Chapter 4. Synthesis of Arctic Alaska Marine Fish Ecology

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Abstract

The compilation of data and information, its review, and the synthesis processes leading to the development of individual species accounts focused on descriptive elements of Arctic Alaska's marine fish fauna. The species accounts reflect the compilation and review of a large body scientific information about the marine fishes off Alaska in United States waters in the northern Bering Sea, north of the Bering Strait, and throughout the circumpolar Arctic. The purpose of this synthesis is to interpret the whole of this biological and ecological information in the context of the marine biogeography of the Chukchi and Beaufort Seas. This interpretive approach provides historical and contemporary perspectives to our descriptions of (1) patterns of species occurrence, habitat and population relationships, and (2) functional ecosystem processes that affect the distribution and abundance of marine fishes, and, with respect to the present, (3) conceptual understanding and information needed for resource management and conservation. The objectives of this synthesis focus on environmental relationships including physio-chemical factors (for example, temperature, salinity, dissolved oxygen, and turbidity), mechanisms (for example, currents, migrations, and movements), and biological processes (for example, competition, predation, colonization, and reproduction) that collectively have limited the distribution, abundance, and productivity of marine fish populations through adaptations to Arctic conditions.

Introduction—A Biogeographic Emphasis

Individual species accounts present a large amount of information about the biology, geography, and environmental factors affecting large-scale patterns of distribution and abundance. Collectively, this compilation of environmental information is foundational for an improved understanding of the descriptive and interpretive components of this region's biogeography (Nelson, 2006). Our focus on the interpretive component (historical and ecological elements of biogeography) provides a meaningful approach for explaining the observed diversity relationships, synthesizing the information presented, and expressing our impressions about outstanding needs. Historical biogeography addresses the origins of distributional patterns as determined from systematic studies. The paleoceanographic record is not well-developed from this part of the Arctic and here we explore species origins in light of possible dispersal and vicariance events as suggested by paleontology and geologic records, climatic histories, and known phylogenetic relationships. Ecological biogeography addresses the environmental relationships including physiochemical factors (for example, temperature, salinity, dissolved oxygen, and turbidity), mechanisms (for example, currents, migrations, and movements), and biological processes (for example, competition, predation, colonization, and reproduction) that limit the distribution, relative abundance, and productivity of a species. Information about body size and trophic position also are reviewed because they are important parameters that correlate with metabolic processes and other life history traits (Romanuk and others, 2011).

The descriptive component of biogeography is addressed in project tasks leading to an updated checklist of marine fishes, presentation of information in the species accounts, and special analyses related to (1) new species occurrences and range extensions, (2) large-scale patterns of abundance from past and ongoing studies, and (3) identification of species likely to occur, but yet-to-be confirmed from the Chukchi and Beaufort Seas. The visualization of species information in new maps and depth profiles provides another dimension to evaluation of the status of baseline information than was previously available. This is especially relevant as it applies to availability of age- or stage-specific information and related habitat relationships. Quantitative relationships between age-and-length and size-at-length have been described for several dominant species, but this information is dated. For almost all species, information about stock structure and population dynamics (that is, differential mortalities between life stages or age classes) remains to be described. Although many science gaps exist, compiling and integrating descriptive and interpretive information-types allows a more detailed examination of linkages between geographic distributions, evolutionary processes (patterns of life history variations), ecological factors, genetic diversity, and population dynamics

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for the fauna as an initial approach to estimating effects of environmental change (Winemiller, 2004; Benton and others, 2006). This approach illustrates why the information presented in the species accounts is relevant to decision making and, for potential indicators species, a rationale for research priorities.

Historical Biogeography

The Chukchi and Beaufort Seas occupy a relatively small region within the zoogeographic realm (Mecklenburg and others, 2011) that has been used by classical ichthyologists to describe the taxonomy and composition of the Arctic marine fishes (Briggs, 1974; Andriashev and Chernova 1994; Eastman, 1997; and Mecklenburg and others, 2011). In Alaska, the Arctic Realm includes the northern Bering Sea and marine environments beyond the EEZ[3]. As such, it does not directly correspond to conventional natural resource management areas in the Alaskan Arctic. The southern boundary of the province in the Bering Sea is ecologically significant because the area demarks a sharp gradient in diversity and abundance of Arctic and Boreal marine fishes that is defined by temperature (<2 °C). As such, a natural rather than administrative faunal separation is represented. For example, NOAA collected 86 species of marine fishes in the northern Bering Sea in 1981 (Thorsteinson and others, 1984) compared to the 300 species reported from the southeastern Bering Sea (Wilimovsky, 1974). The zonation is important to contemporary Arctic issues with respect to extralimital species and northerly shifts in distributions and range expansions associated with climate change and potential fisheries. The importance of the Bering Strait with respect to geologic and climatic history and origins and exchanges of fishes, especially during the late Pleistocene, has been shown to be critical to understanding Pacific influences on Arctic fauna (for example, Mecklenburg and others, 2011).

A systematic comparison of the marine fishes reported from the Arctic province, marginal seas of the Arctic Ocean, and Bering Sea provides clues and insights about the evolutionary processes (origins, rates of endemism) underlying current patterns of taxonomic representation (zoogeographic patterns, chapter 2). The comparison of marine fish faunas from adjacent waters also is instructive with respect to origins (distribution centers), expectation of probable occurrence, or in some instances, understanding founding sources of confirmed species from the U.S. Arctic (table 4.1, additional Arctic seas in Christiansen and others, 2013).

The estimates of marine fish diversity (occurrence) in table 4.1, was from published literature or acquired through reliable sources of written communications, and represent “working” totals from a field of ichthyology that is rapidly changing. These changes relate to new discoveries, increased sampling, and new genetic tools for identification and better understanding of evolutionary relationships. The presence of 15 new marine fishes from the U.S. Arctic not reported in the *Fishes of Alaska* (Mecklenburg and others, 2002) has been confirmed for this report (table 2.2). Many of the authors cited reported significant problems associated with species identifications (related these to unresolved taxonomic issues), deficiencies in geographic sampling coverage, or access to existing data and information. Despite these issues, the systematic comparisons help to begin to explain large-scale patterns of biodiversity including origins of species distributions.

Biogeographic research has shown that fish species in the Pacific and Atlantic Oceans have similar zoogeographic patterns with respect to latitudinal gradients, but not diversity (Christiansen and others, 2008; Christiansen and others, 2013). In each ocean, species richness peaks in the tropics with sharp gradients between tropical and temperate waters. There is leveling off in decline of richness toward the poles (Roy and others, 1998). Using marine gastropod diversity data, Roy and others (1998) examined latitudinal gradients in the Atlantic Ocean with respect to ecological traits (that is, range size, habitable area, and input of solar energy). The greatest correlation reported was between diversity and sea surface temperature (a proxy for solar input) suggesting that, if the relation was causal, it probably was linked through some aspect of production. Because the physical mechanisms of dispersal for marine invertebrates and fishes are similar (or the same), process effects—such as production cycles and events—would similarly influence geographic distribution and abundance patterns.

In areas where regional faunas are relatively well known, Briggs and Bowen (2012) described a high concordance between levels of endemism in fishes, molluscs, and other biota. However, Roy and others (1998) could not explain latitudinal gradients in the North Atlantic based on recent geologic history. By contrast, Vermeij (1991) and Briggs (1995, 2003) described the biogeographic consequences of the opening of the Bering Strait and the Great Trans-Arctic Biotic Exchange (3.5 million years ago [Ma]) on the dispersal of Arctic molluscs and marine fishes, respectively (see table 4.2 for geologic periods). Prior to this opening, the marine barrier formed by Beringia had isolated Pacific and Atlantic faunas for millions of years. Vermeij (1991) determined that of the 295 mollusc species that participated in the interchange, almost 90 percent (n=261) had Pacific origins or were descended from taxa with Pacific origins. Briggs (2003) hypothesized an asymmetrical invasion of marine fishes from a North Pacific evolutionary center (“*centres of origin*” hypothesis) and that at least one species from

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[3] The three provinces described in Sigler and others (2011) relate to Bering, Chukchi, and Beaufort Seas and relate more directly to smaller ecological units in a conservation context. For this discussion, the classical definition for a province is used based on endemism. In this case, the provincial boundaries correspond with the geography of shelf areas of the Arctic Region described by Briggs and Bowan (2012).

Table 4.1. Systematic comparisons of marine fishes occurring in the Arctic marine and adjacent seas or marine areas bordering the U.S. Chukchi and Beaufort Seas.

[**Regions:** Arctic Realm (as defined in this chapter), Arctic Zoogeographic Region described by Mecklenburg and others (2011). OCS, Outer Continental Shelf; ~, approximately; –, not applicable]

Regions	Geography relative to U.S. study area	Estimated total number of				References
		Orders	Families	Genera	Species	
Arctic Realm	Encompasses circumpolar Arctic including the northern Bering Sea	22	45	126	242	Mecklenburg and others (2011)
U.S. Beaufort Sea	Beaufort Sea OCS Planning Area	9	19	44	83	This report
U.S. Chukchi Sea	Chukchi Sea OCS Planning Area	11	22	56	97	This report
Chukchi Borderland	North U.S. Chukchi Sea	4	7	11	12	Mecklenburg and others (2014); Longshan and others (2014)
Canadian Beaufort Sea[1]	East of U.S. Beaufort Sea	21	48	115	189	Coad and Reist (2004)
Yukon	Adjacent to U.S. Beaufort Sea and north of Yukon Territory, Canada	9	14	28	44–46	Coad and Reist (2004)
Russian Chukchi Sea	West of U.S. Chukchi Sea	11	26	68	112	Parin (2004); Parin and others (2014); Datsky (2015)
East Siberian Sea	Northern Russia east of Chukchi Sea	9	14	33	65	Pauley and Swartz (2007)
U.S. Bering Sea	U.S. territorial marine waters south of Chukchi Sea	21	64	190	~375	Mecklenburg and others (2002); Mecklenburg and others (2011 OR1); Maslenikov and others (2013); Love and others, written commun. (2015)[2]
Northern Bering Sea	Bering Sea from the Bering Strait to the south of St. Lawrence Island	–	–	–	(a) 128 (b) 136 (c) 165	(a) OBIS database (http:/www.iobis.org/); (b) Chernova (2011); (c) Datsky and Andronov (2007)
Bering Sea	Entire Bering Sea south of Chukchi Sea	–	–	–	(a) 385 (b) 418	(a) Christiansen and others (2013); Mecklenburg and Steinke (2015) (b) Greenwald and others (2006)

[1] This estimate does not include brackish water species.

[2] Love and others, written commun. (2015) refers to an ongoing updating of Love and others (2005).

Salmonidae, Osmeridae, Hexagrammidae, Cottidae, Agonidae, Liparidae, Stichaeidae, and Pholidae contributed to the Arctic-North Atlantic fauna. The Capelin (*Mallotus catervarius*) is an example of such a Trans-Arctic dispersal during the Pleistocene (Dodson and others, 2007). Similarly, the cod family, Gadidae, is thought to have developed in the North Atlantic and contributed two species to the North Pacific.

Large segments of an ancient fauna of boreal origins are believed to have gone extinct during the late Miocene (Mecklenburg and others, 2011). The opening of the Bering Strait, prevailing ocean conditions and currents probably favored the dispersal of new North Pacific species into habitable Arctic shelf areas during the Pliocene (Eastman, 1997; Briggs, 2003). Ocean connections to the Arctic during this period are hypothesized to have been primarily through the Fram (North Atlantic) and Bering (North Pacific) Straits. The relatively small number of species in the Arctic suggests that widespread dispersal processes were constrained by the separation of basins and absence of a circumpolar current.

Christiansen and others (2013, p. 195) noted that (Arctic) freshwater and diadromous fishes were "*significantly molded by glaciation, deglaciation and geological events during the late Pleistocene and Holocene epochs (i.e. ~ 126,000 and 12,000 years ago, respectively)*" and that (citing Krylov and others, 2008 and Polyak and others, 2010) the evolutionary history of the marine fish fauna "*dates back to the Neogene period as the modern circulation in the Arctic Ocean began to form some 14–17 million years ago*." The Great Exchange occurred during a period of ice-free, boreal conditions. The greater success of Pacific invaders was hypothesized by Briggs (1995) to be related to their "superior competiveness" (for example, behavioral, reproductive rate, individual

Table 4.2. Geologic and climatic history of the Arctic.

Era(s)	Recent geologic history (millions of years ago)	Geologic and climatic significance
Late Cretaceous	80	Beringia (Bering Land Bridge) forms and separates North Pacific and Arctic-North Atlantic faunas.
Paleocene–Oligocene	66–23.03	The Arctic Region was in high latitude position and the climate was temperate with water temperatures of 10–15 °C. Water temperatures gradually cooled during the Eocene and ligocene eras (56–23.03 million years [Ma] ago)
Miocene	23.03–5.3	Arctic land masses reached their present positions and water temperatures dropped below freezing (10–15 Ma). The Bering Strait may have opened during the Cenozoic (6–12 Ma) allowing for limited passage (Briggs, 2003). Additional cooling, ice sheet expansion, lower sea levels, and shallow Bering Strait, limit exchanges between Arctic and Pacific Oceans. Ocean circulation was latitudinal with limited Arctic-North Atlantic exchanges. The southward movement of the warm-temperate zone and its replacement by the cold-temperate zone are hypothesized to have caused mass extinctions of boreal families during the late Miocene.
Pliocene	3.5–3	The opening of Bering Strait allowed many Pacific species to invade the Arctic. Ocean circulation changed with the closure of the Isthmus of Panama (about 3.2 Ma), which strengthened the Gulf Stream, increased precipitation at high latitudes, and contributed to further glaciation in the northern hemisphere. The Atlantic and Pacific Oceans had oceanic connections to the Arctic during the late Pliocene and faunal interchange was possible.
Pleistocene	2.588–0.0117 (11,700 years ago)	The early Pleistocene was a time of glacial advances and retreats, periodic freshwater inputs into the Arctic Basin, and cooling leading to the formation of Arctic sea ice. Permanent ice cover has been present for at least 0.7 Ma and possibly intermittently as long as 2.0 Ma. Some components of the Arctic marine fauna may have persisted from the Miocene and Pliocene eras and exchanges with the Atlantic and Pacific were also possible as the Bering Strait remained open.

size, or vulnerability to predators or parasites) resulting from their evolution in a highly diverse marine ecosystem. Extended cooling between 2.9 and 2.4 Ma is postulated to have led to the extinction of the truly boreal species and given rise to the modern Arctic fauna (table 4.2; see Eastman, 1997; Mecklenburg and others, 2002, 2011; Briggs, 1974, 1995, 2003, 2004). This fauna is characterized by relatively few (numbers) endemic species when compared to the diversity of marine fish fauna from lower latitudes. The low amount of endemism has been hypothesized to be related to evolutionary effects of ocean continuity and lack of geographic isolation over recent time. Briggs (1995) indicated that the Arctic climate repeatedly warmed and cooled until about 3 Ma when present cold conditions stabilized.

In Alaska, the species richness of the marine fish fauna from the high Arctic (includes northern Bering Sea as used here) is similarly low when compared to lower latitudes (chapter 2). Interestingly, the number of endemic species relative to total number of marine fishes reported from the U.S. Chukchi and Beaufort Seas is relatively high. We propose that this relates to the geographic isolation of this region during the last glacial period resulting from a lack of connection between Pacific and Arctic oceans through the Bering Strait, and the absence of shelf environment between openings with the Nordic Seas.

Geographic Perspectives of Marine Fish Diversity

Mecklenburg and others (2011) examined the faunal composition of marine fishes in the Arctic region and confirmed earlier characterizations of the young phylogenetic age of dominant families (for example, Zoarcidae and Stichaeidae) and the apparent lack of successful invaders from the Atlantic (for example, Gadidae and Anarhichadidae). Data in this report support these findings as they extend to Alaska. As an example, the two largest families (Zoarcidae with 17 species and Cottidae with 17 species) were determined to contain almost one-third of the total number of species reported. They were followed, in order of decreasing species numbers, by Salmonidae (12), Pleuronectidae (9), Stichaeidae (8), Agonidae (7), and Liparidae (6). Collectively, seven (7) families accounted for nearly 68 percent of the region's confirmed marine fish diversity. In the western Chukchi Sea, Datsky (2015) noted a similar pattern (without Salmonidae), with members of the Cottidae, Zoarcidae, Pleuronectidae, Stichaeidae, and Agonidae accounting for 66 percent (73 species) of the total number of species identified.

Regional comparisons of the diversity of fishes reported from marine waters adjacent to the U.S. Arctic are qualitative[4]; however, the distributional patterns suggested by presence-absence data suggest dispersal processes. With respect to the U.S. Arctic, the Bering Sea, with more than 400 marine fishes, represents the largest regional source of potential colonizing species. The same is true of the North Atlantic for the Barents and Eastern Siberian Seas. When the species information is examined in the context of prevailing ocean currents and transport processes, a northerly dispersal of species in Pacific Waters, notably in Alaska Coastal Water, seems to be the most probable (with respect to likelihood of success) historical and contemporary mechanism for large-scale colonization of the U.S. Chukchi and Beaufort Seas. The distribution of shared species in the Chukchi Sea (United States and Russian), Chukchi Borderlands, and southeastern Beaufort Sea (United States and Yukon) would seem to reinforce the Pacific transport hypothesis (table 4.2). However, Mecklenburg and others (2014) noted that all 12 species collected from the Chukchi Borderland occur, and many are common in northern Atlantic sectors of the Arctic. Their findings support an Atlantic transport hypothesis in subsurface currents associated with Atlantic water masses. Alternatively, as the authors suggest, the species could have been in the region for thousands of years but simply not discovered until recently because of the previous lack of sampling.

A regional comparison of the presence data indicates a high percentage of shared species between United States sectors of the Chukchi and Beaufort Seas (table 4.3). Although this could be an artifact of existing data collection, it supports a major dispersal pathway in Alaska Coastal Water. The regional data as a whole further support the existence of an inter-regional gradient of declining species richness with increasing latitude. This pattern was reported previously for the U.S. Arctic (Craig, 1984) and was related to the lack of expatriate species from the Bering Sea found in the Beaufort Sea (Crawford and others [2012] citing others). In this case, the transport of Alaska Coastal Water to the east and north of Point Barrow (fig. 1.1) may impede larval dispersal and colonization processes. Cold temperatures, availability of foods, and other physical and biotic prerequisites of the Beaufort Sea coastal habitats could be major constraints to successful colonization.

Table 4.3. Estimated numbers of common or shared species in the U.S Arctic and adjacent marine areas.

[**Russian Chukchi Sea:** Total estimate of 67 assumes Arctic Cod and Pacific Cod occur in the area, but were not reported by Pauly and Swartz (2007). **Arctic:** Includes Chukchi and Beaufort Seas in waters of the United States]

Regions	Chukchi Borderland	Russian Chukchi Sea	United States			Yukon
			Chukchi Sea	Beaufort Sea	Arctic	
Chukchi Borderland	12	4	7	9	7	3
Russian Chukchi Sea		67	46	42	39	22
U.S. Chukchi Sea			97	68	68	31
U.S. Beaufort Sea				83	68	34
U.S. Arctic					109	30
Yukon						44–46

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[4] Comparisons are problematic due to differences in sampling, problems associated with field identifications and nomenclature, and taxonomic uncertainties.

Understanding the diversity of marine fishes in adjacent areas also provides information about extralimital occurrences and a basis for reasoned expectations about probable species occurrences (not yet recorded) and possible founding sources of new species into Alaska waters (table 4.3). Mecklenburg and others (2011) reported the presence of 242 species of marine fishes in a circumpolar Arctic study area that, for Alaska, extends into the northern Bering Sea. Mecklenburg and Steinke (2015) report 122 marine fishes from the Pacific Marine Region, a smaller region that includes northern Bering, Chukchi, Beaufort, and East Siberian Seas. They do not include amphidromous species in their tally of marine fishes. The Center of Biodiversity reports the occurrence of 418 species of marine fish in the Bering Sea (Greenwald and others, 2006) and although this number could not be verified, it is indicative of the high diversity of fishes found south of the Bering Strait. With respect to the U.S. EEZ in the Bering Sea, Mecklenburg and others (2002) reported about 350 species. As part an ongoing effort to update a checklist of marine and estuarine fishes in United States waters by Love and others (2005), the current estimate is between 375 and 400 species for this part of the Bering Sea.

An examination of regional oceanographic and zoogeographic patterns in light of known phylogenetic relations provides additional support for hypotheses regarding the ancestry of Arctic marine fishes. For the United States, the updated list of fishes is indicative of both widespread (Pacific and Atlantic) and endemic (Arctic Ocean) origins. The species derived from Atlantic and Pacific origins further suggest the role of ocean currents on dispersal and the hypothesized importance of the continuity of Arctic shelves to colonization (Eastman, 1997). To illustrate the concept, Carmack and Wassman (2006), estimated that the flow of Atlantic Water into the Arctic Ocean is, on average, more than five times larger than inflow of Pacific Water. This difference was considered to be responsible for the dominance of Atlantic-derived species over much of the northern Russian shelf.

The analysis herein of zoogeographic patterns revealed that Atlantic-derived species account for less than 10 percent of the diversity (n=9 species) of marine fishes confirmed from United States waters. This includes species from Stichaeidae (*Eumesogrammus praecisus*, *Leptoclinus maculatus*, and *Stichaeus punctatus*), Gadidae (*Gadus chalcogrammus* and *Gadus macrocephalus*), Psychrolutidae (*Cottunculus microps*), Osmeridae (*Hypomesus olidus*), Myctophidae (*Benthosema glaciale*) and Pleuronectidae (*Reinhardtius hippoglossoides*). Interestingly, only two stichaeids (*E. praecisus* and *S. punctatus*) are found in both Chukchi and Beaufort Seas suggesting a discontinuous dispersal for members of this family. A slightly broader examination of the distribution of Atlantic-derived species that included marine areas adjacent to Alaska revealed four species from four families in the Russian Chukchi Sea (*G. chalcogrammus*, *E. praecisus*, *L. maculatus*, and *R. hippoglossoides*); five species from five families in the Chukchi Borderland (*G. chalcogrammus, Artedellius atlanticus*, *C. microps*, *L. maculatus*, and *R. hippoglossoides*); and one species from the Yukon (*Ammodytes dubius*) and the possibility of a longitudinal gradient along the shelf break.

Paleontological Connections

Knowledge of the paleoceanographic conditions and how these conditions affect the evolution of Arctic marine fishes is limited. It seems clear from the inventory of known marine fishes from U.S. Arctic waters that endemic species (that is, Arctic, predominantly Arctic and Arctic Boreal fauna) are significant components of Chukchi (58 percent) and Beaufort (>74 percent) assemblages. How the opening and closing of the Bering Strait, interglacials, and formation of shelf ecosystems affected dispersal and speciation processes and faunal distinctions must be related to observed differences in regional oceanography, dispersal corridors, and energy pathways (Barber and others, 1997; Carmack and Wassmann, 2006; Dunton and others, 2006; Cui and others, 2009; Norcross and others, 2010). For example, Pacific water influences on the Chukchi Sea shelf are more direct than advection of regional water masses onto the Beaufort Sea shelf. The hydrography of the Beaufort Sea shelf is affected by winds, upwelling, and river inputs, and presents a variable environment for its fishery occupants (Carmack and Wassman, 2006). Biogeographic data are indicative of Pacific influences on recent (<3 Ma) colonization processes. Regional differences in shelf environments (topographic, bathymetric, hydrographic, hydrologic, currents, and biologic) correspond to broad patterns of observed diversity in adaptive strategies between the Chukchi (greater than numbers/abundance of marine species) and Beaufort (greater than numbers/abundance of amphidromous species) Seas. The latitudinal gradient that forms the southern boundary of the Arctic province is evident in the data presented. A less pronounced subregional gradient is near Point Barrow (Chukchi Sea greater than numbers of Bering Sea species less than Beaufort Sea).

Adaptations in Marine Arctic Fishes

Environmental conditions in the Chukchi and Beaufort Seas pose numerous substantial challenges to their fish populations. As noted by Power (1997, p. 16), "*Fish living in arctic marine waters have to adapt to low temperature, in most places below the usual freezing point of teleost blood; seasonally constrained low productivity; perpetual or long periods of darkness; and an ice-affected shoreline.*" In contrast to waters of Antarctica, Arctic waters may also have substantial annual changes in salinity (Eastman, 1997). The Arctic challenges extend to how, where, and when research has been conducted, and the resulting ecological information is much better for coastally occurring species and for those taken in subsistence fishing, than for truly marine fishes. As a result, Arctic marine fishes are a current emphasis of BOEM research including physiological studies in laboratory and field studies (appendix A) as sea ice retreats and technological advances allow greater access to offshore marine environments for scientists and industry alike.

Many investigations show how large-scale oceanographic processes over coastal, shelf, and slope environments of the Arctic Ocean and marginal seas relate to observed differences in regional productivity and transfer of energy to benthic and pelagic components of the marine ecosystem. These affect the form (anatomical and morphological, for example, Mecklenburg and others, 2002) and function (ecological niche) of individual species and, collectively, the suite of life strategies for marine fishes occupying these waters (chapter 3). Arctic shelves are shallow and often are characterized by the richness and biomass of their benthos. With respect to the U.S. Arctic, Carey and Ruff (1977) and Carey (1987) hypothesized the predominance of benthic- and pelagic-dominated ecosystems in the Chukchi and Beaufort Seas, respectfully, as suggested by the distribution and abundance of infaunal and epifaunal invertebrates. Subsequent research (for example, Grebmeier and others, 2006a) related observed patterns of distribution to ocean features and to the cropping efficiency of herbivorous zooplankton and transport of organic matter to the benthos. The tight coupling (low efficiency) between pelagic and benthic ecosystems reported by Grebmeier and others (2006a) support the Carey (1987) hypothesis for the Chukchi Sea shelf, but the effects of shelf-slope exchange in deeper waters and the Beaufort Sea (Forrest and others, 2007) are far less clear. The low diversity and biomass of benthic invertebrates reported in ongoing benthic surveys (Katherine Wedemeyer, BOEM Alaska OCS Region, Anchorage, Alaska, oral commun., 2015) may lend further support to the pelagic hypothesis especially in eastern sectors of the U.S. Beaufort Sea. Coastal processes and food webs in the nearshore marine (≤10 m depths) are affected by terrestrial, freshwater, and marine influences. Marine exposures and influences generally are relatively greater along the U.S. Chukchi Sea coast than the Alaska Beaufort Sea.

The role of sea ice as a substrate for algal production and marine food webs represents a specialized flow of energy in the Arctic marine environment (Alexander, 1992). The composition, low relative abundance, and low trophic position of the marine fish assemblage reported from the Chukchi Sea are indicative of an invertebrate-dominated benthic ecosystem over shelf waters. The suspected occurrence of large concentrations of Arctic cod in deep waters of the Chukchi and Beaufort Seas (Crawford and others, 2012) suggests more pelagic processes may be occurring over the slope. Nearer shore, the role of terrestrial peat in coastal food webs of the Alaska Beaufort Sea represents a conceptually different but important source of organic matter in coastal food webs and in the adaptation, and interactions of marine fish in ephemeral brackish waters that annually form along the coast (Dunton and others, 2006). As new data from BOEM studies on the distribution and abundance of marine fish and invertebrates from offshore marine areas of the Chukchi and Beaufort Seas, including food habits and bioenergetics become available, greater insights into more specific Arctic adaptive strategies will be possible.

Descriptions of the survival strategies of cold-water fishes in the Arctic environment are provided herein along with considerations of adaptations gleaned from known information about marine fishes living in other polar regions and, to a lesser extent, more temperate waters. However, there is a shortage of research on the physiology and behavior of the fishes of the Chukchi and Beaufort Seas. Although some studies were conducted on taxa like Arctic Cod and Shorthorn Sculpin in other parts of their ranges, most physiological research has been on Antarctic species from a region quite different from the Arctic. At high latitudes particularly, Antarctic waters have been covered in an ice sheet for 10–15 million years. Its inshore waters have been isolated from lower latitudes for about 25 million years (leading to a suite of endemic and closely related species), and it has both temperatures and salinities that are quite stable over the course of a year (Eastman, 1997; DeVries and Steffensen, 2005; Verde and others, 2006). Additionally, the water beneath this ice sheet is super-cooled, leading to the formation of ice crystals to depths of more than 30 m. In contrast, a permanent ice cover has existed in the Arctic for only 0.7–3 million years, so there are no barriers to immigration into the region (leading to a relatively diverse fish assemblage). Water temperatures can vary as much as 15 °C during a year, and at least in some nearshore environments, the variability in salinity is significant (Eastman, 1997; DeVries and Steffensen, 2005; Whiteley and others, 2006). There is no super-cooled water in the Arctic. As an example, over the course of a year, conditions for the nearshore fish assemblage in Simpson Lagoon, Beaufort Sea, included temperatures from at least –2 to 14 °C, freshwater to marine conditions, and clear to extremely turbid waters (Craig and Haldorson, 1981).

Because most of the research on physiological and behavioral adaptations of fishes to polar conditions has been conducted on Antarctic fishes, some of the results of this research should be cautiously extrapolated to Arctic taxa. As noted by Wells (2005, p. 302), “*There is no a priori reason that their [Antarctic fishes] adaptations should parallel those seen in the Arctic fishes.*”

Physical and Sensory Adaptations

Particularly in comparison to fish physiology and biochemistry, physical adaptations to Arctic environments, if any, are poorly understood. Seasonal changes in light and sea ice effect in concert with cold temperatures, geographic vagaries in productivity and coupling of marine pelagic-benthic ecosystems, and the general low abundance of marine fishes are evident in their physical structure and functional morphology. These adaptations relate to how fishes interact and navigate Arctic marine waters in search for prey, potential mates, and optimum habitats. Examples of physical adaptations have been described with respect to sensory organs such as eyes, lateral lines, and barbels; skeletal and musculature structures; egg and larval conditions; and patterns of coloration. The physical placement of eyes and mouth, shape and size of mouth, and arrangement of teeth, reflect examples of morphological adaptations to dietary requirements and evolved predator-prey relationships (for example, piscivores, plankivores, benthivores, and generalists). Collectively, the adaptations relate to various search, capture, and ingestion strategies related to life (that is, moving, feeding, growing, maturing, and reproducing) in the Arctic marine environment.

Little is known about the direct selective effects of cold on sensory organs, although there has been some research on adaptations of the nervous system to lower temperatures (see section, "Physiological and Biochemical Adaptations"). Some work has examined the role that low light levels (either seasonal or during summer under ice cover) might have on sensory system function. McAllister (1975) discussed a number of potential sensory adaptations to low light levels in Arctic fishes. He compared eye diameters between five pairs of closely related fishes— one pair from the genera *Eleginus*, *Gadus*, *Triglops*, *Aspidophoroides*, and *Liopsetta*). In each comparison, one species of the pair was taken from the Arctic; the other species were from boreal or subarctic waters. In each case, the northern representative had larger eyes. He also noted that Arctic-caught Pacific Cod (*Gadus microcephalus*; identified as Greenland Cod, *G. ogac*) and Arctic-caught Atlantic Cod (*G. morhua*) had barbels that were longer (when standardized against orbit length) than those of Atlantic Cod taken in boreal waters. Similarly, the barbels of the Arctic-dwelling Arctic Alligatorfish (*Aspidophoroides olrikii*) are prominent, whereas those of the congeneric and, arguably more boreal-dwelling Alligatorfish are small. McAllister also generalized that the lateral line systems of a number of Arctic gadids and sculpins are composed of exposed filaments rather than filaments inside of canals, a trait found in other members of these families that lived in more southerly waters.

Since McAllister's (1975) review, no research has been done in Arctic waters that attempted to verify his hypothesis. Work on Antarctic fishes has shown that there are some, but not extreme, adaptations to low-light environments in visual, lateral line, chemosensory, and tactile systems. For instance, and apparently similar to some Arctic fishes, many nototheniids have relatively large numbers of free neuromasts, perhaps in response to feeding and avoiding predation at low light levels (Montgomery and Sutherland, 1997; Macdonald and Montgomery 2005). However, it may be difficult to assign the reason for the evolution of this trait. As an example, Coombs and Montgomery (1994) examined the frequent occurrence of free neuromasts on the ventral trunks of Antarctic notothenioid fishes. They argued that this may not be a response to living in low light levels. Rather, it may be a non-adaptive, paedomorphic trait, essentially a holdover from larval structures. However, it is not clear whether a midwater lifestyle or a low-light environment selected for this morphology. McAllister also made the generalization that, with few exceptions, Arctic fishes tend to be drably colored and suggested that the relatively low light levels of that environment might favor species that blend in with that environment.

Numerous attempts have been made to link increasing vertebral number, and its possible ramifications, with adaptation to Arctic conditions. This was first presented by Jordan (1891) as "*in certain groups of fishes the northern or cold-water representatives have a larger number of vertebrae than those members which are found in tropical regions*" and is now called "Jordan's Rule."(McDowall, 2008, p. 502). Nikolsky (1963), McAllister (1975), and other subsequent authors have speculated that greater numbers of vertebrae would be selected for in cold-water species. They noted that the additional myomeres associated with those vertebrae would aid in swimming through more viscous cold waters and help overcome a putative lowered efficiency of colder muscles. However, McDowall (2008) questions whether "Jordan's Rule," as well as several other generalities (that is, "Bergmann's Rule," "Lindsey's Rule," and "Williston's Rule") regarding the interrelationships among water temperature, size of individuals, and number of vertebrae, have any evolutionary significance. McDowall's (2008) position is that (1) there are many exceptions to these "rules," (2) it remains unclear what drives these relationships in an adaptive sense, and (3) there is a lack of understanding regarding whether variation in vertebrae number is under genetic and (or) environmental control.

An additional generalization, summarized in varying degrees in Rass (1941, 1989) and Marshall (1953) is that species living in Arctic waters have larger and fewer eggs (with larger yolks) than do those living in boreal waters. Marshall (1953) suggests that larger and yolkier eggs may be most adaptive in polar waters, where prey may be available only over a short plankton season. The advantages of the larger larvae that emerge from these eggs are "*the smaller food requirements in relation to size combined with increased powers of swimming, leading to a widening of the range of search for suitable food…Hatching at an advanced stage with a shortening of the period leading to metamorphosis is likely to be advantageous in high arctic [sic] and Antarctic waters with a short seasonal plankton production…an increased supply of yolk leads to increased rates of growth of embryos and larvae, thus counteracting the retarding influence of low temperatures…*" (Marshall, 1953, p. 340). Since that time, only a few studies have examined this phenomenon. Miller and others (1991) determined that among 13 species of flatfishes in the Atlantic, the 3 species in Arctic waters had the largest eggs. The operative factor(s) selecting for this trend remain somewhat unclear. Rass (1941) considered water temperature alone responsible, whereas Marshall (1953) considered both physical factors (such as temperature) and biological factors (such as a short planktonic production season) important. The results of several studies imply that, at least in some groups, larger eggs are attributable to differences in spawning seasons rather than directly to temperature clines (Chambers, 1997).

Lastly, we note the observations of Miller and Kendall (2009, p. 439): "*It's interesting to note that on the Arctic and Antarctic shelves, fish eggs are mainly demersal. A review of maternal output in polar fishes (Christiansen et al. 1998) revealed that while there was a pattern of relatively few and large eggs in polar versus boreal fishes this difference did not exist in substrate spawning species with large yolk reserves and long incubation periods (e.g., Greenland cod [Gadus ogac] and arctic flounder [Liopsetta glacialis], whereas most other cods and right eye flounders [Pleuronectidae] have pelagic eggs. It's possible that spawning demersal eggs may protect the eggs against the risk of freezing and/or also against the low salinity of the surface water (where osmoregulation is difficult) during the melting of the ice.*"

Physiological and Biochemical Adaptations

Adaptations related to living at low temperatures generally relate to the "scope for growth" bioenergetics processes that occur at molecular and cellular levels of fish physiology. Much of the available research has focused on antifreeze proteins (AFPs) in fishes from Polar regions. These proteins and other properties of blood chemistry are important adaptations to how Arctic marine fishes may avoid freezing or respond to below freezing conditions (for example, specializations in the nervous system).

Below freezing conditions represent a significant environmental threat to fish species living in polar regions, as the blood plasma of most marine teleosts freezes at about -0.7 to -0.9 °C (Holmes and Donaldson, 1969), well warmer than the freezing point of sea water (that is, -1.9 °C). In response, many fish species that inhabit Arctic waters have evolved the ability to lower the freezing point of their body fluids. Of particular importance to a fish living in subfreezing waters is the ability to prevent the ice crystals that occur in these waters from growing larger, either on that fish's external surface or, after ingestion, within the body (DeVries and Cheng 2005; Cheng and others, 2006).

The freezing point of aqueous solutions, such as those in fishes, can be depressed through elevating the concentrations of dissolved solutes. These solutes include such plasma electrolytes as sodium (Na^+) and chloride (Cl^-) (O'Grady and DeVries, 1982). However, high concentrations of these ions can interfere with a range of biological processes, such as enzyme activity, protein subunit assembly, and protein solubility (Somero, 1992). Fishes also depress their freezing points with a number of organic compounds that have less disruptive effect on these processes (Raymond, 1997). These compounds include glycerol (Raymond, 1992; Driedzic and Short, 2007), trimethyamine oxide (Raymond, 1994; Raymond and DeVries, 1998), urea (Raymond, 1994; Raymond and DeVries, 1998), and glucose (Benziger and Umminger, 1973). All of these ions and compounds depress the freezing point colligatively (acting through the number of ions or molecules in a given amount of solvent and not on their size or mass). Serum-ion concentrations in marine teleosts living in very cold waters generally are relatively high, typically, 40 percent higher than in fishes from more temperate waters (Raymond, 1997).

The concentrations of dissolved solutes in many cold-water dwelling marine fishes (that is, Shorthorn Sculpin, Hew and others [1980]; Sea Raven [*Hemitripterus americanus*], Fletcher and others [1984]; Atlantic Wolffish [*Anarhichas lupus*], Desjardins and others [2006]; see also O'Grady and DeVries [1982]) increase during the winter, probably in response to decreasing temperature and photoperiod (Driedzic and others, 2006). Dissolved solute concentrations may provide sufficient or near-sufficient antifreeze protection for only a few species (for example, Navaga [*Eleginus navaga*], Christiansen and others [1995] and Arctic Smelt, Raymond [1992]), whereas for all others the amount of freezing protection afforded is likely limited (Fletcher and others, 1985b).

All cold-water dwelling fish species exposed to ice protect themselves from freezing by synthesizing AFPs. There are five distinct molecular groups of antifreeze proteins (AFP Types I–IV and antifreeze glycoproteins (AFGPs) (Fletcher and others, 2001); for the purposes herein all antifreeze proteins are referred to as AFPs. The five AFP types (among only distantly related taxa) are sufficiently structurally different from each other as to have evolved independently (Davies and others, 1988; Fletcher and others, 2001). The evolution of AFPs in Northern Hemisphere Arctic teleost fishes (table 4.4) likely occurred within the last 3 million years. This was the first time that these waters were glaciated (ice crystals formed) since the last ice age about 280 million years ago before the rise of teleosts (see Kennett, 1982; Scott and others, 1986; Fletcher and others, 2001; Davies and others, 1988).

Each type of AFP likely is coded for by a gene family (Hew and others, 1988; Scott and others, 1988; Shears and others, 1993; Desjardins and others, 2006). For instance, the number of gene copies of Type III AFP in the Atlantic Wolfish and Ocean Pout (*Zoarces americanus)* is estimated to be 85 and 150, respectively (Desjardins and others, 2006). Although the adult fish ability to inhibit freezing in the presence of ice through the production of AFPs is well documented, there is growing evidence that this ability also is in embryos and larvae of some species (Murray and others, 2002, 2003; Robles and others, 2005; Desjardins and others, 2007) and perhaps in their eggs (Desjardins and others, 2007).

Table 4.4. Species known to have antifreeze-protein or antifreeze-glycoprotein activity in the U.S. Chukchi–Beaufort Sea region.

[All studies listed used fishes taken outside the U.S. Chukchi–Beaufort Sea region. Families are arranged in phylogenetic order (Nelson and others, 2004)]

Family	Common name	Source
Clupeidae	Pacific Herring[1]	Power (1997)
Gadidae	Arctic Cod	Denstad and others (1987); Enevoldsen and others (2003); Nahrgang and others (2010)
	Saffron Cod	Raymond and others (1975)
	Pacific Cod[2]	Van Voorhies and others (1978); Enevoldsen and others (2003)
Osmeridae	Arctic Smelt	Raymond (1992)
Cottidae	Atlantic Hookear Sculpin[3]	Enevoldsen and others (2003)
	Arctic Staghorn Sculpin	Enevoldsen and others (2003)
	Arctic Sculpin	Enevoldsen and others (2003)
	Shorthorn Sculpin[4]	Raymond and others (1975); Hew and others (1980); Denstad and others (1987); Enevoldsen and others (2003)
Liparidae	Kelp Snailfish[1]	Enevoldsen and others (2003)
Stichaeidae	Arctic Shanny	Enevoldsen and others (2003)
Zoarcidae	Polar Eelpout[5]	Davenport (1992)
Pholidae	Banded Gunnel	Enevoldsen and others (2003)
Pleuronectidae	Alaska Plaice[6]	DeVries (1980)

[1] Enevoldsen and others (2003) reported antifreeze proteins (AFPs) from “Pygmy Snailfish” now known as “Kelp Snailfish.”

[2] As Greenland Cod, *Gadus ogac*.

[3] Scientific name for Atlantic Hookear Sculpin is *Artediellus atlanticus*.

[4] Raymond and others (1975), reported AFPs from “*Myoxocephalus verrucosus*” from Saint Lawrence Island, Bering Sea. This is a synonym of *M. scorpius* (Mecklenburg and others, 2002).

[5] Enevoldsen and others (2003) reported AFPs from “Canadian Eelpout” now known as “Polar Eelpout.”

[6] DeVries (1980) reported AFPs from “Arctic Plaice” now known as “Alaska Plaice.”

AFPs may be produced in several parts of the body. In many species, AFPs are primarily (or solely) produced in the liver (Davies and others, 1988). However, in at least some species (for example, Shorthorn Sculpin, Longhorn Sculpin (*Myoxocephalus octodemspinosus*), Winter Flounder (*Pseudopleuronectes americanus*), and Ocean Pout) AFPs are produced in the liver and in the epidermis of structures such as the gills, skin, scales, and fins (Gong and others, 1992; Fletcher and others, 2001; Low and others, 2002; Murray and others, 2002, 2003). The exocrine pancreas appears to be the sole site of AFP production in all Antarctic notothenioid fishes (Cheng and others, 2006); such pancreatic production has not yet been detected in Arctic taxa. Praebel and Ramlov (2005) determined that, in some species, AFPs also are derived from food sources. They examined levels of AFPs in the gastrointestinal tracts of Arctic Cod (*Boreogadus saida*) feeding either on AFP-containing Arctic Cod or on crustaceans that did not produce AFPs. They determined that Ice Cod (*Arctogadus glacialis*) that had fed on Arctic Cod contained significantly higher levels of AFPs in their digestive fluids. Praebel and Ramlev (2005) hypothesized that partly digested, but still functioning, AFPs could be absorbed into the bodies of Arctic Cod.

AFPs do not prevent the creation of ice crystals within the fish; rather they retard the growth of ice crystals that have entered the fish (Raymond and DeVries, 1977; Evans and others, 2011). Each AFP molecule binds preferentially (and likely permanently) to well-defined sites on newly formed ice crystals (rather than to the surrounding water), thus altering their structure and inhibiting their growth (Fletcher, 1977; Fletcher and others, 2001; Davies and others, 2002; Goddard and Fletcher, 2002; Howard and others, 2010). The different types of AFP molecules bind to different surface planes on an ice crystal (Knight and others, 1991; Fletcher and others, 2001). In at least some species, "chaperone molecules," such as glycerol, enhance AFP activity (Gong and others, 2011). Compared to dissolved solutes, AFP molecules act noncolligatively; that is they have little effect on the osmotic balance within a fish (because the action of AFP molecules is not proportional to the number of molecules present).

Preventing the buildup of ice crystals is a two-step process involving preventing ice crystals in the environment from entering the body through the skin and preventing those crystals that do enter the body from growing larger. For fishes encountering freezing temperatures and ice, the first barrier is through prevention of ice crystals entering the body through the epithelium. Fishes living in Antarctic waters (few studies have targeted Arctic fishes) have ice on their skin, gills, and in their gastrointestinal tract, but not in the body fluids, muscles, and most organ systems, except for the spleen (Praebel and others, 2009; Evans and others, 2011). Fish skin appears to be an effective barrier to ice crystal penetration into the fish, with gill epithelium perhaps less so (Valerio and others, 1992). How do fish prevent ice crystals that form on the mucous covering the skin (Praebel and others, 2009) from gaining access to the body interior? Although it is possible that larger ice crystals fall off through frictional forces as the fish moves through the water or as currents pass over the body, it is more likely that these ice crystals are prevented from growing by the AFPs in the mucous covering the skin. Ice crystals also have been found in the gastrointestinal tract, which were carried along with ingested food and as fishes drink seawater (to maintain osmotic balance). Here, these crystals are prevented from enlarging by AFPs in the esophagus and stomach as well as pancreatic secretion into the intestine where the fluid becomes hyposmotic to seawater (Cheng and others, 2006).

In some species, these mechanisms are not sufficient to completely prevent the entry of all ice crystals into the body. When this occurs at least some fish sequester these crystals in the spleen. Evans and others (2011) studied the process by which ice crystals are lodged in the spleen. Using nanoparticles as proxies for ice crystals, they found evidence that (1) AFP-coated ice crystals were removed from the circulatory system and stored by spleen phagocytes and that (2) these phagocytes were able to recognize the difference between AFP molecules alone (which they ignored) and those molecules attached to ice crystals (a process seen in crystallizable [Fc] receptor-mediated phagocytosis induced by immunoglobin-bound foreign particles [Swanson and Hoppe, 2004]). Evans and others (2011) note that there remain several areas of uncertainty. First, it is unclear how high levels of AFP (all of which are first discharged into the intestinal tract) are maintained in the blood and lymph systems. Second, the fate of the stored splenic ice crystals is unknown. If fish find themselves in waters above freezing temperatures, as happens to some Antarctic species (Hunt and others, 2003), these crystals could be removed through passive melting.

Seasonal changes in AFPs in Arctic fishes are poorly understood and vary among species. For instance, although high AFP levels in Arctic Sculpin from the Canadian Arctic do not vary appreciably over the course of a year ([Fletcher and others, 1982], a pattern was observed in numerous Antarctic fishes [DeVries and Lin, 1977]). Arctic Cod taken off Svalbard, Norway (Nahrgang and others, 2010) and Shorthorn Sculpin (location unknown; DeVries, 1980) exhibited reduced AFP activity during summer and increased activity during winter. Generally, seasonal changes in AFP production seem to be widespread in fishes exposed to freezing winter temperatures and warmer summer waters (for example, Winter Flounder [Fletcher, 1981]; Atlantic Cod [Fletcher and others, 1987]; Ocean Pout [Fletcher and others, 1985b]; Eelpout [*Lycodes* spp.; Sorenson and Ramlov, 2001]; and Atlantic Wolffish and Spotted Wolfish [*Anarhichas minor*; Desjardins and others, 2006]), although there is considerable interspecific variation in the timing of this cycle (Fletcher and others, 2001). Given that Arctic waters, particularly relatively nearshore, exhibit considerable summer warming, it might be expected that many species will exhibit seasonal changes in AFP production. However, the degree of seasonal variation of AFP produced by skin cells is much less than that produced by liver cells (Low and others, 2002).

Two environmental parameters, photoperiod and water temperature (sometimes working together), help control annual cycles in AFP production, although the importance of each parameter may vary with species. Photoperiod (mediated through the hypothalamus), for instance, is likely a major controlling factor in Winter Flounder, although water temperatures must be less than 8 °C for a buildup of AFP mRNA in the liver and subsequent production of AFP (Fourney and others, 1984; Davies and others; 1988, Fletcher and others, 1989). However, even in Winter Flounder, water temperature does influence the maintenance of AFPs in the body through controlling its removal from the blood stream and controlling the levels of AFP mRNA in the liver (Davies and others, 1988). On the other hand, Fletcher and others (1987) determined that changes in water temperature alone were primarily responsible for boosting AFP production in Atlantic Cod, because manipulating day length did not affect antifreeze production, whereas lowering water temperature to 0 °C did. Finally, based on laboratory studies, it is likely that both seasonal changes in water temperature and photoperiod play a role in the timing of increases and decreases in AFP production in Atlantic and Spotted Wolffishes (Desjardins and others, 2006; Duncker and others, 2006). The timing of AFP production seems to be at least partially genetically fixed (Fletcher and others, 1985a), although these previously mentioned environmental cues, working through the central nervous system and the pituitary gland (particularly through the release of growth hormone), act to "fine tune" the precise timing of the onset and decrease of AFP production (Davies and others, 1988; Fletcher and others, 2001).

Within a species, concentrations of AFP may vary considerably, even among individuals living close together. As an example, juvenile Atlantic Wolffish hatched together from eggs collected in a single bay in Newfoundland, varied in their blood plasma AFP concentrations between a high of 18.1 mg/mL and a low of 8.5 mg/mL (Desjardins and others, 2007) and similar between-individual variability was observed in sympatric adults of that species (Dejardins and others, 2006). In these two wolffish studies, juveniles and adults harbored similar concentrations of AFPs.

Conspecifics taken from geographically separated areas commonly produce different amounts of AFP. For instance, Ocean Pout living off Newfoundland contained higher levels of AFP than did their conspecifics living off warmer-water New Brunswick, differences linked to the New Brunswick fish having only one-quarter the number of AFP genes than did those from Newfoundland (Hew and others, 1988). Similarly, in a comparison of plasma AFP from Ocean Pout from Denmark and Newfoundland, fish from both areas reportedly had high levels during the winter. However, the warmer-water Danish fish lost most of their plasma AFP during the summer, whereas levels in fish from Newfoundland remained relatively high (Fletcher and others, 1985b; Sorenson and Ramlov, 2001). Similar variability occurs in, among other species, Atlantic Cod and Winter Flounder (Fletcher and others, 1985a; Goddard and others, 1999).

There are differences in AFP production within closely related species. Desjardins and others (2006) compared AFP production in the Atlantic Wolffish and Spotted Wolffish. They determined that although both species produced AFPs only the Atlantic Wolffish produced sufficient AFP to protect an individual down to the freezing point of seawater. Likely of significance is that, although both species encounter subzero water temperatures, the more shallow-dwelling Atlantic Wolffish has more of a chance of encountering ice and freezing conditions.

Even at temperatures greater than freezing, AFPs may protect cells (including perhaps fish cells) against damage. As an example, cells require the ability to expel calcium ions through active transport (thus balancing the passive ion transport that is continually occurring). It is thought that low temperatures may damage a cell’s ability to actively transport these ions out of the cell. Studies by Negulescu and others (1992) determined that AFPs “*inhibited passive Ca entry across the cell membranes*” without inhibiting such normal cell functions as active transport. Antifreeze proteins may also interact with various constituents of cell membranes to inhibit cell leakage and death (Rubinsky and others, 1990; Wu and Fletcher, 2000; Wu and others, 2001).

Lastly, the mechanism(s) of freezing protection in fish eggs are poorly understood. Davenport (1992) reported that the eggs of Capelin can survive as much as 6 hours at temperatures as low as -5.2 °C. He noted that the chorion of these eggs had a “sticky, thick extra outer layer, not found in other species, which appears to have the dual effect of slowing ice crystal penetration” thus implying that there is a morphological component to fish egg protection. However, Goetz and others (2005) determined evidence of what they believed to be an antifreeze protein in the eggs of Atlantic Cod and significant amounts of AFPs exist (and significant resistance to ice propagation exists) in the newly spawned eggs of Antarctic notothenioids (for example, Ploughfish (*Gymnodraco acuticeps*, Cziko and others, 2006).

Cellular and Metabolic Adaptations

Evidence for one long-proposed adaptation, called Metabolic Cold Adaptation (MCA), has been effectively undercut by a relatively recent series of studies. MCA holds that fishes adapted to cold waters appear to have evolved a higher metabolic rate “*when corrected for differences in measurement temperature*” that is 2–4 times that of temperate species (Steffensen and others, 1994, p. 49). The hypothesis was based on fish respiration experiments by Ege and Krogh (1914) and Krogh (1916) and later followed by those of Scholander and others (1953) and Wohlschlag (1960). However, studies on a number of Arctic and Subarctic species (for example, Arctic Cod, Arctic Staghorn Sculpin (*Gymnocanthus tricuspis*), Spatulate Sculpin (*Icelus spatula*), Shorthorn Sculpin, Fish Doctor (*Gymnelus viridis*), Greenland Cod [now known to be Pacific Cod]) strongly imply that MCA is almost certainly an artifact caused by insufficient laboratory acclimation time for fishes in respiration experiments (Holeton, 1974; Mikhail and Welch, 1989; Steffensen and others, 1994; Hop and Graham, 1995; Steffensen, 2002; Karamushko and others, 2004).

Much of the experimental research on the cold-adapted performance of fishes has focused on the selective forces on energy production, particularly on how these forces have influenced mitochondria. Cold temperatures affect the aerobic capacity of mitochondria; the respiration rates of isolated mitochondria generally decrease with decreasing temperature (Johnston and others, 1998). In response, and to maintain sufficient aerobic activity, cold-water species harbor higher volumes and densities of mitochondrial clusters than do more temperate taxa; these may reach 50 percent of the muscle fiber volume in the Antarctic Icefish ([*Champsocephalus esox*] see Johnston and others, 1998; Pörtner and others, 2005). However, several factors limit the amount of mitochondria produced by Arctic fishes. First, there is a maximum limit to mitochondrial densities beyond which there is not space for myofibrils, thus muscle function suffers, and the greater volumes of mitochondria in cold-water fishes only partially compensate for the reduced oxidative capacity the mitochondria afforded at low temperatures (Johnston and others, 1998). Second, an increase in mitochondrial density causes an increase in oxygen demand even under resting conditions and, as noted by Pörtner and others (2001, p. 1,992) this particularly becomes “*detrimental during warming when [oxygen demand] can no longer be covered by oxygen uptake through ventilation and circulation.*” As an example, an increase in ambient water temperatures of only 2.3 °C results in large increases in oxygen consumption in Arctic Cod (Hop and Graham, 1995). Additionally, a comparison of the mitochondrial enzyme capabilities (citrate synthase, cytochrome *c* oxidase, and the electron transport system) of Arctic and boreal populations of Atlantic Cod demonstrate that there also have been cold adaptations in these systems (Lannig and others, 2003).

With greater mitochondrial densities in Arctic fishes has come a shift from carbohydrate to lipid (fatty acid) catabolism by these mitochondria. Although the rationale for this shift and the process by which it occurs remains somewhat obscure, one possible reason is that fatty acids are transported across cell membranes composed of fatty acids at a lower energy cost than those with high levels of carbohydrates (Pörtner, 2002). As a consequence, lipid accumulations in Arctic fish tend to be higher than in many temperate taxa. Additionally, the mitochondrial membranes of Arctic fishes tend to have elevated levels of polyunsaturated fatty acid phospholipids, probably because this type of fat supports efficient energy release rates (proton leakage) through the inner mitochondrial membrane (Brand and others, 1992; Pörtner and others, 2005). This increase in polyunsaturates, combined with the aerobic generation of high-energy phosphates, increases the opportunity for damage by free radicals and, likely in response, Antarctic fishes have high levels of the antioxidants vitamin E and C (Ansaldo and others, 2000; Gieseg and others, 2000; Davison, 2005).

In cold-water fishes, mitochondrial proliferation and associated adaptations come with physiological tradeoffs, as energy demands for these adaptations can be relatively high and would be shifted away from growth and reproduction (Lannig and others, 2003). Pörtner and others (2001) gave an indication of what these tradeoffs might entail. Their work was conducted on Atlantic Cod and Ocean Pout at a number of sites ranging from the European Arctic through the more temperate Baltic and North seas. They determined that in both species growth rates and fecundity declined with increasing latitude (that is, decreasing ambient water temperatures).

Selection for greater metabolic efficiency at fluctuating lower temperatures also may have led to intraspecific polymorphisms in the hemoglobin molecule. Functional differences in polymorphic hemoglobin molecules are known from Arctic Cod (*Boreogadus saida*) and Ice Cod (*Arctogadus glacialis*) (Verde and others, 2006) as well as in Spotted Wolffish, Ocean Pout, and in several Antarctic taxa (Hjorth, 1974; Verde and others, 2002). As an example, some hemoglobin molecules of both *Boreogadus saida* and *Arctogadus glacialis* show a low oxygen affinity and a low Root effect, probably linked to the high concentrations of oxygen in cold marine waters (Verde and others, 2006). Polymorphic hemoglobins, labeled HbI(I) and HbI(2), have been most intensively studied in the Atlantic Cod. First described by Frydenberg and others (1965) and Sick (1965), the frequency of the two alleles shows a north-south cline along the Norwegian and eastern North American coasts. In both instances, a greater proportion of fishes living in cold more northerly, waters carry the HBI(2) alleles. Since that time, a range of studies has demonstrated that the two polymorphisms function most efficiently at different temperatures (Karpov and Novikov, 1981; Pörtner and others, 2001; Brix and others, 2004). For instance, HbI(2) is better fitted to cold temperatures through its ability to transport more oxygen to the tissues by superior oxygen binding capabilities at low temperatures. This, in turn, seems to be responsible for differences in a number of life history parameters. For instance, Atlantic Cod living off northern Norway and carrying the homozygotic HBI(2) allele exhibit faster growth, earlier maturation, and earlier spawning season than do fish carrying the homozygotic HBI(1) allele (Mork and others, 1983). Laboratory studies have also shown that Atlantic Cod held at low temperatures grew faster when carrying the HBI(2) gene (Imsland and others, 2004). Additionally, fish behavior also may be influenced by hemoglobin type as juvenile cod that carry the HbI(2) form seem to preferentially inhabit significantly lower temperatures than do fish carrying the HbI(1) variant (Petersen and Steffensen, 2003). Although few studies have examined the handful of cartilaginous species that inhabit polar waters, the hemoglobin of the Arctic Skate (*Amblyraja hyperborea*) and the Antarctic Eaton's Skate (*Bathyraja eatonii*) seem to be (1) similar to one another and (2) functionally different from those of temperate cartilaginous species (Verde and others, 2005).

Hibernation

Small to moderate levels of reduced activity, feeding, and growth in winter are widespread among fishes, largely because metabolism is directly coupled to environmental temperature. However, true hibernation among fishes has been perhaps best documented in the Antarctic species Black Rockcod ([*Notothenia coriiceps*]; Johnston and Battram, 1993; Coggan, 1996; Campbell and others, 2008). These studies determined that in natural habitats during winter (or in testing situations that simulated winter conditions) Black Rockcod had (1) greatly reduced feeding rates (even when additional food was available) and increased mobilization of lipid reserves, (2) a negative growth rate (the loss of body mass), (3) a 58 percent suppression in total metabolic rate and 29 percent in standard metabolic rate, and (4) a 20-fold reduction in activity and a 6-fold reduction in home range. Thus, despite living in a thermally stable environment where food was readily available throughout the year, *N. coriiceps* exhibits a number of the characteristics of terrestrial hibernators. It is likely that the trigger for hibernation in this fish species is decreasing light levels rather than decreasing temperatures. As Campbell and others (2008, p. 7) note: "*The winter dormancy we have documented…is distinct from the facultative dormancy observed in temperate fish species by the levels, and duration of the reduced physiological state...*"

Hibernation in fishes is likely a continuum (Campbell and others, 2008) ranging from small amounts of metabolic depression in some species to the extreme examples of physiological and behavioral adaptations noted in Black Rockcod. What evidence for hibernation is there in Arctic fishes? To date, no studies have directly addressed this issue in fishes living in the Chukchi and Beaufort Seas. However, results from other research imply that hibernation, or at least dormancy, is a likely strategy for many Arctic species. For example, in the Subarctic waters of Newfoundland Cunner (*Tautogolabrus adspersus*) display numerous attributes suggestive of dormancy (Green and Farwell, 1971; Green 1974; Valerio and others, 1990). At temperatures less than 5 °C**,** Cunner become extremely torpid and shelter in the rocks and boulders of shallow, nearshore waters (at water temperatures as low as -1 °C). Here they remain, without feeding, throughout winter and spring, until water temperatures increase in May or June. Additionally, Cunner produces a thick mucus coat that likely hinders contact between ice crystals and skin and that skin produces antifreeze. Unlike Antarctic fishes, however, these survival mechanisms are imperfect, as extremely stormy winter conditions can drive ice crystals with sufficient force against sheltering fishes that they freeze to death. In the cold waters of laboratory experiments, a North Atlantic species, Winter Flounder, burrow into soft bottom, perhaps to avoid ice crystals (Fletcher, 1975).

Hibernation has not been directly investigated in Arctic fishes. However, the winter behavior of young Arctic Cod in Franklin Bay, southeastern Beaufort Sea off Canada, led Benoit and others (2010) to speculate that these fish were hibernating. During this hibernation period, these fish form extremely dense midwater schools and make only occasional vertical excursions, likely for feeding. Noting the slow digestion rates in this species (about 17 days), Benoit and others (2010) speculated that fish remained for the most part in a torpid state, leaving that state only when sufficiently hungry. Amphidromous species, such as Arctic Cisco (*Coregonus autumnalis*) and Least Cisco (*C. sardinella*), overwintering in the Sagavanirktok River and Colville River deltas in Alaska may become torpid during winter, as feeding ceases or is much reduced (Schmidt and others, 1989). However, during winter these fishes will migrate upstream away from the more saline conditions that occur as winter progresses, so hibernation is not complete. On the other hand, the marine Fourhorn Sculpin (*Myoxocephalus quadricornis*), a dominant benthic species in the nearshore of the Beaufort and Chukchi Seas, shows no sign of hibernation, as it actively feeds throughout the year (Schmidt and others, 1989). Fishes including Arctic Cisco and Least Cisco, Humpback Whitefish (*C. pidschian*) and Broad Whitefish (*C. nasus*), Arctic Cod, Saffron Cod (*Eleginus gracilis*), Fourhorn Sculpin (*M. quadricornis*), and Arctic Smelt (*Osmerus dentex*) are all captured in winter fisheries, implying enough individual activity for them to become entangled in gillnets or to strike hooks (Craig, 1989b).

Other Functional Adaptations

As water temperatures decrease, blood viscosity increases in Antarctic fishes. For instance, blood viscosity in the Emerald Rockcod (*Trematomus bernacchii*) at 0 °C is about 40 percent higher than at 10 °C, thus increasing cardiac workload (Axelsson, 2005). To compensate for this added viscosity, a major adaptation in the circulatory system of Antarctic fishes in extremely cold water has been a reduction in haematocrit (packed red blood cell volume) and mean cell hemoglobin concentration (Egginton, 1996; Davison and others, 1997). Interestingly, there is no evidence for increased flexibility of red blood cells, although this would also reduce the effect of increased viscosity (Lecklin and others, 1995). Additionally, the gross anatomy of Antarctic fish hearts appears to be similar to those of more temperate-water taxa, although the diameter of Antarctic fish heart myocytes (muscle cells) are slightly larger, due to an increased number of mitochondria (Axelsson, 2005). There is no evidence for cold adaptation of vascular control as measured by branchial artery contractility in polar compared with temperate fishes (Hill and Egginton, 2010).

Most research addressing possible adaptations to the nervous system of Arctic fishes also has studied Antarctic species. These studies demonstrate that polar fishes have evolved a number of adaptations to this cold environment. Among these, alterations in the cell membrane to maintain fluidity is one of the most important and is accomplished through an increase in unsaturated fatty acids, thus lowering viscosity that would normally attend ambient lower temperatures (Morris and Schneider, 1969; Macdonald, 1981). Work on Shorthorn Sculpin from the northern Bering Sea demonstrates that at low temperatures this trend of increasing membrane fluidity declines or ceases (Cossins and Prosser, 1978). Conductivity within the axoplasm of nerve cells also has adapted to lower temperatures through an increase in ion concentrations within and around these cells (Dobbs and DeVries, 1975; MacDonald, 1981). The brain gangliosides (molecules in the cell plasma membrane that influence membrane fluidity and are involved in cell signal transduction) of Antarctic fishes seem to be cold adapted through an increase in their concentrations and polarity (Becker and others, 1995). However, this variety of adaptations leads to only a partial compensation for low temperatures. Overall, the nervous systems of Antarctic fishes transmit impulses at a slower rate than in fishes living in warmer environments (Macdonald, 1981; Pockett and Macdonald, 1986), a phenomena also found in the peripheral nerves of Arctic species such as Arctic Cod, Snakeblenny (*Lumpenus lampretaeformis*), and an unidentified eelpout (*Lycodes* sp.) (Moran and Melani, 2001).

Similar to the nervous system, the musculature of cold-water fishes has seen a series of adaptations to maximize function under Arctic conditions. These adaptations include (1) changes in myosin structure (Johnson and Johnston, 1991) and the abilities of cross bridges to generate force (Johnston, 1985; Johnston and Altringham, 1985), (2) increases in rates of Ca^+ accumulations in sarcoplasmic reticulum (McArdle and Johnston, 1980), (3) and changes in the activation enthalpies of the sarcoplasmic reticulum ATPase (McArdle and Johnston, 1980). All these adaptations have helped bolster the force generation, muscle contraction speed, and twitch duration of cold muscles beyond what might be expected. Within the Antarctic notothenioid fishes, there has also been a marked trend toward large white and red muscle fibers (Davison, 2005). However, this may represent an ancestral trait within the group, rather than an adaptation to cold water. As with the nervous system, these compensations (including the changes in aerobic capacity due to increases in mitochondrial densities are relatively modest and muscle function of fishes living in Arctic conditions is significantly impaired compared to those of fishes living in warmer waters (Montgomery and Macdonald, 1984; Johnson and Johnston, 1991). For instance, power output for the Antarctic Icefish at -1 °C is about 60 percent that of the Pacific Blue Marlin (*Makaira nigricans*) at 20 °C (Johnston and Altringham, 1985). Together, this translates to generally lower maximum swimming speeds and low maximum tail-beat frequencies in polar fishes (Johnson and Johnston, 1991) and to relatively poor burst swimming performance in at least some of these species (Archer and Johnston, 1989).

Despite a range of compensatory adaptations, cold-water dwelling fishes remain incapable of maintaining the metabolic rates and active life styles of most temperate species (Macdonald and Montgomery, 1982; Johnson and Johnston, 1991; Lannig and others, 2003). This is true both for the Antarctic (Steffensen, 2005) and for northern Arctic and subarctic fishes, which have the additional burden of coping with significant annual changes in temperature (Lannig and others, 2003). Inevitably, many Arctic species have a relatively sluggish (that is, lowered mobility) lifestyle and shift a significant amount of their energy budgets away from growth and reproduction (summarized in Steffensen, 2005).

Life Strategy Adaptations

Arctic fishes have evolved numerous life strategies for coping with low temperatures, long periods of diminished light conditions, and brief periods of marine production that generally favor benthic-dwelling species (for example, Mecklenburg and Steinke, 2015). These strategies relate to a fish's environmental requirements for food, growth, and reproduction. These requirements involve multiple life history stages, habitats, and behaviors that optimize life processes and opportunities for successful reproduction. Diadromous (migratory) patterns that involve amphidromy or anadromy are common life strategies that link the fish to stable conditions in freshwater and marine environments and, at the species level, are characterized by species that vary widely in their tolerance to salinity, exhibit variable freshwater residencies in immature fish, older ages at first reproduction, and widespread differences in their fidelity, or suspected fidelity, to known spawning and overwintering areas (for example, DeGraaf and Machniak,1977; and Craig, 1989a). The amphidromous species (for example, charr and whitefishes) are iteroparous and generally long-lived, typically living 20 years or more. They tend to mature at 7–8 years and, after their first spawning event, tend to spawn every other year thereafter. Anadromous species (for example, Pacific salmon and lampreys) are semelparous, spending most of their lives at sea. The anadromous fishes tend to live between 2 and 7 years and die shortly after spawning. These species tend to be much larger and more fecund than the amphidromous fishes. Both are conspicuous members of the Chukchi and Beaufort Sea nearshore fish assemblages during summer months. Existing information for many marine fish species suggests shorter life cycles, earlier maturation, and greater relative investments of energy in the production of young (for example, large numbers of eggs). There are exceptions such as sharks, rays, and Pacific Halibut. The location of important seasonal habitats, reproductive ecologies, and life histories of most species from Arctic Alaska remain largely undescribed. It is known that many populations, or segments of populations have important life history linkages to coastal waters for food, reproduction, and migration between seasonal habitats. Examples include all of the amphidromous and anadromous species as well as other coastal dominants such as Arctic Cod, Arctic Flounder, Capelin, Arctic Smelt, and several sculpin species such as the Fourhorn Sculpin. Generally, onshore-offshore movements such as those related to ontological development of species like Pacific Herring and Arctic Smelt, or feeding or spawning of Arctic Cod remain to be described because winter surveys are lacking.

Reproductive Ecology

Although patterns of reproductive ecology (for example, timing of reproduction) vary considerably among species, the spawning seasons and incubation periods of some Arctic fishes, particularly anadromous or amphidromous species, are timed to take advantage of the late spring-early summer breakup of ice and the concomitant increases in photoperiod and temperatures and in primary and secondary production of prey. This synchrony is a "hedge betting" strategy that has evolved to increase the probability for early recruitment. For instance, although many amphidromous species (for example, charr, ciscoes, and other whitefishes) spawn under ice in autumn (Craig, 1989a), the eggs remain in gravel beds for 7–8 months and larvae emerge from April to July (McCart and others, 1972; Yoshihara, 1973; Craig and McCart, 1974; Griffiths and others, 1975; Burns, 1990). In the Beaufort and Chukchi Seas, both juvenile and adult Arctic Smelt overwinter under ice in brackish river deltas and coastal waters; many of the river mouths along the Beaufort and Chukchi Seas harbor overwintering populations (Bond, 1982, Schmidt and others, 1987; Bond and Erickson, 1989, Craig, 1989a;

Sekerak and others, 1992). As winter progresses, fish gather near spawning grounds (Haldorson and Craig, 1984) and spawning occurs in spring, just prior to ice break-up with most spawning occurring in the lowermost, but still fresh, parts of rivers (Belyanina, 1968; Burns, 1990). Compared to autumn-spawning fishes, however, Arctic Smelt eggs hatch quickly, in 10–30 days depending on water temperature (Belyanina, 1968; Morrow, 1980; Gritsenko and others, 1984; Burns 1990). Saffron Cod spawn under ice from December to at least May (Andriyashev, 1954; Stewart and others, 1993) and Arctic Flounder from March to June (Ratynski, 1983; Lawrence and others, 1984). However, the spawning seasons of other marine fishes appear to be less tightly linked to seasonal productivity and are perhaps tied to pelagic-benthic coupling of energy to benthic organisms that comprise the diets of the juveniles of some species. For instance, in the Chukchi and Beaufort Seas, Pacific Herring spawn from June to September (Ratynski, 1983; Gillman and Kristofferson, 1984; Lawrence and others, 1984; Stout and others, 2001), Capelin primarily in July and August (Kendel and others, 1975; Fechhelm and others, 1984; Stewart and others, 1993), and Polar Eelpout (*Lycodes polaris*) likely in autumn or early winter (Andriyashev, 1954; Frost and Lowry, 1983). In some instances, at least part of the adult population spawns during a season where few larvae survive. As an example, Fortier and others (2006) demonstrated that most of the Arctic Cod larvae produced during the relatively cold spring die soon after. However, early spawning persists in this species because the few larvae that survive are larger and better able to survive the following winter than the larvae produced later in the year.

Synchrony

The regional bathymetry of the Chukchi and Beaufort Seas indicates small-scale local variability in the physical location of the shelf break relative to average conditions across larger scales. In many areas, the gradient between 75- and 200-m is relatively sharp, occurs over a short distance, and the corresponding surface area and volume is relatively small. The effects of small-scale physical and biological features resulting from shelf-slope interactions along a shallower, but sharper gradient, especially in the northeastern Chukchi and western Beaufort Seas, could be seasonally important to many species having evolved life history and reproductive ecologies linked to, or concentrated in these environments (Crawford and others, 2012). For marine fishes occupying shelf and slope habitats, this is important because the ecological processes operating over short times and small spatial scales, such as food or prey concentrations, may be especially critical to early life history success (for example, match-mismatch survival of larval fish predators). For instance, *it is common that wind forcing at the shelf break of both seas frequently drives upwelling events that lift nutrient-rich water from the depths to the shelves* (from Crawford and others [2012, p. 180], citing Weingartner [1997] and Carmack and Kulikov [1998]). We hypothesize that shelf-slope processes in areas of sharp gradients are important oceanographically to life history processes. However, from a practical view, the spatial extent of existing data relative to this narrow depth interval is coarse at best. For analytical purposes, this scale of resolution limits our predictive capability and, although we know from many studies (for example, Norcross and others, 2009) that temperature and depth are important determinants of fish distribution, only broad hypotheses are currently possible regarding the relative importance of habitats near shelf break and slope areas in the U.S. Arctic (for example, Crawford and others, 2012). At the population level (for example, reproduction, immigration, and emigration processes), the importance of shelf-slope processes are further suggested by newer biogeographic information presented herein.

Life History and Behavioral Adaptations

Unlike the small number of well-studied nototheniid species of Antarctica that live in a stable environmental regime, the behavioral adaptations of Chukchi and Beaufort Seas fishes to seasonally fluctuating temperature, salinity, turbidity, and variable food conditions are quite poorly understood. Much research, especially in the coastal waters of the Beaufort Sea indicates the existence of many adaptive responses to seasonally dynamic hydrographic and biological properties of nearshore ecosystems and coastal lagoons. Examples include fish migration (for example, bathymetric, between freshwater and marine), reduced activity and potential hibernation, and reproductive specialization (for example, Arctic Cod and sea ice). How reproduction and early life history in marine fishes (that is, timing, habitat locations, and spawning behaviors) have evolved with respect to being in synchrony with biological production events, sea ice, hydrological and meteorological conditions remains to be described. For most species, studies of genetic diversity and population structure are needed to understand the variability in patterns of age and growth that have been observed and genetic relationships in the regional fauna.

Migration is an evolved process that reflects the regular movement of fish populations between habitats important to the completion of their life cycle. Movement, although related, generally describes the immediate tactical responses of fish to environmental surroundings. During winter, ice covers the marine waters of the Chukchi and Beaufort Seas and in some coastal areas freezing occurs throughout the water column. In response, fishes move into unfrozen parts of rivers (that is, amphidromous and anadromous taxa), into river mouths (euryhaline species), into unfrozen, near-shore marine refuges, or perhaps into deeper, more-offshore marine waters. Arguably, seasonal-linked coastal migrations of many amphidromous species (whitefishes) are reasonably well understood. However, there have been few winter studies of Arctic nearshore or, particularly offshore, marine fish species. Thus, the behavior of the generally sluggish, benthic species that occupy these waters is little understood.

With that caveat, examples of life strategy models of known or inferred seasonal movement patterns of some of the most conspicuous or ecologically and traditionally important species inhabiting the Chukchi and Beaufort seas are presented. This focus, illustrated with several prominent species, or groups of species, serves to model key features of the life history strategies and regional variations in migratory patterns in order to explain the range of behaviors and habitat dependencies that have evolved. The models described reflect adaptive strategies for life processes that occur in Arctic marine fishes across the continuum of freshwater, estuarine, and marine habitats:

Amphidromous/Anadromous Model.—This segment of the nearshore fish community is important in subsistence fisheries throughout Arctic Alaska. Prior to the 1990s, most technical reports and publications did not distinguish between the two life strategies and referred only to anadromous species. Craig (1989a) examined the evolution of anadromy in the Arctic as an adaptation related to differences in food quality and availability and energetic benefits conferred by coastal migrations. Most young fish reside in fresh water for 1–3 years prior to their first coastal excursion, the exception being the Arctic Cisco in the Alaska Beaufort Sea. However, although the species undertakes a coastal migration during its first year of life, once re-entering freshwaters in and around the Colville River, they resume the variable residency strategy. Overwintering habitats in freshwaters may be limiting and, where studied, strong density dependence is evident in their population dynamics.

Amphidromy Example: Dolly Varden.—All Dolly Varden (*Salvelinus malma*) overwinter in fresh water habitats. Amphidromous Dolly Varden must return to rivers and streams during summer or early autumn and timing or return often varies with whether they will spawn that year (Craig and McCart, 1975; Griffiths and others, 1975). Except for the rare and small habitat areas kept free of ice by perennial springs (taliks), the upper parts of rivers draining into the Beaufort Sea and southeastern Chukchi Sea freeze solid during winter. Perennial springs are located in rivers and streams flowing from the eastern Brooks Range into the Beaufort Sea (Craig 1989a; Wiswar, 1994). Both spawning and overwintering occurs in those tributaries where perennial springs prevent freezing throughout the water column (Craig and McCart, 1974; Griffiths and others, 1988; Burns, 1990), whereas in rivers flowing to the Chukchi Sea, the lower parts of the waterways also may be partially ice-free (DeCicco,1996; DeCicco, 1997). It is likely that spawning does not occur in low-lying coastal plain rivers of the southwestern Beaufort Sea west of the Colville River because they tend to be connected to lakes and lack the perennial springs that prevent freezing (Burns, 1990; Gallaway and Fechhelm, 1997). Thus, in some waterways, a large segment of a population may be found in a small stretch of water (Burns, 1990).

In Beaufort Sea drainages, most Dolly Varden are thought to overwinter in their natal drainages. For instance, in the Sagavanirktok River, one study determined that an estimated 86 percent of overwintering fish had originated in that river (Crane and others, 2005). In the rivers flowing into the southeastern Chukchi Sea, fish do not show overwintering fidelity to natal waterways and stocks from various rivers share ice-free zones (Armstrong and Morrow, 1980; DeCicco, 1997; Crane and others, 2005).

As they make their return migrations into fresh waters, the timing and behavior of Dolly Varden is quite complex and varies with location, reflective of variable water temperature regimes and states of maturity (DeCicco, 1997; Crane and others, 2005). Spawning occurs in autumn. During those years when a fish will spawn, some spawners will remain in freshwater; others will undertake an abbreviated coastal migration and return to their spawning habitats as early as late June (Armstrong and Morrow, 1980). The lack of, or short-term nature of, the coastal migration of an individual may be an adaptive strategy that allows these fish to occupy and defend premium spawning sites. Additionally, size and bright coloration helps them attract mates and, by remaining resident, or almost resident, allows them to spawn during most optimal times. However, although many Dolly Varden begin returning in July, in most instances most Dolly Varden are thought to return to freshwaters from mid-August and early-September. The environmental trigger for this migratory behavior is unknown but is thought to relate to changing light and hydrographic properties. A return migration may occur as late as October (after ocean freeze-up) before fish move into river systems (Yoshihara, 1973; Kendel and others, 1974; Bendock, 1977; Craig and Haldorson, 1981; Griffiths and others, 1988; Burns, 1990; Thorsteinson and others, 1990).

The migratory behaviors of fish in the southeastern Chukchi Sea drainages are more complex than in the Beaufort Sea drainages and regional differences in summer and autumn spawning populations may be related to differences in thermal regimes and summer durations of open water periods (DeCicco, 1997). There is apparently a greater incidence of summer spawning in Chukchi Sea drainages. Summer spawning fish do not seem to migrate to sea during the spawning year. Rather, in June and early July, they ascend rivers, spawn, and then descend to lower river over-wintering grounds. Summer spawning fish that have overwintered in non-natal rivers move into the Chukchi Sea in June, migrate directly to the spawning grounds, and descend to lower-river overwintering areas. In both instances, fish do not feed in the sea during the spawning year. Fish that spawn in autumn behave more like their Beaufort Sea congeners, migrating to sea in summer, feeding, and then returning to fresh waters in autumn. Recent satellite telemetry studies of Dolly Varden from the Wulik River reconfirm the extensive ocean migrations by adult fish (Courtney, 2014), whereas previous, limited tagging indicated transboundary movements between Alaska and Russia (DeCicco, 1992).

Amphidromy Example: Whitefishes.—The seasonal movements of all of the whitefishes of the U.S. Arctic (Arctic Cisco, Bering Cisco, and Least Cisco, Broad and Humpback Whitefish) have much in common. The degree of tolerance for salinity varies by species and affects the extent of intrusions into marine waters. The Least Cisco life cycle model is broadly representative of most whitefishes and generally illustrates the migratory pattern of this group.

Juvenile Least Cisco may remain in rivers for several years before entering the sea (variable residence). During feeding migrations in coastal waters, Least Cisco schools can maintain this integrity for months (Craig and Haldorson, 1981). Juvenile fishes do not migrate as far away from natal origins as larger adults and tend to remain in brackish habitats (5–10 °C, 10–25 practical salinity units [psu]). Older fishes are more tolerant of both colder temperatures and increased salinity (27–32 psu), and disperse farther along the coast. Most Least Cisco stay within the brackish water lens, although they have been found in river plumes as much as 20–30 km (12–19 mi) off shore (Kendel and others, 1975; Griffiths and others, 1988; Burns 1990, Schmidt and others, 1991; Philo and others, 1993a, 1993b). Most Least Cisco found along Alaska's south central Beaufort Sea are thought to originate from spawning and over wintering grounds in the Colville River (Griffiths and others, 1988). Generally, the extent of coastal migrations is affected by prevailing summer winds (for example, wind direction and speed). Least Cisco from the Colville River migrate farther east in years of persistent westerly winds. Similarly, fish from the Mackenzie River benefit from wind-aid migrations and move farther to the west in years of prevailing easterly winds (Griffiths and others, 1988; Fechhelm and others, 1996; Gallaway and Fechhelm, 1997).

Along Alaska's North Slope, larger fish can swim faster and reach distant feeding grounds before smaller individuals (Fechhelm and others, 1996). Given the short summer season, Least Cisco can travel substantial distances when conditions are favorable. For instance, a fish tagged in Simpson Lagoon was recaptured off Barrow, 300 km to the west (Craig and Haldorson 1981). However, fish leaving the Colville River generally migrate eastward along the coast of the Alaska National Wildlife Refuge because marine waters bathing the nearshore between Smith Bay and Cape Halkett appear to retard westward movement (Gallaway and Fechhelm, 1997; L. Moulton, MJM Research, oral commun., 2012). Most of the fish emigrating from the Mackenzie River travel westward perhaps as far as Phillips Bay (Kendel and others, 1975) and eastwards to the Tuktoyaktuk Peninsula (Percy, 1975).

Between July and September, Least Cisco begin to return to freshwater spawning and overwintering grounds (Jones and Den Beste, 1977; Craig and Haldorson, 1981; Griffiths and others, 1988; Fechhelm and others, 1996). At least in some areas (for example, Prudhoe Bay), the initiation of this migration may be linked to the onset and intensity of the coastal marine water intrusion or to food availability (Gallaway and Fechhelm, 1997). Several researchers have noted that the fish that will spawn in a given year are the first to leave coastal waters, followed by non-spawning adults and juveniles (Mann, 1974; Kendel and others, 1975; Jones and Den Beste, 1977). Both juveniles and adults overwinter in the brackish waters of river deltas (the Colville and Mackenzie Rivers are the largest over wintering areas along the Beaufort Sea), open coast (for example, Tuktoyaktuk Harbor), and the freshwater lakes of the Tuktoyaktuk Peninsula, Canada (Percy, 1975; Bond, 1982; Fechhelm and others, 1996). Except for the Sagavanirktok River (where some overwintering occurs in delta waters), Least Cisco do not seem to either spawn or overwinter in any waterway between the Colville and Mackenzie Rivers (Fechhelm and others, 1996). Although water temperature and food availability likely trigger most of the movements in this species, Schmidt and others (1989) observed that during their under-ice sojourn in the Sagavanirktok River Delta these fish also moved upstream when saline waters increased over the course of the season.

Anadromy Example: Pacific Salmon.—Although all five species of Pacific salmon spawn in rivers entering the Chukchi Sea (Craig and Haldorson, 1986; Craig, 1989b; Healey, 1991, Mecklenburg and others 2002; Stephenson, 2006), currently only Pink Salmon and Chum Salmon are likely to spawn in significant numbers in the rivers of the Beaufort Sea (Stephenson, 2006; Irvine and others, 2009). All of the salmon species spend at least one winter at sea. Given the harsh conditions in the marine nearshore, the location of where Beaufort Sea salmon overwinter while at sea is of increasing interest. Irvine and others (2009) posit three options: (1) Bering Sea Refuge—during their marine sojourn, young salmon migrate westward and live in the Bering Sea and perhaps Gulf of Alaska; (2) Atlantic Layer Beaufort Refuge—salmon remain in the Beaufort Sea, but winter deep under the pack ice; (3) Freshwater Beaufort Refuge—salmon remain in the Beaufort Sea region, overwintering in river plumes. Irvine and others (2009) examined the strontium (Sr):calcium (Ca) microchemistry signatures of otoliths of Chum Salmon from the Colville River (emptying into the Beaufort Sea) and the Tanana River, a tributary of the Yukon River, which drains into the Bering Sea. Although the results were somewhat ambiguous, Irvine and others (2009) reported that "*the most parsimonious explanation is that Arctic chum salmon live in the North Pacific for most of their marine life…[but] may spend their first winter deep within the Beaufort Sea.*"

Nearshore—Marine Model

The movements of the vast majority of species inhabiting the waters of the U.S. Chukchi and Beaufort Seas are not known. However, seasonal data are available for a small number of species, especially those occurring in coastal waters during summer months. The brackish water conditions, especially along the Alaska Beaufort Sea, provide important nursery habitats for Arctic Cod, Capelin, Pacific Herring, snailfish, and probably many other marine fishes that are not adequately represented in the sampling of existing research (Thorsteinson and others, 1991). The (1) roles of deltas, lagoons, and other nearshore habitats for reproduction, incubation, and rearing of early life stages; (2) relative importance of such coastal areas with respect to fish production; and (3) evolutionary significance of these sites with respect to freshwater inflows, substrate, or wind- and current-aided transport or retention of early life stages are expected to be the subject of future studies.

Linked Estuarine—Marine Example: Forage Species.—The spawning, overwintering, and migration patterns of Pacific Herring are highly variable. For example, Bond (1982) reported that many Pacific Herring remained in Tuktoyaktuk Harbor (Canadian Beaufort Sea) for most of the year, leaving the harbor only for a few months during the summer to feed. Of the 10 known wintering sites in the Tuktoyaktuk Peninsula region, 8 were in estuarine coastal habitats, 1 was in the lower Mackenzie River, and 1 in the saline waters of Tuktoyaktuk Harbor (Sekerak and others, 1992). At the other extreme, many herring in the eastern Bering Sea overwinter hundreds of kilometers offshore (at depths of 110–130 m [361–426 ft]) and move into nearshore waters in spring preparatory to summer spawning (Dudnik and Usol'tsev, 1964). It is not known if Pacific Herring use offshore waters in the U.S. Chukchi and Beaufort Seas.

Capelin and Arctic Sand Lance (*Ammodytes hexapterus*) are seasonal dominants of the Chukchi Sea nearshore and are important in the diets of some fish, seabirds, and mammals. Like the Pacific Herring, reproduction, especially in Capelin is linked to inshore and coastal waters. Their distribution over shelf waters and seasonal use of shelf habitats, including onshore-offshore linkages are not well understood. Arctic Sand Lance burrow into sandy substrates of the shelf and are known to spawn coastally. In the Beaufort Sea, Capelin reproduction occurs in the delta habitats of the larger rivers such as the Colville and Sagavanirktok Rivers near Prudhoe Bay. Thorsteinson and others (1990) hypothesized that the successful reproduction of Capelin in these areas was spatially and temporally linked to the first marine intrusion of the year. That is, the success of Capelin spawning, incubation, and offshore transport and recruitment of young fish to other nearshore habitats is related to strong westerly winds and oceanographic conditions that push inshore waters carrying larvae and early-age juveniles offshore along the central coast. The hypothesized wind-driven transport in relatively fresh surficial waters was further suggested to span a critical period for capelin growth and physiological development in which juvenile transformation from living in brackish to marine conditions occurs (Thorsteinson and others, 1990). These authors noted a strong association between young Capelin and Arctic Cod, a predator, in surface catches taken off the Sagavanirktok River, which suggests another adaptive mechanism linking, in this case, brackish and marine environments.

Nearshore—Marine Example: Demersal Species and Other Coastal Dominants.—If the water column does not completely freeze, some nearshore species remain in shallow waters throughout the year. An example of such residency is the Fourhorn Sculpin. In the Beaufort Sea, these fish overwinter along shallow-bottom coastlines (Kendel and others, 1975; Percy, 1975; Jones and Den Beste, 1977; Craig and Haldorson, 1981) and in river deltas (for example, Colville and Sagavanirktok River deltas, see Craig [1989a] and Schmidt and others [1987]). A few winter surveys have determined that at least some individuals of the following species also overwinter more-or-less where they reside during warmer months: Arctic Smelt, Saffron Cod, and unidentified snailfish (Craig and Haldorson 1981, Craig 1989b). The Arctic Flounder, another shallow-water species, however, is known to undertake a bathymetric migration and move slightly offshore in autumn. In the Beaufort and Chukchi Seas, the extent of this winter migration is not known and may not be extensive (Andriyashev, 1954, Craig and Haldorson, 1981). For instance, in Tuktoyaktuk Harbor, fish overwinter in the deep parts of the harbor, at depths of 12 m or less (Bond, 1982). As waters warm in spring, fish move into shallow waters in large numbers, where they remain until autumn (Bond, 1982). Spawning of at least some of these species (that is, Fourhorn Sculpin, Arctic Flounder) occurs in winter and spring under ice in shallow marine waters. Arctic Smelt spawn in fresh or brackish waters under ice in spring, just prior to breakup.

Marine Example: Arctic Cod.—The Arctic Cod is an excellent example of a truly marine, although euryhaline, species. Arguably, this is the most widespread and abundant fish species in the U.S. Arctic. However, although it is clear that these are highly mobile and migratory fish, their movements, particularly seasonal movements, throughout much of the Arctic are poorly understood (Ponomarenko, 1968; Craig and others, 1982; Benoit and others, 2008). Throughout their range, fish are abundant in nearshore waters in summer, the precise time varying between locations and between years at the same location. In the nearshore, schools may move quickly through an area (Craig and Haldorson, 1981; Craig and Schmidt, 1985) or may reside in the same location for weeks at a time (Welch and others, 1993). How much of the overall population migrates into shallow waters is not known, although many fish may not migrate to the shallowest waters (Fechhelm and others, 1984; Frost and Lowry, 1983; Hop and others, 1997). In the Alaskan Beaufort Sea, Arctic Cod tend to be relatively scarce immediately after ice-out, but move into shallow waters as the season progresses especially after the first marine intrusion that typically occurs in mid-July following a west windstorm (Craig and others, 1982; Palmer and Dugan, 1990; Wiswar and others, 1995). The high abundance of colonizing epibenthic invertebrates in lagoonal waters provides a rich prey base for cod and other marine fishes. The species also has been shown in recent studies to be abundant over shelf and slope environments.

Ecological Theory

Adaptations (anatomical, molecular, physiological, and behavioral) of marine fishes to life in Arctic waters are evidenced in strategies (genetically determined life history or behaviors [Gross, 1987]) and demographic characteristics of each population. The strategies relate to how resources are allocated to maximize fitness (in individuals and populations) and are tightly linked to life history parameters (Stearns, 1977). The primary life history traits—size at birth; growth pattern; age and size at maturity; number, size, and sex ratio of offspring; age- and size-specific reproductive investments; fecundity; age- and size-specific mortality schedules; and life span—are poorly known for Arctic fish species. These parameters inform the population dynamics (survival, recruitment, growth rate) of each species and vary in response to temporal variations in ecological traits (for example, habitat, diet, home range, and other ecological traits) and other environmental factors.

Population Theory (r-K Selection)

Life history information provides important insights about selective forces operating on fish populations and their evolution to niches in marine ecosystems. In the absence of reliable population parameters, general studies of environmental effects on species adaptations are possible within an r-K conceptual framework[5]. Considering the postulated recency of marine ecosystem stability and related phylogenetic age of the Arctic fish families, r and K selection models are instructive. At one evolutionary extreme, the amphidromous fish (that is, Salmonidae) are unambiguous K-strategists (for example, Craig, 1989a). Amphidromy, like anadromy, involves the alternate occupation of freshwater and sea habitats by fishes. It involves complex migratory behaviors that ensure population fitness through predictable migrations of populations, or segments of populations, between stable habitats in freshwater, brackish, and marine environments. At the other end of the continuum, r-strategists, like the Pacific Herring and Capelin (for example, published values for instantaneous rate of natural mortality [M] and gonadosomal index [GI] from Gunderson [1980] and Rose [2005]) and Arctic Cod are adapted to seasonal periods of high food abundance followed by periods of relative scarcity. These small pelagic species allocate a greater proportion of their resources to reproduction, produce larger numbers of young, and have short life spans and wide niche widths (unspecialized). Although population sizes are unknown for Capelin and Arctic Cod, it is likely that they are prone to fluctuating stock abundance as is the pattern for similar forage species elsewhere. Life history information presented in the species accounts shows that the vast majority of Arctic species display mixes of r and K traits (for example, Cottidae and Agonidae). The mix of life history traits reported, although mostly incomplete, is thought to have adaptive significance with respect to ecological trade-offs (for example, production of young and longevity) and changes in M (Gunderson, 1980; Power, 1997).

Environmental Stability

The Arctic marine ecosystem is a relatively young system that is characterized by both stable (predictable) and variable (seasonal) environmental features in time and space. The small size and low densities of many species would suggest that many of the marine fishes are living at the abiotic and biotic extremes of their ranges (for example, temperatures between -2 and +2 °C). How body size and abundance co-varies with other traits (for example, temperature tolerance and foods) is an area of increasing interest given the rapidity and potential effects of changing Arctic ecosystems. The relative vulnerabilities (extinction selectivity, see McKinney, 1997) of marine species to climate effects or other large-scale perturbations is presently difficult to assess on the basis of life history and ecological traits not only because information is lacking (that is, environmental tolerances and preferences), but because non-linear threshold effects (population and ecosystem levels) are impossible to estimate. Linked biological and physical models are needed to inform research and assessment processes.

The biological mechanisms linking environment, through the life history, to the population dynamics are complex. As harsh as Arctic environmental conditions may seem, the Arctic marine fishes are adapted to life therein. The presence of sea ice and cold water temperatures are stable features in deep waters and the life histories of some species, such as the Arctic Cod, are intricately linked to sea ice habitats. How variations in environmental conditions (abiotic and biotic factors) influence population demographics is not known for most species and is an important topic for monitoring long-term change. Benton and others (2006) described the potential interplay of these factors in terms of differential mortality and

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[5] The r-K conceptual framework is useful for understanding adaptations to life in the Arctic marine environment. The underlying theory concerns population growth in stable and unstable environments and the respective roles of density-dependent and density-independent factors on population dynamics in each. Carrying capacity (K) is an attribute of the ecosystem (habitat) and the selection of K attributes (long-life spans, slow growth, large size, delayed maturity, iteroparity, few offspring, and stable mortality rate) reflects population growth near in stable environments. At the opposite end of the r-K continuum, r-selected species are adapted (short life expectancy, small size, early maturity, reproduces once, many offspring are produced, variable recruitment rate) to living in unstable, fluctuating environments and density-independent factors (abiotic factors) affect population processes such K values are low and the exponential growth rate (intrinsic rate of growth rate [r]) is characteristic of the population. Density-dependent factors seldom come into play in r-selected species. The r/K concept represents a continuum and many species display a mix of both traits.

survival for different life stages and resulting effects on age structure and abundance of populations (that is, developing life cycle understanding). These authors note the importance of population structure for two primary and related reasons: (1) the life cycle takes time to complete and (2) different ages or stages may be affected differently by environmental effects (that is, potential for cascading effects).

Oceanographic influences on ecosystem conditions and productivity are critical determinants of the distribution and abundance of marine fishes. Marine production cycles in the Chukchi Sea lead to a tightly coupled benthopelagic system supporting a biotic community dominated by benthic invertebrates and small marine fishes (Grebmeier and others, 2006b). It is not known whether inefficient cropping of algal production produced beneath sea ice or in open water environments leads to a similar benthic pattern across the Beaufort Sea shelf and slope. The brackish habitat that forms along the north coast of Alaska (within 10–15 km of the shore) in early summer is often characterized as a wind-driven system subject to rapid changes in temperature and salinity. The brackish conditions are ephemeral and by late summer marine conditions are widespread nearshore. Terrestrial sources of organic matter can fuel invertebrate-driven (epibenthic crustaceans) food webs that are seasonally established along the Beaufort coast (Dunton and others, 2006; 2012). Winter ice, as deep as 2-m coastally, and hypersaline conditions in unfrozen waters, render nearshore and lagoon waters inhospitable to most marine fishes. The temporary conditions of many Arctic habitats makes them “ecological vacuums” for r strategists (Gunderson, 1980) and apparently many mixed-trait species (for example, those favoring a strategy of high investment in reproductive output, short generation times, etc.). The information presented about food habits, physical habitats, size, and reproductive ecology suggests that many species are non-specialists (opportunists), lacking competitive capacity (high dietary overlap in invertebrate foods), and expend large amounts of energy on gonadosomatic development at the expense of large body size.

The combinations of life history and abundance traits conceptually extend to fish assemblages associated with pioneer (developmental) and mature (climax) communities in Arctic marine ecosystems (Vadstein and others, 2004). Pioneer communities have low stability against perturbation and low biological control (that is, r strategists). Other characteristics include low diversity, wide niche width, and low specialization. Mature communities are typically dominated by K-strategists (for example, amphidromous species in Arctic rivers and lakes (for example, Johnson, 1997) in stable systems with high biological control and high resistance (below a specific threshold) to perturbation. The effect of high or low diversity, in the relative sense (that is, generally low across the Arctic) is not known. Other comparisons indicate niche width is wide and specialization is high in mature systems.

Ecological Biogeography

Correlative information about the relations between sea temperature, growth, life span, and marine fish diversity in Arctic conditions (generally -2 to > 6 °C) exists for many species. Much of this information was obtained for marine species studied outside the Chukchi and Beaufort Seas. Winter data regarding habitat requirements and fish behavior is generally lacking. Generalizing from the data presented in the species accounts (chapter 3) and section, “Adaptations in Marine Arctic Fishes” (this chapter), marine fish communities occurring in colder regimes have characteristic tendencies for slow growth (populations), small size, short food chains, and low diversity. Arctic conditions favor large species, populations, and predators in the marine invertebrates. Few species are considered apex predators (for example, sharks) and relatively few species are characterized by large populations. Arctic Cod is the most conspicuous exception and other commonly reported marine species (for example, Capelin, Arctic Sand Lance, and Fourhorn Sculpin) and amphidromous fishes (for example, Dolly Varden, Least Cisco, Arctic Cisco, and Broad Whitefish) also may have large population sizes. Large predators (for example, Pacific Halibut (*Hippoglossus stenolepis*), Pacific Salmon, Walleye Pollock (*Gadus chalcogrammus*), Inconnu (*Stenodus leucichthys*), and at least one shark species) are most abundant in the southeastern Chukchi Sea. Fewer species, such as Dolly Varden and possibly Arctic and Greenland flounders fit this description from the Beaufort Sea. No species from these high latitude seas is strictly piscivorous, which is indicative of the length of food chains and relative importance of invertebrate foods (including fish larvae in the zooplankton community) in energetic pathways.

Environmental Relations

Certain life history parameters (for example, growth rate, age at maturity, and fecundity) are sensitive to changes in temperature and food (that is, ecological conditions). This makes interpretation of field data difficult with respect to causal mechanisms and a requirement for laboratory work necessary (Stearns, 1977). Ongoing fieldwork on marine fish populations in the Chukchi and Beaufort Seas will develop much new information about population dynamics, structure, and community functions. New information about habitat associations will represent snap shots of ecosystem condition and laboratory experiments still will be needed to fill information gaps remaining about the physiological tolerances and environmental preferences of Arctic marine fish. Empirical data will be critical to evaluations of potential effects of climate change and human activities on this fauna (that is, natural and anthropogenic effects).

Temperature effects are especially important as they directly affect growth and survival of individuals and thereby recruitment at the population level. In many analyses of field data, thermal conditions often are used as a proxy for mechanisms affecting survival such as enhanced prey production or advection of young fishes in warmer water masses to nursery or feeding habitats. Because thermal relations are often indirect, temperature is not the only factor affecting recruitment, and correlations often break down. Well-designed experiments addressing the effects of multiple stressors may reduce the uncertainty associated with population forecasts.

Regarding environmental preferences, the species accounts support previous finding about marine fishes (excluding amphidromous and anadromous forms) and their apparent preferences for colder, more saline waters (for example, Logerwell and others, 2011). In the summer, this includes marine waters lying seaward, or underlying, nearshore brackish waters along the Alaskan Beaufort Sea. As summer wanes, the nearshore becomes more saline due to decreased freshwater input from rivers and streams and marine intrusions associated with summer storms. During this time, marine fishes often share nearshore brackish waters with diadromous fishes, primarily to feed on the abundant epibenthic fauna or possibly to spawn (for example, Capelin and Arctic Smelt). In autumn, after most amphidromous fishes have returned to freshwater systems to spawn and overwinter, the marine fishes remain in the nearshore area to feed. Onshore-offshore dimensions of their migratory or movement behaviors are generally unknown, but for important forage species like Capelin and Arctic Cod could be important to ecosystem function.

The use of coastal habitats by Arctic Cod in Simpson Lagoon (near Prudhoe Bay) follows a pattern of increased nearshore abundance with the first major marine intrusions (usually mid-July), seasonal residence through early winter months, followed by an occupation of offshore waters during winter months. How much of the Arctic Cod population undertakes such a bathymetric migration, how it relates to life history patterns (spawning times and locations), and locations of seasonal habitats remain largely unknown for both the Beaufort and Chukchi Seas. There are suggestions that large numbers of fish remain over shelf and slope habitats and, given their importance in regional food webs, there remain important questions to be addressed. Because of reports of nearshore spawning (for example, summaries by Thorsteinson and others [1990] and Pirtle and Mueter [2011]), important questions about reproductive ecology and stock structure remain for Arctic Cod and other dominant species of ecological or subsistence importance (for example, Saffron Cod).

Concern about the potential effects of North Slope oil and gas development on amphidromous species (ciscoes, whitefish, and charr) and coastal habitats have a long-standing history. Because of their subsistence, and until recently commercial values, Arctic Cisco have received special research and monitoring attention. Coastal monitoring data from Prudhoe Bay and harvest records from the Colville Delta extend to the early 1980s. During the late 1980s and early 1990s, the effects of West Dock and Endicott gravel causeways in Prudhoe Bay on physical habitat conditions, especially temperature and salinity properties, and effects on the migrations and movements of amphidromous fishes, were a focus of many fishery studies. More than a decade later, in an innovative research approach, BOEM and its investigators worked with Nuiqsut residents (experts) in 2003 to identify new and continuing information needs relative to Arctic Cisco (Murphy and others, 2007). During the process of expert engagement, they identified issues and developed study hypotheses (n = 27). Within the constraints of existing information, each question was addressed and considered regarding future priorities. A summary of the issues identified from local observations included: fewer fish available to subsistence fishery; reduced size and (or) weight of fish; changes in distribution of fish in the Colville River; changes in the quality of fish (taste, texture, color); deformed fish; food chain effects; and energetics stress. These changes were thought to be related to changes in habitat associated with local industrial developments such as seismic noise, causeways and coastal siltation, ice roads, contaminants, and dredging, or larger scale processes such as ocean and climate changes. The possibility of over harvesting also was considered. Although causeway effects were still of concern, the study was done after a period of oil and gas development in the Colville Delta, and this explains the expanded list of local concerns.

The Murphy and others (2007) study was unique in its comprehensive evaluation of environmental influences on Arctic Cisco and the participation of Nuiqsut residents from beginning to end. Environmental influences were geographically partitioned into three regions including the MacKenzie River Region, Coastal Beaufort Region, and Colville-Prudhoe Bay Region to investigated population effects on immature ciscoes (age 0–5 and 5–7). Environmental factors analyzed included: MacKenzie River—river discharge, air temperatures, regional sea surface temperatures (SSTs), spring ice concentration, and a combined climate index (temperature, ice, discharge); Coastal Beaufort Region—winds, regional SSTs, and ice concentrations; and Colville-Prudhoe Bay Region—air temperature, river discharge, SSTs, sea surface salinities, autumn salinities (delta), ice concentration, Arctic Oscillation (AO), flow through the Bering Strait, and the combined climate index.

The results of the analysis reconfirmed, in part, the importance of east wind conditions on the recruitment of young-of-the-year Arctic Cisco to the Colville Delta.

Murphy and others (2007) reported that 80 percent of the natural variation in recruitment could be explained by these winds. Regional changes in sea ice conditions, winds, coastal circulation, and upwelling are known to affect the geographic extent and duration band and the quality and possibly coastal access to habitat by amphidromous fish; these relationships were examined by Murphy and others (2007). A weak correlation was established between survival rates (age 0–5) and the AO, possibly related to changes in regional circulation. Warming influences on the timing of breakup and river discharges were studied in the Colville-Prudhoe Bay Region and a relation between increased discharge and decreased survival in age 5–7 ciscoes was described. Changes in hydrology and changes in regional upwelling and nearshore prey conditions and competition were suggested as causes of the increased mortality and decreased fish condition. Insufficient information was available to evaluate the effects of siltation effects in coastal habitats in the West Dock area, effects of contaminants (for example, heavy metals), effects of autumn salinities on cisco distributions in delta habitats, or effects of seismic activities (noise and vibration) on fish distribution and abundance. A key finding for Arctic Cisco, and other marine fishes, is the demonstration of how physical drivers interact to affect coastal habitats at different time and spatial scales with differential effects to species throughout their life cycles.

With respect to Arctic Cisco, Murphy and others (2007) noted the lack of population information for this species from the MacKenzie River and need for greater resolution of the age structure of the population in the Colville River. Murphy and others (2007) also noted the need for increased understanding about AO effects on regional marine ecosystems. In response, the BOEM and USGS began researching the genetics and age of fishes in the Colville Delta and a broader study on the influences of AO on recruitment processes in young-of-the-year fish (von Biela and others, 2011; Zimmerman and others, 2013). The genetics research confirmed the MacKenzie River origins of Colville River ciscoes and the aging studies indicated the presence of small numbers of older-aged fishes than previously reported (that is, the presence of fishes to age 11). Large-scale effects of AO on the MacKenzie River focused on annual variability in coastal discharge and interannual effects of marine ecosystem conditions on the abundance and condition of euphausiid prey in coastal plumes. With respect to the latter, von Biela and others (2011) hypothesized that prior year conditions (to the arrival of age-0 migrants), are critical to the growth and condition of euphausiids and prey concentrations in the next year. The temporal connection between euphausiid ecology and early marine survival and growth in Arctic Cisco adds significant new information about another source of natural variation in the recruitment of these fish into Alaskan waters.

Fish Assemblages

DeGange and Thorsteinson (2011) used an earlier classification scheme (Mecklenburg and others, 2008; Minerals Management Service, 2008) to describe primary and secondary marine fish assemblages in the Chukchi and Beaufort Seas. The DeGange and Thorsteinson (2011) classification scheme is consistent with the life history profiles presented herein (for example, vertical distributions) and with respect to partitioning the primary assemblage (all species) into ecological categories. The ecological categories broadly define fish assemblages based on existing knowledge of fish behavior and ecology and associations with prominent oceanographic features (for example, seafloor, shelf break, pack ice, and other features). In this analysis, the ecological categories used by DeGange and Thorsteinson (2011) were re-defined to include regional distinctions in habitat and dominant fauna associated with nearshore (<5 m) and offshore areas (>5 m) of the continental shelf. This separation of inshore and offshore communities is more consistent with hydrographic properties (water mass distributions) of the Chukchi (for example, Norcross and others, 2009) and Beaufort Seas (for example, Craig, 1984; Logerwell and others, 2011). A nearshore assemblage was added to the classification and subdivided into three subregions to capture faunal differences in Kotzebue Sound, in the Barrow area, and in brackish coastal waters along the Alaska North Slope to the east of and including Harrison Bay.

The definitions of regional assemblages now includes: (1) *nearshore assemblages* (in shallow bays and lagoons and along open exposed coastlines); (2) *neritic-demersal assemblage* (at or near the seafloor of the continental shelf); (3) *neritic-pelagic assemblage* (in the water column over the continental shelf); (4) *oceanic-demersal assemblage* (living on or close to the bottom beyond the continental shelf break at 200 m); (5) *oceanic-pelagic assemblage* (inhabiting the water column of oceanic waters seaward of the continental shelf break); and (6) *cryopelagic assemblage* (inhabiting neritic or oceanic waters, but during their life cycle, are associated with sea ice). The dominant species associated with these assemblages are listed in table 4.5.

A *cryopelagic assemblage* was not included in table 4.5 and is considered separately due to the special role of Arctic Cod in sea-ice community dynamics. The cryopelagic assemblage and role of the Arctic Cod in the marine ecosystems are unique to the Arctic (Bradstreet, 1982). The term “cryopelagic” describes fishes that actively swim in neritic or oceanic waters but, during their life cycle, are associated with drifting or fast ice. Both young and adult fishes can be associated with ice or water immediately beneath the ice. These relationships can be trophic in nature or related to refuge and possibly reproduction and nursery for young.

Table 4.5. Marine fish assemblages in the Chukchi and Beaufort Seas.

[**Marine fish assemblages:** Cyropelagic assemblage is described in text. **Neritic-pelagic:** Salmon, Pacific Herring, and Yellowfin Sole from southeastern Chukchi Sea]

Community dominants (family/species)	Marine fish assemblages						
	Nearshore			Neritic-Demersal		Neritic-pelagic	Oceanic-demersal
	Southeast	Northwest	North Slope	Chukchi	Beaufort		
Petromyzontidae	Arctic Lamprey						
Squalidae				Spiny Spotted Dogfiish			
Rajidae				Arctic Skate	Arctic Skate[1]		
Clupeidae	Pacific Herring					Pacific Herring	
Osmeridae	Arctic Smelt, Pacific Capelin	Arctic Smelt, Pacific Capelin	Arctic Smelt, Pacific Capelin		Pacific Capelin, Arctic Smelt	Pacific Capelin	
Salmonidae	Chum Salmon, Pink Salmon, Least Cisco, Inconnu, Dolly Varden	Pink Salmon, Least Cisco, Dolly Varden	Dolly Varden, Arctic Cisco, Least Cisco, Bering Cisco, Broad Whitefish, Humpback Whitefish			Chum Salmon, Pink Salmon	
Gadidae	Arctic Cod, Saffron Cod, Walleye Pollock	Arctic Cod	Arctic Cod	Arctic Cod, Saffron Cod, Walleye Pollock	Arctic Cod, Saffron Cod, Ice Cod, Walleye Pollock	Arctic Cod, Saffron Cod, Ice Cod	Arctic Cod, Ice Cod
Gasterosteidae			Ninespine Stickleback				
Hexagrammidae	Whitepotted Greenling						
Cottidae	Hamecon, Arctic Staghorn Sculpin, Fourhorn Sculpin, Ribbed Sculpin	Antlered Sculpin, Fourhorn Sculpin	Fourhorn Sculpin, Twohorn Sculpin	Hamecon, Arctic Staghorn Sculpin, Arctic Sculpin, Shorthorn Sculpin, Ribbed Sculpin, Eyeshade Sculpin	Hamecon, Arctic Staghorn Sculpin, Spatulate Sculpin, Ribbed Sculpin, Eyeshade Sculpin, Fourhorn Sculpin		Polar Sculpin, Bigeye Sculpin, Atlantic Hookear Sculpin[1]
Agonidae	Arctic Alligatorfish	Veteran Poacher		Arctic Alligatorfish	Arctic Alligatorfish		
Liparidae				Nebulous Snailfish, Variegated Snailfish, Kelp Snailfish	Gelatinous Snailfish, Variegated Snailfish, Kelp Snailfish, Nebulous Snailfish	Gelatinous Snailfish, Variegated Snailfish	Slender Eelblenny, Sea Tadpole

Table 4.5. Marine fish assemblages in the Chukchi and Beaufort Seas.—Continued

[**Marine fish assemblages:** Cyropelagic assemblage is described in text. **Neritic-pelagic:** Salmon, Pacific Herring, and Yellowfin Sole from southeastern Chukchi Sea]

Community dominants (family/species)	Marine fish assemblages						
	Nearshore			Neritic-Demersal		Neritic-pelagic	Oceanic-demersal
	Southeast	Northwest	North Slope	Chukchi	Beaufort		
Zoarcidae				Marbled Eelpout, Saddled Eelpout, Polar Eelpout, Fish Doctor	Marbled Eelpout, Polar Eelpout, Fish Doctor		Adolf's Eelpout, Longear Eelpout
Stichaeidae			Slender Eelblenny	Arctic Shanny, Slender Eelblenny, Stout Eelblenny, Fourline Snakeblenny	Arctic Shanny, Fourline Snakeblenny		Daubed Shanny
Ammodytidae	Arctic Sand Lance	Arctic Sand Lance		Arctic Sand Lance	Arctic Sand Lance	Arctic Sand Lance	
Pleuronectidae	Yellowfin Sole, Starry Flounder	Longhead Dab	Arctic Flounder	Bering Flounder, Yellowfin Sole, Alaska Plaice	Bering Flounder, Greenland Halibut, Arctic Flounder	Bering Flounder, Yellowfin Sole	Greenland Halibut

[1] Fishery data suggest occurrence in assemblage.

Andriyashev (1970) was among the early investigators to find Arctic Cod in abundance in marine habitats associated with broken ice or near the ice edge. In spring, as ice thaws and breaks up, phytoplankton blooms and zooplankton colonize these habitats and provide food for Arctic Cod. The substrate formed by the underside of sea ice supports an amphipod-diatom ice community that is believed to provide an important source of food for cod. Other species, such as Capelin and Pacific Herring have been mentioned in this assemblage, and this relates to limited observations in broken-sea ice conditions or near the ice edge. Ecological linkages for these fish species with sea ice, and others, and the importance of polynyas (biological hotspots), are not known.

Diadromous fishes (migratory fishes), especially salmonids, are prominent members of nearshore fish assemblages and represent an important source of traditional foods for Arctic villagers. Diadromy involves regular occupation of fresh, brackish (5–10 °C, <15 psu), and marine waters. Fish migrations to, or movements between, reflect the response of a population (or segment of the population) to various biological stimuli, such as feeding or reproduction, or ecological factors, such as temperature, oxygen level, or specific spawning-habitat need. Diadromous fishes display a wide range of migration behaviors including once-in-a-lifetime events, repetitive multiyear events, spawning migrations, feeding migrations, and seasonal movements between environments. Diadromous fishes inhabit various habitats including many of the lakes, rivers, streams, interconnecting channels, and coastal waters of the North Slope. Common amphidromous species include Arctic, Least, and Bering Ciscoes; Arctic Smelt; Humpback and Broad whitefishes; Dolly Varden; and Inconnu. Common anadromous species include Pink and Chum salmon, Ninespine Stickleback, and Arctic Lamprey.

The highest densities and diversity of amphidromous fishes occurs in river-deltas, such as the Colville and the Sagavanirktok Rivers along Alaska's North Slope. Pacific Salmon and Arctic Lamprey are in greatest abundance south of Point Lay and in Kotzebue Sound in the southeastern Chukchi Sea. Lakes that are accessible to the sea typically are inhabited by diadromous fishes and many species have evolved resident forms (for example, Dolly Varden and Arctic Lamprey). The Least Cisco is the most abundant species in sea-connected Arctic lakes. With the exception of the Arctic Cisco, the amphidromous species are characterized by a variable freshwater residence for juvenile fishes that lasts 1–3 years before they undertake their first migration to sea. Fish and invertebrate prey are seasonally more abundant in coastal waters than in freshwater habitats; therefore, amphidromy represents a physiological adaptation to food availability (Craig, 1989a).

The primary marine fish assemblage found over the continental shelf is composed of relatively few species of small size and biomass when compared to similar ecosystem attributes of lower latitudes (Irvine and Meyer, 1989). As an example, most species are less than 15 cm (FL). Small schooling species such as the Arctic Cod can be abundant over shelf waters and near the shelf break (Crawford and others, 2012). Ecological processes (for example, Smetacek and Nicol, 2005; Grebmeier and others, 2006a, 2006b; Jay and others, 2011) and associations of fishes in Alaska coastal water, Pacific summer water, and Pacific winter waters (for example, Crawford and others, 2012) provide stable habitat conditions for shelf-affiliated assemblages, especially adult fishes, in the Chukchi Sea. The intermingling of these water masses with Atlantic water along the shelf break, slope, and deep waters of the Chukchi and Beaufort Seas results in conditions that are more inhospitable and fewer fish. The use and importance of fish habitats in river deltas and coastal lagoons have received the most research attention. The relative importance of other habitats such as those along exposed coastlines, near the ice edge and in polnynas, or located at special features, such as the Hannah Shoal, for feeding, reproduction, and other life activities have been postulated, but in most instances, remains to be described.

Trophic Relations

The available food habits data (stomach contents, fatty acids, isotopes) from across all habitats reviewed in chapter 3 suggest that most Arctic marine fishes are primary carnivores that feed across trophic levels T2 and T3. Invertebrates are significant in their diets with pelagic species feeding on zooplankton herbivores compared to demersal species preying more frequently on early life history stages of benthic detritivores. Freshwater invertebrates swept downstream can be an important source of food for anadromous and amphidromous species as they move downstream into the coastal sea.

Trophic level status is an important indicator of diversity or ecosystem change (that is, changes in community, animal size, and consumption in pelagic and benthic environments) and has been used to study fishing and other effects on species abundance in the northeast Pacific Ocean. More than 90 percent of Arctic marine fauna are secondary consumers. Secondary consumers feed on various fish and invertebrate prey by feeding across trophic levels. The trophic position thus occurs at intermediate levels of the marine ecosystem. The average trophic level position for all Arctic marine fishes (juveniles and adults combined) is 3.27 (range: 2.99–4.6)[6]. Of the tertiary consumers, only two species—Arctic Lamprey and Pink Salmon—are common in their occurrence in the southeastern Chukchi Sea.

The trophic positions of each species were estimated in FishBase (Froes and Pauly, 2012) and many assumptions relative to availability and recency of data are involved. Despite these limitations, the mid-level positions indicated are considered to be reasonably accurate. This determination is based on the widespread consumption of small invertebrate prey, benthic and pelagic species, almost universally reported in most species diets. The stomach contents indicate significant dietary overlaps in co-habitating species in marine and nearshore habitats. The abundance of invertebrate foods in each habitat type is related to carbon cycling associated with the delivery of marine-derived organic matter (primary production) to benthic systems offshore and transport of terrestrially derived carbon to nearshore systems. Of interest, the different life strategies that have evolved in the Arctic for marine fishes (anadromy, amphidromy, and marine) are adapted to an invertebrate food base and many species seem to lack specialization with respect to feeding behavior and diet. The generalist strategy may be an effective adaptation of marine fishes living in the invertebrate-dominated shelf systems of the Chukchi and Beaufort Seas. Although most marine fishes are lower-order carnivores, some of the larger, especially pelagic, predators are highly piscivorous during adult stage phases of their lives (for example, Pacific salmon and Inconnu). The absence of exclusive tertiary consumers and relatively few secondary consumers that cross over the T4 level (feed upward) are indicative of the pelagic-benthic coupling and energy pathways characteristic of invertebrate-dominated shelf environments.

Most Arctic marine fishes appear to feed at similar trophic levels and on similar prey comprising the trophic spectrum of available food and prey items available to them in near- and off-shore habitats. It is hypothesized that competition for food resources with invertebrate competitors on the shelf may, in concert with environmental temperature, contribute to observed abundance patterns and the hypothesized ecological redundancy of many cryptic species. In brackish marine environments, such as the open and pulsing lagoons along the North Slope, epibenthic foods (for example, amphipods and mysids) are seasonally abundant, tend to drive coastal food webs, and are not considered to be limiting. Competition between fish competitors in the nearshore marine such as between Arctic and Saffron cods may be significant in some locales and intensified in others through shifts in distribution or changes in ecosystem function brought forth by climate change. Predation pressures on the slope by marine fish, especially on benthos, were not historically considered great (for example, Carey and Ruff, 1977). However, recent data suggesting large standing stocks of Arctic Cod on the slope suggest a need for a re-examination of this hypothesis.

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[6] According to Romanuk and others (2011) omnivores, which consume plants or detritus as well as animals, have trophic levels between 2.2 and 2.79 and carnivores have trophic levels greater than 2.8. Secondary consumers (carnivores) have trophic levels between 2.8 and 4.0 and tertiary consumer levels are greater than 4.0.

Relative Abundance

Spatial patterns of relative abundance for nearshore and shelf fish assemblages can be generalized from a compilation of regional fishery data and related to the diversity estimates (table 4.1), characterization of marine fish assemblages (table 4.5), and advection model developed by Grebmeier and others (2015, presented in chapter 1 of this report) (table 4.6). The species composition of the nearshore was historically known from fish catches in passive gear collections (that is, fyke nets and gill nets) from inshore habitats and expressed in indices of catch-per-unit-effort (CPUE). Sampling over the shelf has involved active sampling methods including bottom trawling (near the bottom), seining, and plankton tows (surface and water column). The fish catches reported from active sampling gears is expressed in densities of fish (in numbers or biomass) per area trawled or volume sampled. The various sampling and enumeration methodologies required development of a simple, unifying classification of abundance (rare, uncommon, and common) to describe regional patterns in the marine fish assemblage (chapters 2 and 3).

The diversity of Salmonidae species throughout the Pacific Arctic Region (table 4.6) reflects the plasticity of this group and its adaptive linkage to freshwaters. All five species of Pacific salmon are abundant in the northern Bering Sea having important spawning grounds in the Yukon and Anadyr Rivers. In the west, sockeye salmon are more abundant than in Norton Sound, USA in the east relating to spawning habitats in the Anadry River, Russia, and its tributaries. North of the Bering Strait, Pink and Chum salmon are the abundant salmon species although successful colonization has not demonstrated in Alaskan habitats north of Kotzebue Sound. Coho Salmon are present in Kotzebue Sound drainages and along the Chukotka coast.

Many of the common species, or functional groups of species, are benthic, or demersal, in their habitat orientation (table 4.6). Densities are low and small-sized fishes such as snailfish, poachers, and pricklebacks predominant over shelves. The small size and low densities of many species suggests that they may be living at the abiotic and biotic extremes of their ranges (for example, temperatures between -2 and +2 °C). How body size and abundance co-varies with other traits (for example, temperature tolerance and foods) is of increasing interest given the rapidity and potential effects of changing Arctic ecosystems. The relative vulnerabilities (extinction selectivity, see McKinney, 1997) of marine species to effects of climate or other large-scale perturbations are presently difficult to assess on the basis of life history and ecological traits not only because information is lacking (that is, environmental tolerances and preferences), but because non-linear threshold effects (population and ecosystem levels) are not possible to describe.

These abundance patterns, and the classification used, are consistent with published literature and, the high number of rare and uncommon species reported raises questions about their functional roles in the marine ecosystem. Biodiverse environments were described by Mouillot and others (2013) as having large numbers of rare species whose functional importance in ecosystems is largely unknown. When the diversity of marine invertebrates is considered, the U.S. Arctic waters can be characterized as biodiverse. The occurrence of roughly 30 percent of the marine fishes from catches in the Beaufort Sea and 20 percent from the Chukchi Sea is described as rare. Even greater numbers are considered uncommon. Only 41 percent of the marine fishes found in the Beaufort Sea, and 53 percent in the Chukchi Sea, are described as common. According to Mouillot and others (2013), rare species in species-rich areas are generally considered to have little influence on ecosystem functioning and may fulfill the same ecological roles as common species. Because of their low abundance, they have less effect, a phenomenon known as functional redundancy (Mouillot and others, 2013). The redundancy hypothesis suggests that rare species serve as an insurance policy for the ecosystem in the event of severe disruption or regime shift and ecological loss. Thus, the ecological role of the individual species, especially in benthic ecosystems in the Arctic where invertebrates predominate and many marine fish are rare or uncommon, is probably best assessed for the demersal assemblage as a whole, rather than single species contributions to food webs and energy flows. Disruptions, such as the cascading effects of ecosystem change reported by Grebmeier and others (2006a; 2006b) related to climate change, would tend to favor pelagic species (for example, salmonids and cods) and potential switch from an invertebrate-dominated system to a gadid-dominated system. In this scenario, the pelagic community would be enriched through increased productivity and immigration at the potential expense of abundant invertebrates such as snow crabs. The potential effect on rare and uncommon fishes could be positive (reduced competition for foods) or negative (less food available). If the hypothesized effects of the cold water pool in the Bering Sea are true, this thermal barrier may protect many of the low density, benthic fishes living in the Arctic from extinction or northward shifts in the decades ahead.

The disruption of the marine food chain could lead to reduced growth rates, lower abundance of some marine fish populations, and restructuring of the fish assemblages. Regime shift effects on pelagic and benthic ecosystems, as hypothesized by Grebmeier and others (2006a; 2015), are driven by decoupling mechanisms (for example, influx of heat in Pacific waters, changing sea ice conditions, reduced transport of organic matter to the benthos, and remineralization), which result in the destabilizing of shelf environments (for example, increased use of pelagic habitats by salmon, reduced benthic productivity and abundance of invertebrate foods, changes in animal distribution relative to prey conditions) from current conditions. In an analysis of potential effects of climate change, Mueter and others (2009, p. 108) concluded that

Table 4.6. Most abundant species of Arctic marine fish in northern Bering Sea, Chukchi Sea, East Siberian Sea, and Beaufort Sea regions of the Pacific Arctic Region.

[Pacific Arctic Region is as described by Grebmieir and others (2015). **Habitat/shelf region:** Pelagic refers to species occurrence in water column; demersal refers to species occurrence at or near the seafloor]

Northern Bering and Chukchi Seas					
Arctic Sea	**Habitat/shelf region**		**Fish abundance**		
			East ←	**Community dominants and species groups**	**→ West**
			Nearshore	**Offshore**	**Nearshore**
Northern Bering	Pelagic		Pacific Salmon, Dolly Varden, Pacific Herring, Arctic Smelt, Capelin	Pacific Salmon, Pollock, Pacific Herring	Pacific Salmon, Dolly Varden, Pollock, Arctic Smelt
	Demersal		Arctic Lamprey; Starry Flounder and other flounders; Pollock, Arctic and Saffron Cods; pricklebacks	Pollock; Pacific Cod; Pacific Halibut; Bering Flounder, Yellowfin Sole, Alaska Plaice and Northern Rock Sole; Capelin; Pacific Herring; eelpouts; snailfish	Pollock, Pacific Cod, Saffron Cod, flounder, sculpins
Chukchi	South	Pelagic	Chum and Pink Salmon; Pacific Herring; Capelin, Arctic Smelt; Least Cisco; Inconnu	Chum and Pink Salmon; Dolly Varden; Pacific Herring	Chum and Pink Salmon, charr, Least Cisco
		Demersal	Arctic Lamprey; Arctic Cod; Saffron Cod; Pollock; Hamecon, Arctic Staghorn and other sculpins; Arctic Sand Lance; Yellowfin Sole; Starry Flounder; Whitespotted Greenling	Spiny Dogfish; Arctic Skate; Arctic and Saffron Cods; Arctic Sand Lance; Bering Flounder; Yellowfin Sole, Alaska Plaice and other flounders; numerous species of eelpouts, pricklebacks, poachers, and snailfish	Chum and Pink Salmon, charr, Least Cisco
	North	Pelagic	Pacific Herring, Capelin	Arctic and Saffron Cods	
		Demersal	Arctic Cod, Four Horn Sculpin, Veteran Poacher, Arctic Sand Lance, Arctic Flounder	Arctic Skate; Arctic and Saffron Cods; Arctic Sand Lance; Bering Flounder; Yellowfin Sole, Alaska Plaice and other flounders; numerous species of eelpouts, pricklebacks, poachers, and snailfish	Chum and Pink Salmon, charr, Least Cisco

Table 4.6. Most abundant species of Arctic marine fish in northern Bering Sea, Chukchi Sea, East Siberian Sea, and Beaufort Sea regions of the Pacific Arctic Region.—Continued

[Pacific Arctic Region is as described by Grebmeier and others (2015). **Habitat/Shelf region:** Pelagic refers to species occurrence in water column; demersal refers to species occurrence at or near the seafloor]

East Siberian and Beaufort Seas			
Arctic Sea	**Habitat/shelf region**	**Fish abundance**	
		East ← Community dominants and species groups → West	
		Nearshore	**Offshore**
Beaufort	Pelagic	Dolly Varden; Arctic and Least Ciscoes, Broad Whitefish; Pacific Capelin; Arctic Smelt; Ninespine Stickleback; Pacific Herring	Arctic Cod; larval and juvenile forms of demersal fish species
	Demersal	Arctic Cod; Fourhorn and Twohorn Sculpins; Arctic Flounder; Slender Eelblenny; snailfish	Arctic Skate; Pacific Capelin; Arctic Smelt; Arctic Cod; Saffron Cod; Arctic Sand Lance; Greenland Halibut; Arctic Flounder; Hamecon, Fourhorn, Arctic Staghorn, and other sculpins; snailfish, eelpouts, blennies
East Siberian Sea	Pelagic	Char, Arctic and least ciscoes, broad whitefishes, Arctic smelt	Meroplankton (fish larvae)
	Demersal	Saffron and Arctic Cods, Arctic Flounder, sculpins	Bering Flounder and other founders, sculpins, eelpouts, snailfish

"…*further shifts in spatial distribution and northward range extensions are inevitable and that the species composition of the plankton and fish communities will continue to change under a warming climate. While overall productivity is likely to increase in the northernmost systems as the region changes from Arctic to subarctic conditions, some (primarily subarctic) species will increase, while other (primarily Arctic) species will decrease or retreat northward*." These analyses demonstrate linkages between climate and species distributions and, when considered in light of sea-ice retreat and marine ecosystem effects toward the poles (for example, Doney and others, 2012), suggested a heightened vulnerability of the pelagic fish community over the Chukchi shelf to widespread environmental change.

The life cycles of marine fishes (eggs, larvae, juveniles, and adults) variously link pelagic and benthic systems and nearshore and offshore through evolved life strategies and behavioral patterns. Many shelf species have a benthic life history stage and depend on the benthic environment for some part, or all of their lives. Cascading effects from pelagic to benthic ecosystems, without immediate additions of demersal fishes from the Bering Sea, are possible, and already may be occurring. Changes in productivity, competition, and predation as noted by Mueter and others, (2009) would accompany changes in habitat and affect population processes including growth and survival. The different species (for example, salmonids, forage fishes, flatfishes, and cods) will be affected differently by changes in the pelagic community. For instance, flatfishes live on the ocean bottom and typically release eggs into the plankton drift. Most eelpouts and sculpins dwell on the bottom and their eggs, larvae, and juveniles develop on the bottom. Saffron Cod adults occur at various depths; however, they lay their eggs on the bottom and the eggs develop there. Key information gaps about the abundance, life history, migrations, and reproductive ecology (for example, spawning times and locations) of Arctic Cod, Capelin, and other forage species will be needed to inform assessments of trophic cascades and effects of ecosystem change.

The fish assemblages of nearshore and shelf waters of the Chukchi and Beaufort Seas are under current fishery investigation (appendix A). Previous research has shown that, although many marine species such Capelin and Arctic Sand Lance commonly are detected in nearshore and offshore habitats, Arctic Cod are by far the most common marine species in the U.S. Chukchi and Beaufort Seas. In reviewing the life history and ecology of Arctic Cod, Crawford and others (2012) reported temperature preferences of early life history stages to be the same as those associated with cold marine waters (that is, larvae and fry development between 1.5 and 3.0 °C with highest survival rates between 0.5 and 3.0 °C). Juveniles and adults were tolerant of a wider range in temperatures conditions. Adults have been sampled in abundance in coastal waters >13 °C and in marine habitats typically no warmer than 6–7 °C. Although specific physical and biological information about migratory behaviors, reproductive ecology, and importance of offshore habitats for this species is lacking, its keystone role is supported by its widespread occurrence, dominance in fish assemblages, and importance in regional food webs.

Population Dynamics

Estimating how marine fish populations respond to changing environments requires an understanding of the mechanisms by which the environment (its mean and variability) creates changes in population dynamics. A life cycle approach that includes a numerical assessment of differential effects at different ages or stages enhances predictive capability and understanding of the contribution of individual effects to the population level (Benton and others, 2006). Environmental effects are mediated through changes in demographic rates and population size, which may result from functional responses at molecular and genetic levels of organization. In population ecology, the most important environmental factors are those that have the greatest effect on mortality, growth, and spawning and recruitment rates (Reist and others, 2006; Allen and Hightower, 2010). In the U.S. Arctic, research has addressed environmental effects on *physiology* (food and growth)[7], *dispersal* (active and passive transport mechanisms), and *predation mortality* (predator-prey). How physical influences (for example, sea ice, light, temperature, salinity, currents, pH, and dissolved oxygen [DO]) affect these processes (directly or indirectly) and ultimately the distribution and abundance of fishes is an increasingly important part of ecosystem-based management and a focus of integrated science. The role of disease and parasitism in Arctic marine fish population dynamics, although thought to be significant, are unknown and baseline information has not been included. At present, the effects of fishing mortality on Arctic marine fishes are of negligible effect to their population dynamics.

Population Parameters and Models

Population size, the number of individuals within a geographic range, is a fundamental demographic parameter. In surveys of marine fishes, it is not possible to count all individuals in a census and therefore a number of techniques have been developed to estimate abundance and monitor change. These methods commonly include estimates of population density, the size of the population in relation to the space it occupies. Population density is affected by density-dependent factors (competition, predation, migration, and disease) and density-independent factors (for example, weather, storms, currents, temperature). The structure of populations often is studied with respect to age- or size-related cohorts (for example, juveniles or adults) and related distributions of gender (sex ratios) to describe the reproductive potential of the population and its current and future growth. Genetic information is commonly obtained to further characterize population structures and elucidate evolutionary relationships. Age- and stage-structured analyses show how some individuals will have a greater effect on population-level processes. In this context, fecundity is an important parameter that describes the numbers of offspring an individual or population is able to produce in a given amount of time. In marine fishes, fecundity (number of eggs) varies by species and age/size of fish with younger smaller fish typically producing fewer eggs, and larger, older fish producing more eggs. Environmental conditions often affect the physiological condition of a fish and the number and quality of eggs produced, and for some species whether or not spawning occurs. Another individual trait that affects population growth is mortality, the measure of deaths per unit of time. Life tables are regularly used to display age-specific statistical patterns of a population's survival patterns.

Many different kinds of models (for example, exponential and logistic) have been developed to study growth in fish population to aid fisheries management, environmental impact assessment, or restoration of stocks that have been exploited or somehow reduced. Stock models range from surplus production models (for example, Schaefer, Fox, and Pella and Thomlinson models) to more detailed and age-structured demographic models (for example, yield-per-recruit, delay difference, and Beverton and Holt stock-recruitment models. The most common uses of population models have been to estimate recruitment (young fish entering the population) and yield (harvestable amount) in managed fisheries. The greatest challenge in these model systems is in their ability to realistically capture the "*complex causation driving population dynamics*"; the greatest value may be in the identification of the general mechanisms, which map the environment, through the life history, to the dynamics (from Benton and others, 2006, p. 1,173). In most instances, the scattered and fragmented nature of the existing Arctic data sets and lack of time series does not allow quantitative approaches to population modeling.

The ideal is to have the capability to estimate (1) long-term fluctuations in abundance and biomass production due to human perturbations or environmental variations, and (2) temporal-spatial responses of fish populations to change (Monterio, 2002). Surplus production models generally require much less biological information than age-structured models. In data-rich regions, like the southeastern Bering Sea, the role of the physical environment in predictions of resource availability is increasingly the focus of ecological (coupled physical and biological processes) models (for example, Miller, 2007).

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[7] The studies stop short of linking bioenergetics (energy expenditures) and population dynamics (mortality, survival, and population growth).

Measures of growth, such as age-length and length-weight relationships are often used in stock assessments, in models that estimate habitat or ecosystem productivity, and in assessments of the health of individuals. However, it is not presently possible to model the population dynamics of most Arctic marine fishes with actual data collected from the Chukchi and Beaufort Seas. Regional-scale resource assessment surveys have been recently designed to collect data for the purpose of parameter estimations (that is, BOEM-sponsored NOAA and UAF surveys). Earlier baselines surveys produced information about species occurrences, relative abundance, and habitats. The collection of population data has, in the whole, been somewhat limited to length-weight and in some instances, age-length (size-at-age) relationships. In appendix B, age-length and length-weight relationships are presented for 19 nearshore species of Arctic fishes. In fishes, both growth rates and length-weight relationships are highly variable reflecting differential changes in population responses to environmental parameters such as water temperature, prey quality, population density, and direct human interaction, such as fishing (Courcelles, 2011; Loher, 2012). Species specific and interspecific differences in population growth rates and age and weight relationships are evident within and across years and by geography from various locations in Chukchi and Beaufort Sea study areas (appendix B). These differences demonstrate the plasticity in age and growth noted by Courcelles (2011) and Loher (2012) in Arctic marine fishes. The sources of age-length data and regression analysis are appended to this report (appendix B) and the species and locations of data collection from outside the U.S. Chukchi and Beaufort Seas are listed in table 4.7.

The length-weight regressions are dated, but at the time of their collection, allowed the estimation of fish condition and growth rates at scattered locations around the Arctic coast. Their historical value will be in comparison with contemporary estimates of these parameters and a potential benchmark to evaluate the effects of changing climate and environmental conditions (for example, Chen and Sakurai, 1993 for Saffron Cod). Given the status of existing information, a structured information management process, such as the Bayesian modeling approach used by Jay and others (2011) for Pacific walrus, could be used to evaluate needs and priorities for population dynamics modeling relative to offshore oil and gas development, climate change, and ecosystem-based management.

Current Understanding of Population Dynamics

There are typically four reasons to study population dynamics. First, population effects are often considered the most relevant response to environmental (ecosystem) perturbation. Second, population viability analyses (time to extinction) are used to manage endangered species. Third, they are critical determinants of sustainable yields in fishery management. Fourth, population processes are critical to understanding ecosystem dynamics and ecological processes (for example, regime shifts and trophic cascades). The first and fourth reasons are the most germane to the present Arctic management need and qualitative approaches to each are possible. Considerable research attention is being applied to developing quantitative understanding of population dynamics in light of changing Arctic conditions and potential fisheries.

Knowing how fish respond to variable environmental conditions and demographic changes in their populations is central to effective environmental assessments, potential fishery management, and informed Arctic policy. Knowledge about the demographics of marine fish population in the U.S. Arctic, while sparse, varies by season and distance from shore. More population data and information are available from nearshore areas during ice-free months simply because this is where the most research has been conducted. Offshore data collection has been of a reconnaissance nature and has allowed useful descriptions of the distribution and abundance of species for given areas and times. In the nearshore, the greatest amount of population information is available from inshore waters (<2 m) of the Alaska Beaufort Sea. This relates to the seasonal habitats for iconic species (Arctic Cisco and Least Cisco, Broad Whitefish, and Dolly Varden), logistical constraints of sampling, and coastal locations of industrial developments. Age-and-growth and size-at-age relationships, sex ratio, age- and size-at-maturity, fecundity, and other life history traits (for example, gonadosomal indices) have been described for Dolly Varden, Arctic and Least Ciscoes, Broad and Humpback Whitefish, Arctic Cod, Arctic Flounder, and Fourhorn Sculpin with most data collections occurring between the mid-1980s and early-2000s[8]. Life history characteristics of Arctic Smelt sampled in the Colville River delta were summarized by Haldorson and Craig (1984).

The nearshore emphasis noted for the Beaufort Sea also extends to the amount of process-oriented research in Simpson Lagoon and Prudhoe Bay. For fishery components of the ecosystem, process studies have examined population movements and migrations with respect to prey availability, trophodynamic relationships, and coastal hydrodynamics.

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[8] Population information obtained through NOAA and MMS sponsored studies for the Alaska OCS Region; British Petroleum (Alaska), Inc. and the North Slope Borough fish monitoring in Prudhoe Bay; and U.S. Fish and Wildlife coastal resource inventories of the Arctic National Wildlife Refuge.

Table 4.7. Age-length and length-weight relationships of fishes in the U.S. Arctic, with available data only from outside the U.S. Chukchi and Beaufort Seas.

Age-length relationships

Species	Location	Source
Acantholumpenus mackayi	Tuktoyatuk Harbour, Yukon Territory, Canada	Hopky and Ratynski (1983)
Ammodytes hexapterus	Lower Cook Inlet, Alaska, USA	Robards and others (2002)
Gadus chalcogrammus	Eastern Bering Sea, Alaska, USA	J. Ianelli, oral commun. (2010)
Gadus macrocephalus	Bering Sea, Alaska, USA Gulf of Alaska, Alaska, USA	Stark (2007)
Gymnelus viridis	Northwest Territories, Canada	Green and Mitchell (1997)
Hippoglossus stenolepis	Northeast Pacific	Forsberg (2011)
Limanda aspera	Eastern Bering Sea, Alaska USA	Wilderbuer and others (1992)
Lumpenus fabricii	Tuktoyatuk Harbour, Yukon Territory, Canada	Hopky and Ratynski (1983)
Pleuronectes quadrituberculatus	Eastern Bering Sea, Alaska, USA	Zhang and others (1998)
Squalus suckleyi	Hecate Strait, British Columbia, Canada Georgia Strait, British Columbia, Canada	Ketchen (1975)
	Georgia Strait, British Columbia, Canada	Ketchen (1975)
		Saunders and McFarlane (1993)
Triglops pingelii	Kamchatka, Russia	Tokranov (1995)
Reinhardtius pingeli	Eastern Bering Sea, Alaska, USA	Ianelli and others (2007)
Zaproa silenus	Kuril Islands/Kamchatka, Russia	Tokranov (1999)
	Northeast Pacific, Alaska, USA	Smith and others (2004)

Weight-length relationships

Species	Location	Source
Acantholumpenus mackayi	Tuktoyatuk Harbor, Yukon Territory, Canada	Hopky and Ratynski (1983)
Ammodytes hexapterus	Lower Cook Inlet, Alaska, USA	Robards and others (2002)
Gadus chalcogrammus	Eastern Bering Sea, Alaska, USA	J. Ianelli, oral commun. (2010)
Gadus macrocephalus	Eastern Bering Sea, Alaska, USA	Thompson and others (2007)
Gymnelus viridis	Northwest Territories, Canada	Green and Mitchell (1997)
Hippoglossus stenolepis	Northeast Pacific, Alaska, USA	Sadorus and others (2012)
Limanda aspera	Eastern Bering Sea, Alaska, USA	Wilderbuer and others (1992)
Lumpenus fabricii	Tuktoyatuk Harbor, Yukon Territory, Canada	Hopky and Ratynski (1983)
Pleuronectes quadrituberculatus	Eastern Bering Sea, Alaska, USA	Zhang and others (1998)
Reinhardtius pingeli	Eastern Bering Sea, Alaska, USA	Ianelli and others (2007)
Squalus suckleyi	Washington, USA	Wildermuth (1983)
Triglops pingelii	Kamchatka, Russia	Tokranov (1995)
Zaproa silenus	Northeast Pacific, Alaska, USA	Smith and others (2004)

Field and laboratory experiments have focused on physiological responses to natural variability in the physical conditions of habitats in bays, lagoons, and exposed coastlines as well as changes in conditions resulting from coastal construction. Years of research and monitoring in the vicinity of Prudhoe Bay has yielded a wealth of information about the life histories, habitats, and harvests of the coastal fishes and increasingly in the area around Point Barrow. Information about genetic relationships (diversity and structure) is more limited with respect to population dynamics. Genetic studies have been conducted on Arctic Cisco, Dolly Varden, Arctic Cod, and there is growing interest in Saffron Cod. The importance of these species in subsistence fisheries, possible effects of offshore oil and gas development, and possible effects of changing climate conditions, have, or currently are, responsible for these studies.

Salmon, charr, and whitefishes are regionally significant as traditional use species in subsistence fisheries and are of increasing value as recreational resources in Arctic watersheds. However, among these species, especially for those stocks occurring in North Slope drainages, harvest rates have not historically warranted management concerns about fishery effects on population sustainability. As an example, Arvey (1991) estimated sport fishery harvests to be 1,000–3,000 fish annually, and subsistence catches to be two to six times this amount. Freshwater habitats, especially overwintering sites, are thought to be most limiting to this species, and thus the possible effects of climate change have raised concerns about their management and conservation (Viavant, 2001; Crane and others, 2005; Greiner, 2009). These concerns have translated into efforts to identify and map overwintering locations and feasibility studies for enumeration of Dolly Varden at major overwintering sites including evaluation of the genetic stock composition at key index areas (for example, Hulahula River, Saganavirktok River, and tributaries). Population monitoring methods include aerial counts of overwintering abundance with possible validation by mark-recapture studies (that is, Ivishak, Anaktuvuk, Canning, and Hulahula Rivers, see Viavant, 2009; Rat River, see Harwood and others, 2009) and use of Dual Frequency Identification Sonar (DIDSON) technology and various species validation techniques (for example, underwater camera and hook and line sampling) in the Hulahula River (Greiner, 2009).

Information about the demographic traits for most marine fish populations in the Chukchi Sea is lacking largely due to the absence of large-scale fisheries operating in the region and corresponding lack of resource assessments and demographic data. Some population information is available from surveys sponsored by BOEM during the early 1990s. As an example, demographic information was developed for Bering Flounder and Arctic Staghorn Sculpin in the northwestern Chukchi Sea by Barber and others (1994). New research being conducted and planned by NOAA and the University of Alaska is expected to address many of the gaps in life history and demographic traits for marine fishes in the Chukchi and Beaufort Sea shelf habitats.

Modeling Environmental Effects on Population Dynamics

The quantitative approaches to population ecology studies of Arctic fish, although limited, are most appropriately considered in light of traditional research associated with physiological responses, dispersal processes, and food web relations.

Physiological research in the nearshore Alaska Beaufort Sea has focused on seasonal growth rates (VBGM growth parameters), body condition (Anderson and Gutreuter, 1983), as part of long-term monitoring of coastal habitats (<2 m) most affected by oil and gas development[9]. The monitoring was designed to obtain biological information about key indicators (notably Arctic Cisco and Broad Whitefish), their use of habitats (generally in the area between the Colville and Saganavirktok Rivers), and population responses to variable hydrographic conditions. Shallow coastal waters are responsive to wind-driven circulation, regional upwelling, and, in the Prudhoe Bay area, localized changes in temperature and salinity associated causeway construction (for example, breaching and wake eddy effects at West Dock and Endicott projects). The long-term monitoring provided seasonal indices of fish abundance and samples for age and growth analysis and trophic studies for indicator species across a large segment of the coast. Physical data collections included observations about wind and weather conditions and hydrographic profiles associated with fish collection efforts. Fish catch records from the Colville River delta are another source of long-term population data. Genetic samples (mtDNA) were obtained for Broad Whitefish from freshwater habitats in the Colville and Saganavirktok Rivers to determine if they were distinct populations (Patton and others, 1997).

The monitoring in Prudhoe Bay was designed to evaluate potential causeway effects on coastal habitats and amphidromous fish populations and related effects to subsistence and commercial fisheries. In a 5-year study, Griffiths and others (1992) studied growth patterns in young (age-1 and age-2) Arctic Ciscoes and Broad Whitefish collected around the causeways (Fechhelm and others, 1995a; 1995b). Growth (increase in length) in each species was positively correlated with temperature and body conditions. Negative correlations between condition and salinity were reported for larger Broad Whitefish and Griffiths and others (1992) suggested that the availability of prey and food benefits associated with marine waters moved inshore, outweighed

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[9] A listing of scientific publications associated with long-term monitoring studies in the Prudhoe Bay area, Alaska, is available from LGL Limited (2014).

negative effects on their growth due to temporary exposures to colder-higher salinity conditions. Reduced growth in about 4–6 percent of each was attributed to causeway effects (for example, thermal barriers and wake eddies).

Numerous ichthyoplankton surveys have been done in the Chukchi and Beaufort Seas. The studies were designed as reconnaissance surveys rather than dispersal studies although the results, as reviewed in this report, shed considerable light on diversity patterns and processes. Research directly focused on *dispersal processes* was used to study population trends and origins of Arctic Cisco in northern Alaska. A delay-difference population model (Deriso, 1980) was used by Gallaway and others (1983) to estimate biomass production of Arctic Ciscoes targeted in a local fishery in the Colville River[10]. Harvest records for the autumn gillnet fishery have been available since they were first collected in 1967 (Fechhelm and others, 2007; Moulton and others, 2010). The Deriso model, classified as a partially age-structured model, was used to investigate annual abundance patterns in the fishery relying on data obtained from (1) 15 years of catch records, (2) CPUE obtained in coastal surveys, and (3) population information acquired from tagging studies associated with those surveys. The model was parameterized with biological information about estimated growth, recruitment, survival and age structure, of fish captured in the Colville River fishery. In this case, the modeling allowed for time lags in the dynamics of the stock for Arctic Cisco (stocks are known for their slow growth and late age of entry to the fishery) and accounted for observed fluctuations in annual abundance as reflected in the catch. Importantly, the model generated a hypothesis about Mackenzie River origins for this Alaskan stock and annual transport of young-of-the-year ciscoes (Gallaway and others, 1983). A dispersal mechanism in wind-aided currents was described by Fechhelm and Fissel (1988) and its effects on recruitment processes in the Colville River fishery by Fechhelm and Griffiths (1990). The interaction of fish, winds, and currents on young-of-the-year (YOY) migration patterns was numerically modeled by Colonell and Gallaway (1997) and results considered in light of interannual fluctuations in abundance of fish in coastal monitoring in Prudhoe Bay and catch rates in the fishery[11]. A simulation model was developed to investigate wind effects on interannual variations in summer dispersal patterns of juvenile Least Cisco in the Prudhoe Bay area (Fechhelm and others, 1995a). The study of age structure in Colville River harvested Arctic Cisco (Zimmerman and others, 2013) may result in the improved population modeling recommended by Murphy and others (2007).

Predator-prey studies, mostly in the form of stomach content analyses and more recently using stable isotope and fatty acids (for example, Pirtle and Mueter 2011) are important components of habitat and community analyses including understanding ecological relations with respect to the maintenance of important populations or evaluations of potential cascading effects of regime shifts (for example, Suryan and others 2009; Carey and others, 2013). Many investigations in the Chukchi and Beaufort Seas have indicated the critical role that Arctic Cod have in Arctic marine food webs (for example, Bradstreet and others, 1986; Springer and others, 1986; Pirtle and Mueter, 2011) and their intermediate position in top-down and bottom-up energy pathways (Hunt and McKinnell. 2006). The results of marine fishery surveys invariably list this species, regardless of depth, season, or year, as the most abundant; usually far exceeding all other species reported in survey catches (Pirtle and Mueter, 2011[12]). Given this abundance and its central role in energy pathways, Arctic Cod must be viewed as a keystone species. This does not detract from the ecological significance of lipid-rich Capelin (Carscadden and Vilhjálmsson, 2002; Rose, 2005) and Arctic Sand Lance (for example, Bluhm and Gradinger, 2008) and, to a lesser extent Pacific Herring (for example, Mueter and others, University of Alaska-Fairbanks, oral commun., 2013) and Arctic Smelt (Craig and others, 1984a). These populations are subject to greater interannual changes in abundance, but have been shown to be locally abundant at various coastal locations and to be important in regional food webs.

The role of invertebrate prey in carbon cycling in Arctic marine ecosystems (Dunton and others, 2006) and in the diets of marine fishes and many higher-level consumers is significant (Craig and others, 1984b). In the Beaufort Sea, especially, the annual colonization of coastal waters by epibenthic amphipods and mysids, pelagic copepods, and other species (Craig and others, 1984b) forms the basis of the nearshore food web. Craig (1989a) and Craig and others, 1984b) discussed the availability of food in coastal habitats to standing crops of macroinvertebrate prey in freshwater habitats as being a significant factor in the evolution of anadromy (amphidromy) in the Arctic. The role of the epibenthic invertebrate food base is a key premise of time-tested conceptual models of fish habitat use in the Beaufort

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[10] Arctic Cisco are harvested between October and November each year. The availability of fish varies annually and Gallaway and others (1983) reported total catches ranging between 9,268 (1979) and 71,575 (1973) fish per year. The size of individuals captured in the fishery ranged from 240 to 380 mm (FL). From 1985 to 2004 about 38,600 Arctic Cisco have been harvested annually in commercial and subsistence fisheries (Least Ciscoes averaged about 18,600 annually during the same period). The average annual removal rate for Arctic Cisco was 8.9 percent of the available fish; the average annual removal rate for Least Cisco was 6.8 percent

[11] Zimmerman and others (2013) re-examined the Mackenzie River hypothesis in light of new genetics data, otolith microchemistry, and potential climate change effects on the coastal migration of YOY fish. Their analysis did not refute Mackenzie River origins for Arctic Cisco found in the Colville River.

[12] Pirtle and Mueter (2011) report peak densities of adult Arctic Cod at 150,000 fish per ha^{-1} at bottom depths of 100–350 m, and peak densities of YOY Arctic Cod at 160,000 fish per ha^{-1} at bottom depths of 20–75 m in the U.S. Beaufort Sea.

Sea (Craig and others, 1982; Craig, 1984) and bioenergetics of coastal fishes in Prudhoe Bay (Fechhelm and others, 1995a; 1995b). Marine food webs for fishery resources in the offshore Beaufort Sea are less studied, but likely are similar to shelf and slope areas of the Chukchi Sea. Planktonic species and under-ice fauna (phytoplankton, amphipods, copepods, euphaussiids, and larval fish) are important food resources for marine fishes in pelagic systems (for example, Gadidae Salmonidae, and others). Invertebrate species associated with the seafloor (for example, shrimp, amphipods, polychaetes, and benthic fauna) for marine species occupying benthic systems (for example, Pleuronectidae, Liparidae, Sticheaidae, and others).

In both nearshore and offshore environments of the U.S. Beaufort and Chukchi Seas, a broad generalization can be made that fish are also important in the diets of many fish species (for example, Gadidae, Salmonidae, Pleuronectidae, and others), particularly older, larger-sized individuals. Like other gadids, the Arctic Cod is cannibalistic. Thorsteinson and others (1990) hypothesized that the observed differences in coastal habitat used by YOY Arctic Cod and older cod in Camden Bay, Alaska, were an adaptive response to cannibalism. Similarly, some species, such as the Dolly Varden, are much more piscivorous than other dominant members of the coastal assemblage, but like most other species are opportunistic in their selection of foods. Although the food habits of some marine fishes are better known than others, the application of bioenergetics approaches to population dynamics modeling suffers from a (1) quantitative data about predator-prey relationships; (2) lack of seasonal information (spring and winter months especially); and (3) lack of long-term population data for most species of interest. For a small number of species in which appropriate data are available (for example, Broad Whitefish and Arctic and Least Ciscoes), bioenergetics applications to population ecology studies in coupled models may be possible. In the absence of data, other approaches to reduce uncertainties associated with selecting population models to evaluate responses to environmental influences (Katsanevakis, 2006), such as changes in recruitment and growth, have been done for Arctic Cisco (for example, von Bielea and others, 2011). In the latter instance, YOY recruitment into the Colville River was used examine the long-term response (1978–2004) of the population to climate change using multi-model inferences to study relations between trends in abundance and YOY growth and various environmental parameters (AO Index, air temperature, east wind speed, sea-ice concentration, and MacKenzie River discharge) and their influences of primary production and life stages of important cisco foods.

Biological Interactions

Estimation of ecosystem functions (for example, primary, secondary, and tertiary productivity; nutrient fluxes; carbon fixation; and organic matter mineralization and suspension removal) are feasible measures of biodiversity importance (Weslawski and others, 2006). The ecological effects of marine production cycles on the distribution and abundance of the Arctic marine fishes has received relatively little attention in the United States Arctic. In a large-scale analysis, Smetacek and Nicol (2005) compared the biological productivity reported in the Barents (Russia) and Chukchi Seas to the Siberian and Canadian shelf seas. The much higher productivity in the Barents and Chukchi Seas—gateways to the Arctic—were related to the advection and retention of nutrients in these systems. With respect to the Chukchi Sea, currents flowing through Bering Strait are rich in nutrients which, when mixed with iron (Fe) in shelf water and melting ice, fuels the high primary productivity of the region. Because of the Chukchi Sea's shallow depth and lack of a well-developed pelagic community, much of the bloom biomass (organic matter) settles out on the sediments and supports a rich, especially invertebrate, benthic fauna (Jay and others, 2011). The carbon sink and intense nutrient recycling occurring near the seafloor are critical processes supporting the region's benthic communities. In contrast, the Barents Sea is deeper and a greater proportion of phytoplankton production is retained in the water column. "*The exceptionally high copepod biomass of the western Barents Sea, largely attributable to advection from the adjoining Norwegian Sea, supports, or has supported, huge stocks of planktivorous fish including capelin and herring and their predators, particularly Atlantic cod*" (from Smetacek and Nicol, 2005, p. 364).

Trophic Linkages

Knowledge about ecosystem functions is foundational to understanding biological interactions of marine fishes. Fishes and zooplankton not only are important prey, but also are critical conduits of energy in regional food webs (for example, Chukchi Sea—Piatt and others, 1989). The large-scale animal distribution patterns (fishes, birds, and mammals) are driven by food availability, not the absence of predators (Hunt and McKinnell, 2006). These authors noted that at regional scales, current predation or past predation events likely have shaped local distributions, at least in marine birds and pinnipeds. Wasp-waist control occurs when one of the intermediate trophic levels is dominated by a single species, which may be the case with Arctic Cod in the Chukchi and Beaufort Seas.

Considerable research underscores the critical function of Arctic Cod in Arctic marine ecosystems because no alternate food source of equivalent trophic value exists. Processes in these ecosystems may have features that result in a switch from bottom-up to top-down control (Hunt and McKinnell, 2006) given the variable abundance of small pelagic species in response to changing environmental conditions. A moderating influence of sea ice in the population dynamics of Arctic Cod is hypothesized; however, loss of sea ice due to climate warming and unknown associated effects on the ecology of this species is of environmental concern[13]. Similarly, the potential effects of large oil spills and related clean-up activities on Arctic Cod could affect marine ecosystem functions.

The Arctic Cod is a key prey of many marine mammals and seabirds as evidenced by their occurrence in the diets of belugas and ringed and bearded seals, Pacific walruses (occasionally), Thick-billed (*Uria lomvia*) and Common Murres (*U. aalge*), Black Guillemots (*Cepphusgrylle*), Black-legged Kittiwakes (*Rissa tridactyla*), Northern Fulmars (*Fulmarus glacialis*), Arctic Terns (*Sterna paradisaea Pontoppidan*), and Glaucous (*Larus hyperboreus*), Sabine's (*Xema sabini*), Ivory (*Pagophila eburnea*), and Ross's Gulls (*Rhodostethia rosea*) (Hunt and McKinnell, 2006). Arctic Cod also are of indirect importance to Polar bears (*Ursus maritimus*) and Arctic foxes (*Vulpes lagopus*), because their primary marine food, the ringed seal, also relies on them as food.

Other fishes are important in regional food webs. Pirtle and Mueter (2011) summarized the known trophic linkages for seven species of marine fish (Arctic Cod, Capelin, Arctic Sand Lance, Pacific Herring, and Saffron Cod, and Arctic and Least Ciscoes) in the U.S. Beaufort Sea. Some aspects about trophic linkages between marine fish and invertebrate communities are described in detail in the species accounts (chapter 3). Depending on season and location, many of the marine species are major food resources for regional populations of seabirds, marine mammals, other fishes, and humans. As an example, the largest seabird colony in the North American Arctic is located at Capes Lisburne and Thompson in northwestern Alaska. Arctic Sand Lance, Capelin, and Arctic Cod are important prey for kittiwakes and murres at the colony during the breeding season (including pre-breeding and post-fledging periods). Pacific Herring and Arctic Cod are important foods of other fish (Inconnu, Chum and Pink Salmon, Dolly Varden), birds, and marine mammals in the Bering Strait and southeastern Chukchi Sea. Least Cisco is an important summer food of the Red-throated Loon in coastal habitats along the Chukchi Sea. Arctic Cod and Saffron Cod are notably important in the diets of most marine animals common to the Chukchi and Beaufort Seas including many seabirds, cetaceans, seals, polar bears, and Arctic foxes. The amphidromous fishes (whitefishes and charr) in the nearshore Beaufort Sea are preyed upon by Beluga whales (*Delphnapterus leucas*) and Ringed Seals (*Pusa hispida*).

Marine Fish Disease Ecology

In spite of obvious effects to humans and captive animals, fisheries managers often ignore disease as a significant factor affecting the abundance of wild populations because the effects are difficult to observe and quantify. Historically, most fish-health research has been directed toward identification, treatment, and prevention of diseases of hatchery fishes; however, recent studies (for example, Hershberger and others, 2013) from marine, freshwater, and terrestrial environments indicate that infectious and parasitic diseases can be responsible for population oscillations, extinction of endangered species, reduced host fitness, and increased susceptibility to predation as well as an important component of natural mortality. The recognition of disease as a population-limiting factor for wild fish is partly the result of the emergence of high profile pathogens and changes in environmental conditions that shift the host-pathogen balance in favor of disease. Among such environmental changes, global warming associated with climate change is seen to be a particularly important threat for poikilothermic vertebrates, such as fish, for which environmental temperature is a controlling factor in their physiology and immune response. The emergence of *Ichthyophonus* infections[14] in adult Yukon River Chinook Salmon, Pacific Halibut in the northeast Pacific, and Atlantic herring (*Clupea harengus*) off Iceland, are examples of disease conditions with links to global warming and possible transmission through trophic linkages (Woodson and others, 2011; Dykstra and others, 2012; Jim Winton, U.S. Geological Survey, oral commun., 2013). The disease is associated with adverse flesh quality and possible pre-spawning losses.

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[13] Arctic Cod are the most abundant forage fish and play a central role in the transfer of energy from plankton to higher-level consumers like ringed seals and polar bears (Hunt and McKinnell, 2006). As warming alters sea ice conditions, northward shifts in the distribution of marine fishes are expected. Such food-web impacts would propagate through the ecosystem, from sea-floor organisms to their predators, and, ultimately, to the subsistence users whose livelihoods largely depend on having reliable access to marine mammals, fish, and other wildlife. Shifts in marine biodiversity will partly depend on whether species are associated with the open ocean or with seasonal sea ice (Hunt and others, 2013).

[14] Phenotypic (Hershberger and others, 2008) and genotypic (Criscione and others, 2002; Rasmussen and others, 2010) differences have been identified among isolations of *Ichthyophonus hoferi* from the northeastern Pacific, suggesting that there are multiple sympatric species in the region. Due to this taxonomic uncertainty, the parasite is referred herein by its generic name.

Human Interactions

Subsistence Fisheries

Generally, subsistence is considered hunting, fishing, and gathering for the primary purpose of acquiring, sharing, or bartering traditional foods. Craig (1987; 1989b), Braund and Kruse (2009), and DeGange and Thorsteinson (2011) summarized the relative importance of marine fishes in the traditional economies of 11 Arctic communities using data obtained from the Alaska Department of Fish and Game[15] and others. Depending on village location, Pacific salmon, Dolly Varden, Arctic and Least Ciscoes, Broad and Humpback whitefishes, and Inconnu were the major fish species harvested. Arctic Cod, Saffron Cod, flounders (for example, Arctic Flounder), and sculpins (for example, Fourhorn Sculpin) and other marine fishes, such as Capelin and Pacific Herring, that occur in inshore waters, are of more limited, but still important usage. The subsistence survey data summarized by DeGange and Thorsteinson (2011) that Alaska Native Arctic residents are actively engaged in subsistence fishing and that fish are important foods (5–10 percent or more of traditional diet); fish is consumed on a daily basis in many villages, and in some cases provides more of a dietary contribution than any other food source. In the Kotzebue Sound area, fully one-third to one-half of the total subsistence harvest by weight consists of fishes. Although the inhabitants of the North Slope often depend much less on fishing and more on marine mammal and caribou (*Rangifer tarandus*) hunting, significant fish harvests are still made. The fact that fishes comprise more than 10 percent of the total subsistence harvest of Point Barrow is remarkable, considering the number and biomass of bowhead whales (*Balaena mysticetus*) harvested there annually (DeGange and Thorsteinson, 2011). At a larger scale, communities north of Bering Strait harvested 23 bowhead whales (about 750 tons) in 2008; the subsistence catch of marine fishes for the same area in Alaska was estimated at 60–70 percent of this amount. At Nuiqsut (Colville River), fish are the largest single contributors to the subsistence economy at nearly 40 percent of the total harvest.

According to an Alaskan catch reconstruction study (Booth and others, 2008), the total yearly subsistence harvest of fishes from Wales to Kaktovik in 1950 was approximately the same as in 2006 (450–500 tons). Changes in subsistence use at Wainwright, Barrow, Nuiqsut, and Kaktovik pre- and post-2000 were reported by Braund and Kruse (2009) and, within the constraints of existing data, show consistency over time for most species, and increasing catches of Pacific salmon (Carothers and others, 2013). Fish landings in the Chukchi Sea are primarily for local consumption (North Pacific Fishery Management Council, 2009). The most important species are salmonids, especially Chum Salmon and Inconnu, although 15 species of marine fishes are used. In Kotzebue Sound, Dolly Varden, Pacific Herring, and several species of flounder also are regularly harvested. About 90,000 fish are harvested annually and, in recent years, about 25,000 salmon were captured (Magdanz and others, 2011). Small numbers of five Pacific salmon found in Arctic Alaska are occasionally caught as far to the east as Amundsen Gulf, Canada. Generally, the closer a community's proximity to the more temperate and productive Bering Sea, the greater the number of salmon species caught and the greater the contribution of salmon to the local population's diet. This corresponds directly to the distribution of spawning populations of various salmon species. In the U.S. Arctic, Chum and Pink Salmon have the widest range and subsistence values.

The whitefish species are significant subsistence fishery resources in the 11 coastal villages where data are available (DeGange and Thorsteinson, 2011). Georgette and Sheidt (2005) documented their importance in Kotzebue Sound including the seasonality and methods of catch and complexity of Iñupiaq taxonomy. Farther north and east of Kotzebue Sound, various whitefish and cisco species and Dolly Varden comprise the marine basis of regional subsistence fisheries. Inconnu are important in the area of the central Kotzebue Sound and in the Mackenzie River Delta, Canada, but nowhere between. Least Cisco are important in local fisheries east of the Saganavirktok River, Alaska, but are little used by villagers at Kaktovik. Capelin, Arctic Smelt, Arctic Cod, other gadids, and some sculpins are eaten at Point Barrow. A small commercial and subsistence fishery for Least and Arctic ciscoes occurred until recently in the Colville River Delta, near Prudhoe Bay. In 2010, the Helmerick family terminated the commercial fishery for Arctic Cisco, but subsistence fishing continues by villagers from Nuiqsut. The Arctic Ciscoes captured in this fishery originate in the MacKenzie River, Canada; the Colville River, by virtue of its size, is the major overwintering site for Arctic Cisco in Arctic Alaska. The subsistence gill net fishery is size selective for 5- and 6-year-old fish, which are used by residents of Nuiqsut and Barrow, Alaska. Long-term fishery monitoring in Prudhoe Bay indicates increasing abundance of some marine fishes, such as Arctic Smelt and Arctic Flounder (Fechhelm and others, 2006), and suggests the possibility of their increased use by coastal residents in Nuiqsut and Barrow.

Dolly Varden is an important subsistence resource throughout the coastal Chukchi-Beaufort Sea region from the Seward Peninsula east to Kaktovik. Reliance on this species by humans is greatest in the villages of Wainwright and Kaktovik and in Kotzebue Sound. Located in the eastern Alaska Beaufort Sea, Kaktovik is situated near Dolly Varden spawning grounds in the Brooks Range (Craig, 1989a).

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[15] See http://www.subsistence.adfg.state.ak.us/CSIS/.

The timing and location of subsistence fisheries are intimately linked to the life cycle and habitats of targeted fishes. Environmental conditions, such as temperatures for drying and freezing of the fish flesh also are important. Marine and estuarine species are vulnerable to coastal fishing and the amphidromous/anadromous species are captured in both freshwater and coastal sites. Overwintering species, such as Arctic and Least ciscoes are targeted in autumn and winter fisheries with gillnets fished under ice. Coastally, during summer months, many species are captured in hook-and-line fisheries. Other species, such as Dolly Varden and Pacific Salmon can be captured in these fisheries. The marine connections of some lagoons, such as those in Kotzebue Sound, often are blocked by storm-induced gravel barriers near the end of summer, forming natural traps, or ditching, for desired species, such as Least Cisco (Georgette and Shiedt, 2005). Under certain conditions, gill nets are seined and fish weirs (traps) are used in Kotzebue Sound.

Commercial Fisheries

Commercial fishing in the U.S. Arctic is currently prohibited by Federal and international regulations (for example, National Pollution Funds Center (NPFC) and International Halibut Commission) because most fish stocks in the Chukchi and Beaufort Seas cannot support commercial harvesting (Wilson and Ormseth 2009). Three stocks (snow crab [*Chionoecetes opilio*], Arctic Cod; and Saffron Cod) were identified as sufficiently abundant to support potential fisheries. However, additional research (life history, interactions, and population dynamics) and resource assessments (monitor abundance and productivity) are needed to design sustainable harvest strategies (Levin and others, 2009; Fluharty, 2012). The current knowledge and understanding of fishery managers is that Arctic Cod and Saffron Cod are too important in regional food webs (for example, marine mammal and seabird predators) to be the targets of new, offshore commercial fisheries. Ongoing research by BOEM, NOAA, and NPRB involves ecological baseline surveys that may provide the basis for age- or length-based stock assessments for management of marine fish and shellfish resources in the Arctic. Oceanographic measurements and data on abundance, stock structure, growth, food habits, and energetics data, are being collected to develop quantitative information about the populations and responses to environmental changes including those resulting from human interventions.

Policy Interface—Ecological and Biologically Sensitive Areas

The Convention of Biological Diversity considered the ecological significance of Arctic marine fishes in defining Ecological and Biologically Sensitive Areas (EBSAs; Speer and Laughlin, 2011). Seasonally important habitats for many fishes, birds and mammals were identified along the ice edge, in polynyas, in coastal lagoons and on barrier islands, and in bays and river deltas. In the U.S. Pacific Region (Arctic Monitoring and Assessment Programme [AMAP]), the EBSAs include St. Lawrence Island, Bering Strait, Chukchi Beaufort Coast, Wrangell Island and polar pack ice. The global significance of these EBSAs is based on ecosystem functioning and with respect to marine fishes in the U.S. Chukchi and Beaufort Seas includes the Bering Strait, Chukchi Beaufort Coast, and Polar ice pack.

Bering Strait

The Bering Strait[16] exhibits the highest levels of fish and wildlife productivity and diversity in the Arctic and is the only connection between the Pacific and Arctic Oceans. Arctic Cod and other species of forage fishes are abundant and important to many marine predators, and the region supports populations of whitefishes and charr, which are important seasonally for native community subsistence.

Chukchi Beaufort Coast

The Chukchi Sea has massive phytoplankton blooms, which along with annual sea ice algae production, cannot be fully exploited by the zooplankton communities resulting in an impressively high biomass of benthic infauna and epifauna. Capelin occurs along the sandy seaward beaches of barrier islands in the area of Points Lay and Barrow. Coastal waters provide whitefish nursery areas and migration corridors for whitefish, ciscoes and Dolly Varden. The spring lead and Hanna Shoal (Chukchi Sea) retain sea ice, making it an important area for seabirds in spring and pinnipeds in late summer when sea ice is absent over the rest of the continental shelf.

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[16] The importance of the Bering Strait, as a gateway to the Arctic is widely recognized in national science policy (Speer and Laughlin, 2011; Wilson and Ormseth, 2011; Clement and others, 2013; National Ocean Policy Implementation Plan, 2013; U.S. Arctic Research Commission, 2013) and marine research associated with the Northern Bering Research Area (NPFMC) and Distributed Biological Observatories (National Science Foundation [NSF] and Alaska Ocean Observing System [AOOS]) and other large-scale ecosystem initiatives (that is, NRPB, BOEM, and NSF).

Polar Pack Ice

The multiyear pack ice provides habitat for distinctive fauna and flora. The extent of the multi-year ice is extremely variable inter-annually and is not a static geographic area, but rather an ever-changing feature that provides critical habitat for many animals. Arctic Cod is a key species in short food chains leading to seal and polar bear consumers.

Arctic Climate Change

Non-linear responses of marine ecosystems and populations to atmospheric forcing and warming are major sources of scientific uncertainty as they pertain to estimating probable outcomes of climate scenarios and describing the vulnerability of key biotic resources. The major sources of variation can be characterized as short-term effects on physical (for example, wind, waves, currents, temperature, stratification, nutrients, precipitation, and freshwater input) and biological (for example, phenology, primary production, food availability, and recruitment) environments, and long-term ecological changes (for example, temperature regimes, distributional shifts, and trophic cascades). Because warming effects are occurring more quickly toward the poles, both short- and long-term effects of these changes will be amplified in the Arctic. At the Arctic basin scale, marine ecosystems are affected by the interactions of physical and biological processes occurring at multiple scales of spatial and temporal resolution (for example, global—warming, regional—regime change, local—predation and survival). At a geographic scale, atmospheric forcing—related to the geography, persistence, and teleconnections of continental pressure systems—affects ecosystem function and structure at different spatial and temporal scales (Grebmeier and others, 2006a; 2006b). At smaller scales (centimeters to meters), recruitment processes can be affected by the dispersal and survival of larval fishes.

Ocean Connections

In association with atmospheric influences, Arctic marine ecosystems are also connected through ocean circulation and the long distance transport and mixing of north Atlantic and northeast Pacific waters. Marine waters over the Chukchi Sea shelf tend to be colder and more nutrient rich than water in the Beaufort Sea because of upwelling processes in the northern Bering Sea and transport of marine nutrients of deep northeast Pacific origins. Hydrographic conditions on the shelf indicate the presence of three main water masses that move to the north along the Alaska coast, across the Bering Sea from the northeast Pacific, and to the south along the Russia coast (Crawford and others, 2012). Farther north, the offshore Beaufort Sea is influenced by a mixing of Chukchi Sea water masses and north Atlantic-derived waters (transported to the east) and circulation of other Arctic waters in the Beaufort Gyre (transported to the west). An ephemeral band of brackish water forms along the coast of the North Slope during summer months. As summer advances, the frequency of west winds along the North Slope increases, resulting in marine intrusions and colder, higher salinity water nearshore.

Marine Ecosystem Effects

Extensive and rapid losses of sea ice in the Arctic are already affecting marine ecosystems and raising conservation concerns for ice-dependent fishes, birds, and mammals (Marz, 2010; Jay and others, 2011; Wiese and others, 2015). Sea ice melt and break-up during spring strongly drive phytoplankton production by enhancing light and stratification and stabilization of the water column. The intensity and magnitude of the events is therefore determined in large part due to temperature and salinity, light conditions, and nutrient availability as well as composition and fate of the plankton community. Generally, the annual production event, including algal growth under sea ice, forms the base of the marine food web, which in turn supports higher trophic level consumers including zooplankton, fishes, birds, and mammals. The consumption of phytoplankton by the herbivorous zooplankton in the Chukchi Sea tends to be inefficient (incomplete grazing) leading to a tight coupling between pelagic and benthic ecosystems and deposition of significant amounts of organic debris (decaying phytoplankton) to the benthos. In areas of high deposition, sea floor habitats have a diverse and abundant benthos that provides important feeding grounds for a rich invertebrate community and benthic feeding animals such as walrus and bearded seals. Biological hotspots have been identified in the Barrow Canyon and Hannah Shoal in the northeastern Chukchi Sea near Barrow, Alaska.

Climate-induced changes in growth conditions for primary producers could affect the timing, productivity, and spatial extent of biological hot spots—areas of elevated food web activity (Leong and others, 2005). As an example, Frey and others (2011) reported a 20 percent increase in production throughout the Arctic Ocean during 1998–2009; an estimate that included a 48 percent increase in primary production for the Chukchi Sea. The increases were thought to reflect increased bloom durations in open water in time and space. Zooplankton communities may be particularly sensitive to such changes as their seasonal life cycles are in synchrony with the timing of ice-breakup and phytoplankton blooms (Smith and Schnack-Schiel, 1990; Deibel and Daly, 2007). With warming and changing sea ice conditions, northerly shifts in the distribution of marine fish have been projected. Although commercial concentrations of marine fish are not anticipated in the near term (probably decades due to temperature constraints), conditions that are more favorable for energy use by pelagic species (gadids, salmonids, and other marine fishes) in the Chukchi Sea may result from ecological changes associated with regime shift (Grebmeier and others, 2006b). In this instance, changes in the food web, such as reduced standing stocks of benthic invertebrate foods, could potentially affect the distribution and abundance of predators. Such changes in distributional patterns already are being observed in Pacific walrus (David Douglas, U.S. Geological Survey, Juneau, Alaska, oral commun., 2013).

In a study of possible responses of the Atlantic Cod to climate change, Pörtner and others (2008) examined functional interactions of ecological and physiological processes and effects on this species at various levels of biological organization. The potential effects associated to exposures beyond optimal temperatures can be broadly generalized to other Arctic marine fish species. At the ecosystem level, the thermal disturbance (warming) could result in changing biogeography, biodiversity, seasonal timing, species interactions (mismatch), food web relationships, and overall ecosystem (including social interactions) function (Harley and others, 2006). At the population level, reduced densities might be expected as a result of changes in growth, reproduction, recruitment, and mortality. Changes in fish behaviors and demographic traits altered the physiological scope for growth in individual fish with cumulative effects on population processes. The physiological mechanisms operate at cellular and molecular levels and can change metabolic processes, and alter an organism's functional integration, condition and health, and susceptibility to disease. Within this conceptual framework, it is also possible to envision more positive effects if warming enhances thermal conditions for a particular species life functions and behaviors resulting in possible population growth and expansion.

Ocean Acidification

Changes in ocean chemistry, known as ocean acidification, are an expected outcome of global warming. Ocean acidification (OA) occurs when increases in atmospheric carbon dioxide (CO_2) cause an increase in the oceanic uptake of CO_2. This in turn leads to an increase in marine production of carbonic acid, reducing the pH of marine waters—ocean acidification. Ocean acidification changes ocean chemistry by reducing calcification rates and lowering calcium carbonate saturation (Mathis and Questel, 2013). Calcium carbonate is a key mineral used in calcareous shell production and other biological processes (Doney and others, 2009). The changes in ocean chemistry from ocean acidification are expected to be amplified in the Arctic Ocean[17] with potential biological effects to food webs (that is, shell forming organisms such euphausiids) and marine fish populations (development and survival of early life stages of marine fish and foods) could be significant. In the U.S. Arctic, the ecological effects from amplification of potential acidification in freshwater discharges from the Yukon (195 km^3/yr) and Mackenzie (306 km^3/yr) Rivers (Milliman and Meade, 1983), including nutrients, organic matter, and sediments into Chukchi and Beaufort Seas are not known. For comparison, the freshwater discharge from the Mississippi River into the Gulf of Mexico is 580 km^3/yr.

Shifts in Distribution of Marine Fish Populations

Climate change effects in the Arctic marine environment include loss of sea ice in summer, increased stratification, and shifts in the timing and intensity of the seasonal production cycle (Slagstad and others, 2011; Wassmann and others, 2011). Several authors have attempted to project how these changes will affect marine fish populations (Reist and others, 2006; Huse and Ellingsen, 2008; Mueter and Litzow, 2008; Pörtner and others, 2008; Cheung and others, 2009; Bluhm and others, 2011; Mueter and others, 2011; Sigler and others, 2011; Hunt and others, 2013) and suggest potential effects on biogeography (for example, shifts in distributional), physiology (reproductive timing) and behavior (diet; Hollowed and others, 2013). Cheung and others (2009) projected that expanding bioclimatic windows would result in increased biodiversity in the Arctic. In contrast, Sigler and others (2011), projected that the shallow sill separating the northern Bering Sea and the Chukchi Sea, and the persistent presence of the cold water over the northern Bering Sea shelf (Stabeno and others, 2012a), would serve as a barrier to invasions of fish species into the region. Fishery baselines are changing rapidly throughout the Arctic; the possibility of new fisheries has increased the urgency for scientific attention to biodiversity and stock assessments (Christiansen and others, 2014).

Mueter and Litzow (2008) described the southern edge of the *cold water pool* as defining the ecotone between Arctic and subarctic communities in the northern Bering Sea. The ecotonal boundary reportedly moved 230 km northward since the early 1980s, and Mueter and Litzow (2008) reported that community-wide shifts in distributions and related increases in biomass, species richness, and average trophic level occurred as subarctic species colonized new habitats. The warming temperatures were indicated as the primary cause of changing community distribution and function although other factors were implicated. Importantly, specific responses of individual populations to temperature changes were more difficult to estimate. The range extensions reported in this report are not indicative of significant new additions of subarctic fish species to the Arctic fauna. The effects of winter sea ice and thermal effects of the Earth's inclination at high latitudes suggest cold water temperatures will persist in the Arctic and act to impede successful widespread expansions of many harvestable stocks

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[17] Global warming trends have been amplified in the Arctic region relative to the global mean, and increased vulnerability of the Arctic, is due to the effects of increased freshwater input from melting snow and ice, temperature, and from increased CO_2 uptake by the sea as a result of ice retreat (Fabry and others, 2009).

from the Bering Sea. Given the ecological significance of Arctic Cod in Arctic marine food webs and energy cycling, a special analysis was done to describe climate change effects on Arctic and Saffron Cod in the northern Bering Sea (see chapter 5).

In an Arctic-wide climate-change assessment, Hollowed and others (2013) examined the vulnerability of 17 commercially exploited species in the Bering, Barents, and Norwegian Seas to move farther into the Arctic. The vulnerability assessment was based on exposure (to variations in the environment resulting from climate change), sensitivity (degree to which a species responds to variations in the marine environment that will be affected by climate change), potential affect (probable combined effects of exposure and sensitivity), and adaptive capacity (a species physiological or behavioral abilities to mitigate the effect). The potential for movement of the stocks was evaluated on climate change projections and expert opinion relative to life history (for example, reproductive ecology, feeding, and migratory behavior) and environmental preferences for temperature. Several of the Bering Sea species considered (that is, Walleye Pollock, Pacific Cod, Arctic Cod, Capelin, Arctic Skate, Greenland Halibut, Yellowfin Sole, and Bering Flounder) already occur in the Chukchi (all species listed) and Beaufort (Walleye Pollock, Arctic Cod, Arctic Skate, Capelin, and Greenland Halibut) Seas. Pacific Ocean Perch (*Sebastes alutus*) and Northern Rock Sole (*Lepidopsetta polyxystra*) were considered as having a low potential to move into the Arctic. Neither species has been collected from the U.S. Beaufort and Chukchi Sea. The potential for expansion of Walleye Pollock and Pacific Cod was determined to be low due to temperature and spawning site fidelity, respectively. Greenland Halibut and Capelin potentially could expand in the Arctic if temperature and conditions for larval transport and survival, or prey concentrations, respectively, were sufficient to sustain increased populations. Three stocks (Arctic Cod, Bering Flounder, and Arctic Skate) were determined to have a high potential to expand or move into the Arctic. Arctic Cod spawning occurs under ice and spawning areas will likely change if winter ice cover is lacking in the traditional spawning areas.

For many of the species identified by Hollowed and others (2013), the issue may not be the potential likelihood for northward movements, but climatic and habitat conditions (temperature , foods, substrates, and other conditions) for all life stages that increase the viability and relative abundance and expansion of small populations already present in the Arctic. Our analysis of marine fish diversity indicates that Pacific Cod and Greenland Halibut are uncommon in the Chukchi and Beaufort Seas. Alaska Plaice has been confirmed from the Chukchi Sea but not the Beaufort Sea. Yellowfin Sole is common in the Chukchi Sea but is rare in the Beaufort Sea.

Available data support a hypothesis that natural selection favors individuals that maximize growth and energy efficiency at the expense of ranges of thermal tolerance (Pörtner, and others, 2008). Capelin is a cold water, circum-Arctic species (temperature preferences from -1 to 6 °C; Rose, 2005). In the U.S. Arctic, this species is locally abundant at various locations along the coast as spawning occurs in nearshore deltaic areas. The vulnerability of the species, or stocks adapted to Arctic conditions, to warming and their sensitivity to exposures exceeding a narrow range of temperature optima, is probably great. Under warming conditions, physiologically-motivated shifts in distribution and seasonal abundance could result in cascading effects on regional food webs and changes in foraging behaviors. The disappearance of Capelin in the Gulf of Alaska during the temperature regime shift beginning in the mid-1970s was hypothesized to be in response to elevated temperatures (Anderson and Piatt, 1999; National Research Council, 1996). Generally, other marine species evaluated by Hollowed and others (2013) that are already occurring in the northern Bering Sea or southern Chukchi Sea (with the possible exception of Pacific Cod because of the species fidelity to spawning areas in the Bering Sea) increased abundances of species in the Chukchi Sea and further expansions onto the Beaufort Sea shelf and slope are considered a highly probable response to climate change.

Effects on Salmon Colonization

Pink and Chum Salmon are the most commonly reported species in the Alaska Arctic north of Point Hope (Nielsen and others, 2012). Small commercial fisheries operate in Kotzebue Sound and subsistence fishing occurs farther north. Small numbers of spawning Chum and Pink Salmon have been observed in rivers as far east as Prudhoe Bay in the southeastern Beaufort Sea (Craig and Haldorson, 1986). Whether the spawning observations to the north of Point Hope represented putative populations or straying continues to be unclear. Lack of suitable spawning habitats and extremely cold temperatures have been cited as reasons why this salmon straying has not led to sustainable populations (Irvine and others, 2009; Nielsen and others, 2012). However, each year increasing numbers of Chinook Salmon are being captured at Point Barrow and other sites along the coast. Over the next 30 years, as thermal barriers to migration and successful reproduction break down and, as freshwater, coastal, and marine habitats improve for salmon (for example, extended growing seasons, increased productivity, and other improvements) range expansions for chum, pink, and Chinook Salmon in Alaskan Arctic rivers seems certain. The successful colonization of these habitats by salmon is more difficult to estimate (Nielsen and others, 2012).

Salmon Disease Ecology

Ichthyophonus in adult Chinook Salmon in the Yukon River has been linked to global warming and, because it is prevalent in marine fishes elsewhere in the northeast Pacific (for example, Pacific Halibut in the Gulf of Alaska), represents a potential threat to Arctic marine fishes (James Winton, U.S. Geological Survey, oral commun., 2013). Other diseases of fish, notably viruses of the Rhaddoviridae family (for example, viral hemorrhagic septicemia and infectious hematopoietic necrosis virus) would be novel pathogens in the Arctic marine fauna and potentially threaten members of the Salmonidae. Some ways that global warming can affect the severity and distribution of infectious diseases of fish include changes in the growth rate of pathogens, the types or strains of pathogens present, the distribution or biological carriers and reservoirs, the density or distribution of susceptible species, the diets that can alter resistance to disease, and the physical habitat that can affect disease ecology (Woodson and others, 2011). Although disease information is generally lacking, the anticipated effects of climate change, especially global warming, on fish diseases will include warmer temperatures and, in freshwater, lower flows that will exacerbate diseases caused by endemic parasites and pathogens, increase growth rates of pathogens, favor pathogens or strains that replicate at higher temperatures, and alter the strength and speed of host immune response disease (Hershberger and others, 2013). Additionally, altered freshwater and ocean conditions could change the distribution or density of hosts as well as the overlap with vectors, carriers, or reservoirs of infection. These altered habitats can produce biotic and abiotic stressors that will decrease the resistance to disease, and finally, a greater disease burden and associated fitness losses will increase the disease component of natural mortality among populations of fish.

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Summary

Historical biogeography objectives of this synthesis describe the probable origins of distributional patterns as determined from systematic studies. The description of origins is complicated and largely hypothetical because the paleoceanographic record is not well-developed from the U.S. Arctic. Despite this, species origins were examined in light of possible dispersal and vicariance events as suggested by paleontologic and geologic records, climatic histories, and known phylogenetic relations. Information is limited, but when the known histories are compared with the phylogenetic record, preliminary results suggest that most marine fish species currently in the U.S. Chukchi and Beaufort Seas evolved from a Pacific ancestor. Ecological biogeography objectives addressed the environmental relations including physiochemical factors (for example, temperature, salinity, dissolved oxygen, and turbidity), mechanisms (currents, migrations, and movements), and biological processes (competition, predation, colonization, and reproduction) that limit the distribution, relative abundance, and productivity of a species. Global warming effects on this part of the Arctic are occurring at twice the rate of change in lower latitudes. Changes in regional sea ice coverage, physical and chemical oceanography, and hydrology are expected to have profound effects on coastal and marine ecosystems. Northerly shifts in the distributions of many migratory marine fishes, such as Pacific salmon, are expected with physical changes in temperature and process changes associated with benthic-pelagic coupling over shelf waters.