	-0.02	-0.03	0.12	0.02	0.10	0.05	0.09	-0.04	0.00	0.01	-0.03	0.02

Bsa60 HO077536, allele size range 171-248, # alleles-13, 4 bp repeat (TGAA)

Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	132	130	164	149	130	123	149	149	97	148	1460
N_A	7	7	9	7	9	7	9	6	6	8	6	7.4
N_S	7.00	6.64	7.96	6.04	7.84	6.61	8.38	5.82	5.92	7.75	5.92	6.90
H_o	0.57	0.42	0.49	0.51	0.47	0.51	0.50	0.43	0.42	0.47	0.44	0.48
H_e	0.60	0.48	0.57	0.53	0.53	0.52	0.58	0.51	0.51	0.54	0.51	0.53
F_{is}	0.05	0.14	0.19	0.04	0.13	0.03	0.14	0.15	0.18	0.12	0.14	0.12

Bsa101		HO078113, allele size range 130-158, # alleles-15, 4 bp repeat (GATA)										
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	128	139	162	149	126	129	149	146	97	147	1461
N_A	10	10	12	10	10	11	9	9	10	10	12	10.27
N_S	10.00	9.33	10.68	9.55	9.38	10.53	8.96	8.57	9.65	9.75	10.48	9.72
H_o	0.79	0.74	0.83	0.80	0.72	0.76	0.78	0.72	0.80	0.80	0.76	0.77
H_e	0.81	0.76	0.77	0.78	0.77	0.76	0.77	0.78	0.78	0.76	0.78	0.77
F_{is}	0.03	0.03	-0.07	-0.03	0.06	-0.01	0.00	0.08	-0.03	-0.06	0.02	0.00

Gmo8		AF159238, allele size range 101-138, # alleles-13, 4 bp repeat (GACA)										
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	133	121	164	149	122	129	149	149	97	148	1450
N_A	4	4	2	3	4	4	3	7	3	2	3	3.5
N_S	3.91	3.59	2.00	2.52	3.14	3.39	2.88	5.70	2.57	2.00	2.57	3.11
H_o	0.07	0.14	0.08	0.10	0.13	0.07	0.11	0.11	0.07	0.13	0.07	0.10
H_e	0.07	0.14	0.08	0.09	0.13	0.06	0.12	0.15	0.07	0.14	0.10	0.10
F_{is}	-0.02	0.04	-0.04	-0.05	-0.01	-0.02	0.08	0.22	-0.03	0.07	0.23	0.04

Gmo32		DQ191392, allele size range 100-118, # alleles-7, 3 bp repeat (TTG)										
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	133	140	165	146	135	137	147	148	97	149	1486
N_A	4	2	2	3	2	2	2	2	2	2	2	2.3
N_S	3.91	2.00	2.00	2.52	2.00	2.00	2.00	2.00	2.00	2.00	2.00	2.22
H_o	0.21	0.17	0.06	0.19	0.18	0.19	0.16	0.14	0.22	0.20	0.09	0.16
H_e	0.23	0.16	0.06	0.17	0.17	0.18	0.16	0.13	0.19	0.18	0.08	0.16
F_{is}	0.07	0.00	-0.03	-0.10	-0.02	-0.03	0.00	-0.07	-0.12	-0.10	-0.04	-0.04

Gmo127		EU735055, allele size range 259-315, # alleles-13, 4 bp repeat (CAGA)										
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	87	129	137	165	148	133	137	148	148	96	144	1472
N_A	6	8	7	5	9	6	7	8	6	8	7	7
N_S	5.98	6.96	6.57	4.99	7.30	5.64	6.61	6.95	5.57	7.76	6.26	6.42
H_o	0.70	0.64	0.66	0.61	0.66	0.67	0.60	0.61	0.61	0.71	0.56	0.64
H_e	0.63	0.65	0.64	0.59	0.62	0.64	0.61	0.61	0.65	0.67	0.58	0.63
F_{is}	-0.11	0.01	-0.03	-0.03	-0.06	-0.05	0.01	0.01	0.05	-0.05	0.02	-0.02

Sai13		allele size range 194-304, # alleles-24, bp repeat (GTCC/CT)										
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	85	128	137	160	150	134	132	149	148	95	148	1466
N_A	11	13	13	17	14	11	13	14	13	13	14	13.3
N_S	11.00	11.94	10.99	14.00	11.62	10.36	12.05	13.20	11.67	12.76	12.09	11.97
H_o	0.53	0.52	0.63	0.66	0.64	0.57	0.65	0.68	0.59	0.63	0.65	0.61
H_e	0.76	0.78	0.79	0.80	0.79	0.81	0.80	0.80	0.80	0.80	0.79	0.79
F_{is}	0.30	0.33	0.21	0.18	0.19	0.29	0.19	0.16	0.26	0.21	0.18	0.230

Sai25		allele size range 280-289, # alleles-4, 3 bp repeat (TCA)									
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	133	140	165	150	135	135	149	147	97	147	1487
N_A	2	2	3	3	2	3	3	3	3	3	2	2.6
N_S	2.00	2.00	2.61	2.77	2.00	2.63	2.86	2.57	2.58	2.88	2.00	2.45
H_o	0.25	0.17	0.14	0.26	0.29	0.27	0.22	0.25	0.20	0.20	0.20	0.22
H_e	0.22	0.18	0.15	0.23	0.27	0.26	0.23	0.24	0.18	0.21	0.19	0.21
F_{is}	-0.14	0.067	0.02	-0.14	-0.05	-0.04	0.05	-0.04	-0.10	0.07	-0.04	-0.03

Tch5		AF178495, allele size range 174-264, # alleles-73, 4 bp repeat (GATA)										
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	132	137	165	147	134	133	147	148	97	148	1477
N_A	38	48	47	45	47	46	46	48	41	47	46	45.4
N_S	37.67	41.39	40.25	37.13	40.66	39.71	40.58	41.35	36.22	44.91	39.70	39.96
H_o	0.92	0.95	0.92	0.93	0.97	0.95	0.97	0.97	0.95	0.96	0.95	0.95
H_e	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.97	0.95	0.96
F_{is}	0.04	0.01	0.04	0.03	0.00	0.01	-0.01	0.00	0.01	0.01	0.02	0.01

Tch6		AF178496, allele size range 77-177, # alleles-33, 4 bp repeat (GTCT)										
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	128	139	163	149	130	137	149	146	97	147	1474
N_A	19	20	22	22	21	19	24	23	23	21	22	21.5
N_S	18.86	17.84	20.48	19.72	18.57	18.02	21.77	19.64	21.20	20.47	19.83	19.67
H_o	0.89	0.88	0.91	0.80	0.92	0.89	0.95	0.85	0.90	0.93	0.88	0.89
H_e	0.91	0.88	0.91	0.90	0.91	0.87	0.91	0.90	0.91	0.91	0.90	0.90
F_{is}	0.02	0.00	0.00	0.11	-0.01	-0.02	-0.04	0.06	0.02	-0.02	0.03	0.01

Tch11		AF178501, allele size range 122-374, # alleles-58, 4 bp repeat (GATA)										
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	85	133	133	165	150	135	132	149	147	97	145	1471
N_A	29	38	37	38	35	34	37	39	34	33	35	35.4
N_S	29.00	32.77	32.96	31.71	30.80	31.06	32.46	34.56	29.51	31.69	31.47	31.64
H_o	0.94	0.95	0.96	0.93	0.93	0.93	0.95	0.97	0.94	0.90	0.92	0.94
H_e	0.94	0.95	0.95	0.95	0.95	0.95	0.95	0.96	0.95	0.95	0.95	0.95
F_{is}	0.00	0.00	-0.01	0.02	0.03	0.03	0.00	-0.02	0.01	0.05	0.04	0.01

Tch20		AF178509, allele size range 160-366, # alleles-48, 2 bp repeat (GA)										
Collection	1	2	3	4	5	6	7	8	9	10	11	Total
N	89	128	136	162	149	131	136	149	145	96	149	1470
N_A	31	35	35	38	38	37	37	37	39	34	39	36.4
N_S	30.86	30.02	32.67	33.96	33.97	35.03	33.84	34.26	35.57	33.36	34.33	33.44
H_o	0.93	0.95	0.93	0.98	0.96	0.95	0.96	0.96	0.98	0.96	0.95	0.96
H_e	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96	0.96
F_{is}	0.03	0.01	0.03	-0.01	0.00	0.00	0.00	0.00	-0.02	0.00	0.01	0.00

Appendix 2. 591 bp of the COI gene sequenced in *B. saida.* 37 haplotypes were identified among 351 individuals. Names (in bold), corresponds with the haplotype column in the accompanying raw data file. Number of individuals exhibiting that haplotype is noted in parentheses.

1 (222)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1A (1)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCCGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1B (2)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTAATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1C (1)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATTACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1D (1)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTATCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1E (1)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCGCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1F (1)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTGCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1G (1)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTACTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT
(2)

1H (1)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATACCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1I (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCAGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1J (3)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATTGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1K (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCCTCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1L (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCCTCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGTTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1M (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTGTCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1N (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTTATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1O (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTTATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTGTTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1P (2)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCAGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

1Q (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
GGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

2 (27)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTACAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATGAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGATCCTGCTGGAGGAGGTGACCCCATTT

2A (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTACAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATGAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTGTATCCCCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGATCCTGCTGGAGGAGGTGACCCCATTT

2B (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTACAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATGCCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATGAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCCCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGATCCTGCTGGAGGAGGTGACCCCATTT

2C (2)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATGAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCCCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGATCCTGCTGGAGGAGGTGACCCCATTT

2D (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATGAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGAGCTGGAACAGGCTGAACTGTATATCCCCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGATCCTGCTGGAGGAGGTGACCCCATTT

2E (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGATCCTGCTGGAGGAGGTGACCCCATTT

3 (30)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCAC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

3A (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCAC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCGTCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

3B (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCAC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCCCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

3C (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCAC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGAGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCAC
TATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAGC
AATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCAG
CTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

3D (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCAC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACGATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

3E (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTCACAGCAC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTACTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

4 (13)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTACTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

4A (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATTGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTACTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

4B (1)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTACTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCCGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

4C (2)

TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTACAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTACTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

4D (2)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTGTATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTACTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

4E (1)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGGACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTACTAATTACAGCTGTACTCCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

5 (18)
TAAGCCTGCTCATTCGAGCAGAGCTAAGTCAACCTGGTGCACTCCTTGGTGACGATCAAATTTATAATGTGATCGTTACAGCGC
ACGCTTTCGTAATAATTTTCTTTATAGTAATACCACTAATAATTGGAGGCTTTGGAAACTGACTCATTCCTCTAATGATCGGTGC
CCCAGATATAGCTTTCCCTCGAATAAATAATATAAGCTTCTGACTTCTTCCTCCATCTTTCCTTCTCCTTTTAGCATCCTCTGGTGT
AGAAGCTGGGGCTGGAACAGGCTGAACTGTATATCCTCCTTTAGCCGGAAACCTCGCTCATGCTGGAGCATCTGTTGATCTCA
CTATCTTTTCTCTTCATCTAGCAGGTATTTCATCAATTCTTGGGGCAATTAATTTTATTACCACAATTATTAATATGAAACCTCCAG
CAATTTCACAGTACCAAACACCCCTCTTTGTTTGAGCGGTGCTAATTACAGCTGTACTTCTACTATTATCTCTTCCCGTCTTAGCA
GCTGGTATCACAATACTTCTAACTGACCGTAATCTTAACACTTCTTTCTTTGACCCTGCTGGAGGAGGTGACCCCATTT

March 3, 1849

The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under US administration.

The Bureau of Ocean Energy Management

As a bureau of the Department of the Interior, the Bureau of Ocean Energy (BOEM) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS) in an environmentally sound and safe manner.

The BOEM Environmental Studies Program

The mission of the Environmental Studies Program (ESP) is to provide the information needed to predict, assess, and manage impacts from offshore energy and marine mineral exploration, development, and production activities on human, marine, and coastal environments.