Pinniped Movements and Foraging: Seasonal Movements, Habitat Selection, Foraging and Haul-out Behavior of Adult Bearded Seals in the Chukchi Sea

FINAL REPORT

By

Peter L. Boveng and Michael F. Cameron
National Marine Mammal Laboratory
Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle, WA 98115

Prepared for
U.S. Department of Interior
Bureau of Ocean Energy Management
Alaska Outer Continental Shelf Region
Environmental Studies Section
3801 Centerpoint Drive, Suite 500
Anchorage, AK 99503-5823

This study was funded by the U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM), through Inter-agency Agreement M07RG13317 with the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, as part of the MMS Alaska Environmental Studies Program.

DISCLAIMER

REPORT AVAILABILITY

This document is available to the public through:
National Technical Information Service
5285 Port Royal Road
Springfield, Virginia 22161
FAX: (703) 605-6900

And at

http://www.boem.gov/Environmental-Stewardship/Environmental-Studies/Alaska-Region/Index.aspx

CITE REPORT AS

Boveng, P.L. and M.F. Cameron. 2013. Pinniped movements and foraging: seasonal movements, habitat selection, foraging and haul-out behavior of adult bearded seals in the Chukchi Sea. Final Report, BOEM Report 2013-01150. Bureau of Ocean Energy Management, Alaska Outer Continental Shelf Region, Anchorage, Alaska, USA. 91 Pp + Appendix.

PROJECT ORGANIZATION

Peter Boveng; NMFS, Seattle, Washington:
Principal Investigator and report author

Michael Cameron; NMFS, Seattle, Washington:
Co-Principal Investigator and report author

Alex Whiting; Native Village of Kotzebue, Kotzebue, Alaska:
Community Co-Investigator

Jason Herreman; North Slope Borough, Barrow, Alaska:
Community Co-Investigator

John Goodwin; Kotzebue, Alaska:
Field Project Leader

Carl Nayakik; Barrow, Alaska:
Field Project Leader

Enoch Oktollik; Wainwright, Alaska:
Field Project Leader

Josh London; NMFS, Seattle, Washington:
Data Manager

Jay Ver Hoef; NMFS, Seattle, Washington:
Statistician

Brett McClintock, NMFS, Seattle, Washington:
Statistician

Shawn Johnson; Johnson Veterinary Services, Vacaville, California:
Field Project Veterinarian

ABSTRACT

Bearded seals (*Erignathus barbatus*) are one of the most important subsistence resources for the indigenous people of coastal northern and western Alaska, as well as key components of Arctic marine ecosystems, yet relatively little about their abundance, seasonal distribution, migrations, or foraging behaviors has been documented scientifically. Ice-associated seal populations may be negatively impacted by offshore oil and gas development as well as by climate change. Our ability to predict impacts, however, is limited by inadequate knowledge of seal population structure and foraging ecology. By working cooperatively with Alaska Native subsistence hunters we developed methods for live-capturing bearded seals in the Chukchi Sea using nets set in the shallow coastal waters where bearded seals were foraging. Capture efforts were based out of Kotzebue and various locations in the North Slope Borough from Wainwright to Barrow in June and July from 2009 to 2012. In all, 7 seals were caught (2 adults and 5 sub-adults; 4 males and three females; ranging in length and weight from 159 cm and 116 kg to 216 cm and 253 kg), all from Kotzebue Sound. Each seal was sampled for health and condition and released with two different types of satellite-linked, geo-locating data recorders (SDRs): the SPOT SDR, attached to a rear flipper, provided information on the timing of hauling out and on the seal's location for up to three years; the MK10 SDR, glued to the top of a seal's head, provided the same information as the SPOT SDR and also provided data on the timing and depths of dives, for up to ten months.

Upon release, all seals left Kotzebue Sound and moved north along the Alaskan coastline to Point Hope. Though two moved offshore, preferring to occupy the central Chukchi Sea north of 70°N, most continued north and west in shallow, nearshore waters (e.g., three continued into the Beaufort Sea). All seven individuals spent substantial amounts of time within the Chukchi and Beaufort Sea planning areas (CSPA and BSPA, respectively), often occupying locations near or in the lease sale areas. Of all the locations obtained from bearded seals in the CSPA, 21.8% were within 50 km of a lease sale area (5.5% were within 10 km). In the BSPA, 75.0% of the locations obtained were within 50 km of a lease sale area (and 53.0% were within 10 km).

In the fall, all seals began moving south with the advancing ice and, by December, all had passed into the Bering Sea where they spent the winter and early-spring. The tagged, male bearded seals exhibited strong winter site fidelity in the Bering Sea, establishing their preferred sites even as sub-adults and returning year-after-year to the same localized areas. The females spent the first winter after tagging in

the Bering Sea, as well, but data on subsequent winter locations were incomplete or as of the end of this reporting period. In spring, all seals returned north through the Bering Strait and into the Chukchi Sea, some even reoccupying Kotzebue Sound on their way north. As such, the bearded seals found in Kotzebue Sound during late June are associated with a population or sub-population that winters and breeds in the Bering Sea, but makes extensive seasonal use of the Arctic seas to the north.

The vast majority of dives made by all seals were to depths less than 70 m and between 6 and 10 minutes in duration, throughout all seasons and times of day. Dive depth and dive duration appeared to be related to seafloor depth, with seals occupying deeper waters diving deeper and for longer periods than those in more shallow waters. For example, the few records of dives deeper than 150 m and with durations of roughly 20 minutes, were made by individuals that were over canyons or the continental shelf break in the Beaufort and northern Chukchi Seas. Though analysis of patterns in the diving behavior will help to document the areas that appear to be most important to bearded seals, a larger sample will be needed for more comprehensive identification of important summer and autumn foraging habitats and to make general inference about the population as a whole.

An examination of the timing of hauling out indicated that in July, bearded seals occasionally used available sea ice to haul out for periods up to 38 hours, but from August through October bearded seals occupied areas that were nearly or entirely ice free, and so rarely hauled out. In winter, even in areas of abundant sea ice, the seals rarely hauled out, preferring instead to remain in the water, perhaps for foraging or thermoregulatory reasons. Perhaps reflective of preparations for whelping and nursing pups and for setting up breeding territories, haul-out bouts increased in frequency and duration in early spring, though these were still relatively rare. These bouts were of shorter duration compared with those in July, mostly lasting less than 24 hours with evening being the most preferred time of day to haul out onto the ice. Most aerial surveys for ice-associated seals are conducted in the late-spring and early-summer. Unfortunately, we do not have hauling out data available for this time period which precludes our ability to directly calculate a correction factor for these surveys. Acquisition of reliable haul-out data for bearded seals remains a high priority for research and monitoring.

KEY WORDS: bearded seal, *Erignathus barbatus*, satellite telemetry, Arctic, Bering Sea, Chukchi Sea, Beaufort Sea

CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Bearded seals (*Erignathus barbatus*) are large phocid seals, inhabiting circumpolar Arctic and sub-Arctic waters in relatively shallow water depths that are seasonally ice-covered (Figure 1). The common name, bearded seal, derives from the prominent, light-colored, down-sweeping vibrissae (whiskers) that often curl when dry. Bearded seals are also called mukluk or maklak (Yupik Eskimo term in southwest Alaska, St. Lawrence Island, and southern Chukchi Peninsula), and ugruk or similar Inupiat or Inuit terms used from the Chukchi Peninsula east to Greenland (Chapskii 1955, Burns and Frost 1979). Their distribution appears to be strongly influenced by water depth and prey biomass (Kelly 1988) and, to a lesser degree, by ice condition (Burns 1981).

Two subspecies of bearded seals are widely recognized; *E. b. barbatus* often described as inhabiting the Atlantic sector, and *E. b. nauticus* inhabiting the Pacific sector (Rice 1998). The geographic distributions of these subspecies are not separated by conspicuous gaps. In Alaska waters, they are distributed over the continental shelf of the Beaufort, Chukchi and Bering Seas between 85°N and 57°N (Ognev 1935, Johnston et al. 1966, Burns 1981). Bearded seals are benthic feeders, consuming clams, shrimp, crabs, benthic invertebrates and fish, primarily at depths less than 200 m (Burns 1967, Lowry et al. 1980, Stirling et al. 1982, Kingsley et al. 1985). During the winter in the Chukchi and Bering seas, these seals are most common in broken pack ice (Burns 1967, 1981) and, in some areas, shorefast ice. Bearded seals migrate south and away from the shore with the advancing ice edge in winter (Burns 1967), and in summer, most bearded seals are believed to move north with the receding ice, though some juveniles remain along the coast (Burns 1967, 1981).

Bearded seals are distinctive in appearance by virtue of their generally unpatterned, gray to brown coat (though the dorsal surface can be slightly darker) of short straight hair; wide girth; small head in proportion to body size; long mystacial vibrissae; and square-shaped fore flippers. When bearded seals are on the ice, they are readily recognized by their large size and their habit of resting singly at the edge of floes, oriented toward the water. Adults average 2.1-2.4 m in standard length and weigh up to 360 kg (Chapskii 1938, McLaren 1958, Johnson et al. 1966, Burns 1967, Benjaminsen 1973, Burns 1981). In some regions females appear to be slightly larger than males, but the differences are not statistically significant (Chapskii 1938, Benjaminsen 1973, Burns 1981).

Bearded seals primarily feed on benthic organisms that are more numerous in shallow water where light can reach the sea floor (Fedoseev 1965). As such, the bearded seals' effective range is generally restricted to areas where seasonal sea ice occurs over relatively shallow waters, typically less than 200 m, where they are able to reach the ocean floor to forage (Kosygin 1971, Heptner et al. 1976, Burns and Frost 1979, Burns 1981, Fedoseev 1984, Nelson et al. 1984, Fedoseev 2000, Kovacs 2002). Aerial surveys conducted in the Beaufort Sea indicated that bearded seals preferred areas of open ice cover and water depths primarily of 25-75 m (Stirling et al. 1977, Stirling et al. 1982), and aerial surveys in the Canadian High Arctic suggested that bearded seals in this region preferred water depths of less than 100 m (Kingsley et al. 1985). Tarasevich (1963) collected bearded seals in the Kara Sea in late September through the beginning of October. In areas with depths of 20-50 m, he collected mostly males, but in areas where water depth was less than 20 m, he collected males and females in similar numbers (Tarasevich 1963). In contrast, during winter surveys in northern Baffin Bay, most bearded seals were observed on ice in areas where water depths exceeded 200 m or even 500 m (Finley and Renaud 1980). Although these are much greater depths for bearded seal habitat than are usually reported, adults have been recorded to dive to depths near 300 m (Kovacs 2002, Cameron and Boveng 2009), and six of seven pups with dive recorders reached depths greater than 488 m (Gjertz et al. 2000).

Bearded seals are closely associated with sea ice -- particularly during the critical life history periods related to reproduction and molting -- and can be found in a broad range of different ice types (Fay 1974, Burns and Frost 1979, Burns 1981, Nelson et al. 1984). Ice provides a platform on which the seals haul out to bear and nurse pups and to rest and molt (Nelson et al. 1984). Of the ice-associated seals in the Arctic, bearded seals seem to be the least particular about type and quality of ice on which they are observed (Fay 1974). They appear to prefer low ice floes that have not become hummocky; however, the floes can be either very large or so small that it appears the seal is resting on the water (Heptner et al. 1976). They also seem to choose floes that are "clean" and white over those that are "soiled" or dirty. The seals are usually seen resting near the edges of ice floes, within a few feet of open water, with their heads facing the water and their bodies' perpendicular to the axis of the lead, and they avoid lying near large, highly compacted ice (Heptner et al. 1976, Burns and Harbo 1977). The presence or absence of snow cover is not normally a defining characteristic of bearded seal habitat. Smirnov (1927) and Rutilevskii (1939) reported that bearded seals occasionally make snow shelters or subnivean lairs on the ice like the ringed seal, though this behavior has never been described elsewhere and the reports are now considered to be unreliable (Heptner et al. 1976, Smith 1981).

Bearded seals generally prefer ice habitat that is in constant motion and produces natural openings and areas of open water, such as leads, fractures, and polynyas for breathing, hauling out on the ice, and access to water for foraging (Heptner et al. 1976, Fedoseev 1984, Nelson et al. 1984). They usually avoid areas of continuous, thick, shorefast ice and are rarely seen in the vicinity of unbroken, heavy, drifting ice or large areas of multi-year ice (Fedoseev 1965, Burns and Harbo 1977, Burns and Frost 1979, Burns 1981, Smith 1981, Fedoseev 1984, Nelson et al. 1984, Kingsley et al. 1985). In a study of bearded seal habitat use in the Bering Sea, ice floes were categorized into three size classes: brash ice (>2 m), cake floes (2-20 m), and large floes (>48 m); and mixed-floes habitat comprised a mix of floe sizes that could not be defined by a single size class (Simpkins et al. 2003). Aerial surveys conducted near St. Lawrence Island indicated that bearded seals selected habitat with medium ice coverage (70-90% cover) and mixed-floes habitat and avoided areas with heavy ice coverage (90-100% cover) and large floes. They appeared to prefer the transitional habitat between small and large floes (Simpkins et al. 2003). In a similar study in April and May, bearded seals in the Bering Sea were found to most likely occupy ice concentrations ≥75% (Ver Hoef et al. 2013). The highest densities of bearded seals in the eastern Chukchi Sea in May and June were in the offshore pack ice where high benthic productivity has been recorded (Bengtson et al. 2005), and bearded seals in June and July in the Canadian Arctic Archipelago selected areas of ice concentration in the 6/8 to 7/8 range (Kingsley et al. 1985). In late fall and winter, as ice begins to freeze up at the coasts and moves into bays, seals are seen farther out to sea among areas of drifting, broken ice floes, and near open water (Heptner et al. 1976). In the Beaufort Sea, bearded seals are most numerous in a narrow flaw zone, which is an area where drifting pack ice interacts with fast ice, creating leads and other openings (Burns and Frost 1979).

Sea ice provides the bearded seal and its young some protection from predators during the critical life history periods of whelping and nursing (Burns 2002); it allows molting bearded seals to get out of the cold water, raising skin temperature and facilitating epidermal growth (Feltz and Fay 1966); and it is important throughout the year as a platform for resting and perhaps thermoregulation (Lydersen and Kovacs 1999). Being so closely associated with sea ice, particularly pack ice, the seasonal movements and distribution of bearded seals are linked to seasonal changes in ice conditions. Bearded seals generally move north in late-spring and summer as the ice melts and retreats and then move south in the fall as sea ice forms to remain associated with their preferred ice habitat (Johnson et al. 1966, Burns

1967, Potelov 1969, Fay 1974, Heptner et al. 1976, Burns and Frost 1979, Burns 1981, Nelson 1981, Simpkins et al. 2003, Frost et al. 2008).

The region that includes the Bering and Chukchi Seas is the largest area of continuous habitat for bearded seals (Burns 1981, Nelson et al. 1984). The Bering-Chukchi Platform is a shallow intercontinental shelf that encompasses about half of the Bering Sea, spans the Bering Strait, and covers nearly all of the Chukchi Sea. Bearded seals can reach the bottom everywhere along the shallow shelf and so it provides them favorable foraging habitat (Burns 1967). The Bering and Chukchi Seas are generally covered by sea ice in late winter and spring and are then mostly ice free in late summer and fall, a process that helps to drive a seasonal pattern in the movements and distribution of bearded seals in this area (Burns 1967, 1981, Nelson et al. 1984). During the breeding season in May-June, bearded seals in the Bering Sea are near the ice front, but in contrast to ribbon (*Histriophoca fasciata*) and spotted seals (*Phoca largha*), which stay closer to the edge, bearded seals are usually farther north and in heavier pack ice (Fiscus and Braham 1976, Braham et al. 1981). As the ice retreats in the spring most adults in the Bering Sea are thought to move north through the Bering Strait where they spend the summer and early fall at the southern edge of the Chukchi and Beaufort Sea pack ice and at the wide, fragmented margin of multi-year ice (Fay 1974, Heptner et al. 1976, Burns and Frost 1979, Burns 1981, Nelson et al. 1984). A smaller number of bearded seals, mostly juveniles, remain near the coasts of the Bering and Chukchi Seas for the summer and early fall instead of moving with the ice edge (Burns 1967, Heptner et al. 1976, Burns 1981). These seals are found in bays, brackish water estuaries, and river mouths, and have been observed to travel up some rivers (Burns 1967, Heptner et al. 1976, Burns 1981). As the ice forms again in the fall and winter, most seals move south with the advancing ice edge through Bering Strait and into the Bering Sea where they spend the winter (Burns and Frost 1979, Frost et al. 2005, Cameron and Boveng 2007, Frost et al. 2008, Cameron and Boveng 2009). This southward migration is less noticeable and predictable than the northward movements in late spring, early summer (Burns and Frost 1979, Burns 1981, Kelly 1988). During winter, the favorable conditions of shallow waters combined with broken, drifting and fractured pack ice, occur more often in the temperate Bering Sea than the Chukchi Sea (Burns 1981). These conditions may be related to the central and northern parts of the Bering Sea shelf having the highest densities of bearded seals at this time (Fay 1974, Heptner et al. 1976, Burns and Frost 1979, Braham et al. 1981, Burns 1981, Nelson et al. 1984). In late winter and early-spring, bearded seals are widely but not uniformly distributed in the broken, drifting pack ice ranging from the Chukchi Sea south to the ice front in the Bering Sea. In these areas, they tend to avoid the coasts and areas of fast ice (Burns 1967, Burns and Frost 1979). Young-of-the-year bearded seals seem to range widely through the Bering Sea at this time, with some travelling as far as the southern coast of the Kamchatka Peninsula (Cameron 2006, Frost et al. 2008). Despite this range, satellite tagging also indicates that adults, subadults, and to some extent pups, focus on localized feeding areas, often remaining in the same general area for weeks or months at a time (Cameron 2005, Cameron and Boveng 2009).

Despite their importance to Alaska Native subsistence communities, and their apparently unique role in circumpolar arctic marine ecosystems, bearded seals and their habitat requirements are poorly understood. Bearded seals are known to concentrate in specific areas for breeding and molting; identification of these areas is crucial to the assessment of potential impacts from industrial activities. Vocalizations are critical to bearded seal mating systems (Stirling & Thomas 2003, Van Parijs et al. 2003, Van Parijs et al. 2004), which could potentially be disrupted by industrial noise. As inhabitants of the broken pack ice and open water zones, bearded seals are vulnerable to impacts of spilled oil, both from direct contact with oil and from indirect effects through the benthic organisms on which they feed. Although they may be capable of feeding on sympagic (under-ice) and mid-water prey, bearded seals are primarily benthic feeders and are therefore strongly associated with the shallow continental shelf zones that would likely be subject to petroleum exploration and extraction. Any potential industrial impacts on bearded seals could potentially be mitigated or magnified by climatic-induced change in the physical and biological habitat. Magnification of impacts seems the most likely, especially because reductions in sea ice may de-couple the co-occurrence of suitable ice and suitable benthic prey communities in those areas that have become traditional breeding and molting grounds for bearded seals. Ice-associated seal populations may be negatively impacted by offshore oil and gas development (Smith and Geraci 1975; Geraci and Smith 1976; Englehardt 1978; Kelly 1988) as well as by climate change. Therefore, understanding the timing of haul-out behavior is of critical importance because abundance estimates are needed for developing sound plans for conservation, management, and response to potential environmental impacts of planned oil and gas activities.

A primary reason they are less studied than most other seal species is the difficulty of approaching, capturing, and handling live bearded seals for ecological, behavioral or physiological studies. Little funding has been available to address these challenges, but recent developments in live-capture techniques indicate that a focused, collaborative effort between researchers and Alaska Natives with local knowledge of bearded seals can greatly expand the capabilities for employing techniques such as satellite telemetry (Frost et al. 2005, Gjertz et al. 2000, Krafft et al. 2000). Satellite telemetry is a powerful tool for addressing many aspects of bearded seal ecology and behavior. In this study, we deployed SDRs on sub-adult and adult bearded seals to investigate their marine habitat use, movements, distribution and diving behaviors as a basis for evaluating potential impacts of oil and gas industry activities and accidents, such as oil spills. Additionally, we use these data to examine the haul-out patterns of bearded seals and create correction factors for existing and future aerial abundance surveys. Finally, we have collaborated with other researchers and organizations to obtain outside support for the analysis of tissue samples collected during capture activities to assess nutritional status, health, contaminant load, and population structure.

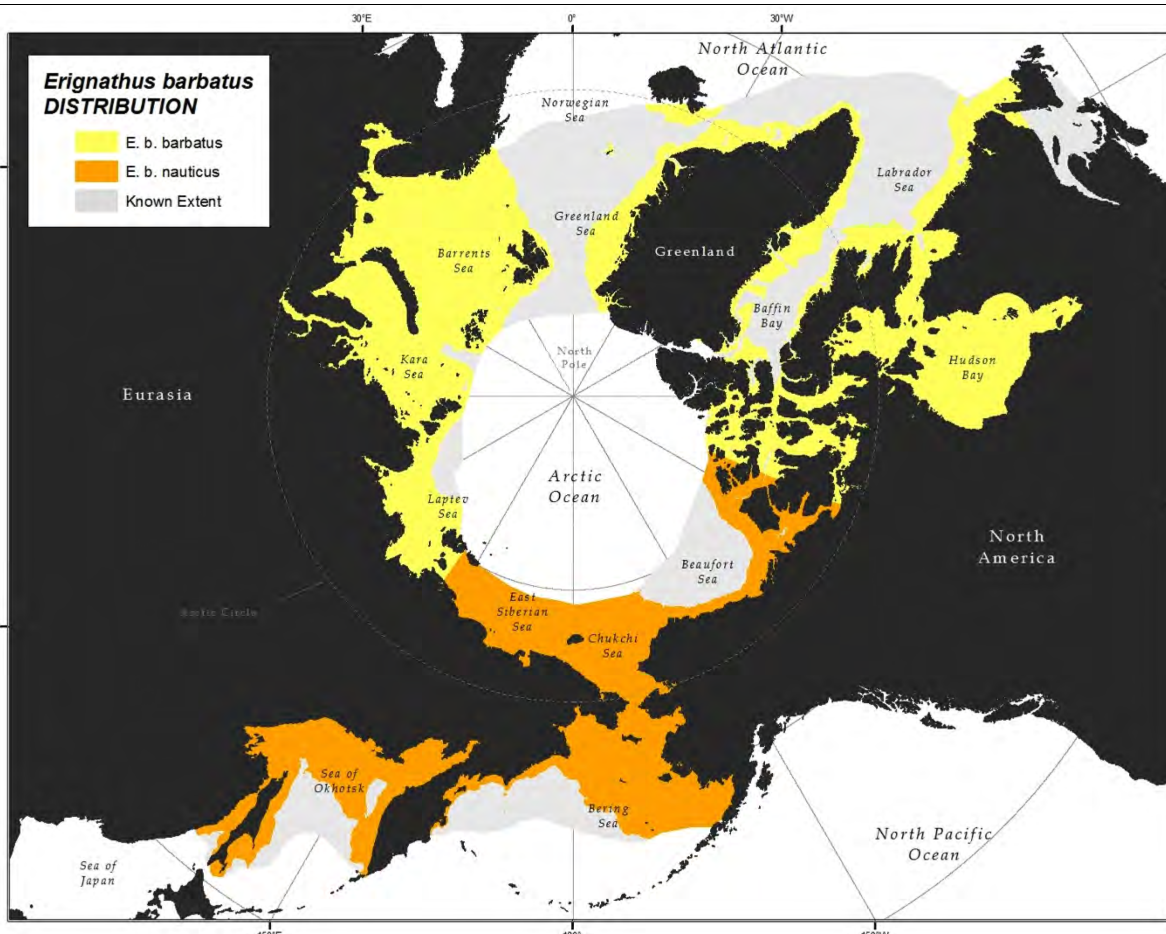

Figure 1. The global distribution of bearded seals as adapted from maps of extent in Burns (1981) and Kovacs (2002). The colored areas of core distribution are those areas of known extent that are in waters <500 m deep. The subspecies range boundaries were approximated from the literature.

GOAL AND OBJECTIVES

Goal:

The goal of this study was to provide scientific information to support analyses of the potential effects of oil and gas development activities on the movements, behavior and seasonal habitat use patterns of bearded seals in the Chukchi Sea Planning Area.

Objectives:

1. Estimate the seasonal movements and patterns of distribution and behavior of bearded seals in the Chukchi Sea Planning Area. Emphasis was placed on movements of seals between near-shore areas where they are hunted for subsistence and offshore areas where industrial development is anticipated, such as potential high biomass areas in the vicinity of the Berger Prospect and Hanna Shoal.
2. Identify specific marine habitats in the Chukchi Sea Planning Area associated with key life history events of bearded seals, such as breeding, pup rearing, foraging, and molting, and rank them according to importance of use.
3. Improve the accuracy and precision of estimates of bearded seal abundance in the Chukchi Sea Planning Area by developing a haul-out correction factor that can be used to adjust existing survey counts for the proportion of seals that are at sea and not observed during aerial surveys.

BACKGROUND

The Interagency Agreement (IA) was conveyed to NOAA in June, 2007, and final clearance to begin work was completed in March, 2008. The original plan outlined in the IA described conducting a single workshop with Alaska Native subsistence hunters, and U.S., Russian, and Norwegian scientists to discuss, develop and refine techniques for live-capture and handling of adult bearded seals, and to identify locations in the Chukchi Sea where such capture operations would likely be successful. Owing to logistical challenges of scheduling a large workshop of scientists and hunters (with diverse schedule constraints), and to the recommendations of the Alaska Native Ice Seal Committee (ISC), the plan was eventually replaced by a series of smaller meetings with individual communities, and opportunistic discussions with scientific colleagues at various workshops and symposiums.

The Principal Investigator of the study was Peter Boveng, and the Co-Investigators were Michael Cameron, and Jay Ver Hoef. The study was organized as two projects based in Kotzebue and the North Slope Borough. For each project, the NMML contracted with a local organization to administer the funds and designate a Co-Investigator and Field Project Leader (a hunter and research participant with good community relations and previous experience in collaborations with agency researchers). For the Kotzebue project, Alex Whiting of the Kotzebue IRA was the Co-Investigator and the Field Project Leader was John Goodwin. For the North Slope Borough project, Jason Herreman of the North Slope Borough was the Co-Investigator, the Barrow Field Project leader was Carl Nayakik, and the Wainwright Field Project Leader was Enoch Oktollik. By partnering with these communities we endeavored to make the best use of local expertise and logistics resources for accomplishing mutual research goals and enhancing capacity for marine mammal research.

Funding for the collaborative projects was provided to the local organizations by a contract from NOAA. The Co-Investigator for each project was the primary liaison with NOAA for local administration of the funds, planning and execution of the field work, and jointly communicating research results to communities in the project region. The Field Project Leader worked with all Co-Investigators to coordinate and lead the efforts to capture bearded seals for tagging, taking into account the timing and condition of ice in the area, safety of all participants, and avoidance of conflict with hunters.

The Co-Investigators and Field Project Leaders participated in the analysis and interpretation of project results and formulation of questions for further research. A goal of this study was to facilitate the mutual exchange of knowledge and expertise between Alaska Native community members and researchers. All aspects of the research were carried out with the intent of demonstrating and sharing both scientific and traditional techniques for working in and observing the arctic environment.

The NMML entered into joint research agreements with the Kotzebue IRA (Native Village of Kotzebue) and the North Slope Borough Wildlife Department (NSB). The Kotzebue IRA and the NSB coordinated with the communities on where and when to conduct bearded seal captures so as not to interfere with subsistence hunting. This mostly entailed working in areas far away from traditional subsistence hunting locations after the majority of hunting had occurred.

The NMML also obtained all necessary MMPA research permits. In 2009, the NMML operated under MMPA permit 782-1765-00. This permit expired in late 2009, and was replaced by MMPA Permit 15126, issued in 2010 and valid until 2015. Finally, NMML research is subject to review and oversight by an animal care and use committee (IACUC) to ensure compliance with the Animal Welfare Act. This project was reviewed in April 2010 and was authorized under IACUC Number A/NW 2010-3 through 2013.

METHODS

Study area

Although the focus of this study was on bearded seals in the Chukchi Sea, the study as a whole encompassed portions of the Bering and Beaufort seas, as well. This broader area is shown in Figure 2 with the BOEM planning and lease sale areas, and with labels for the place names used in this report.

Figure 2. Map of the study area with labels for geographic names used in this report. The Chukchi and Beaufort Sea planning areas (dashed lines) and lease sale areas (grids) are shown.

Field research and capture activities

As part of this IA with BOEM, the NMML consulted in 2008 with other researchers, members of the ISC and other Alaska Native subsistence hunters to develop a method for capturing and tagging adult bearded seals after the annual pelage molt. In late-June and early-July, 2009, NMML researchers, in cooperation with participating subsistence hunters with the Kotzebue IRA conducted the first field work, a 10-day effort in Kotzebue Sound. Individual bearded seals hauled out on pack ice were slowly approached in small boats, typically causing the seals to enter the water. One or two tangle nets were deployed in water nearby. These large-mesh (12-22” stretched) twisted-filament nets were made of 1 to 3 net panels, each 90 ft. long x 24 ft. deep. The float line was made of a 3/4” dia. foam core wrapped in nylon and the lead line was 1/4” diameter, light enough to allow a captured seal to reach the surface to breathe. The nets likely were visible to the seals, but some individuals, apparently out of curiosity, approached the nets and became entangled.

Entangled seals were restrained alongside one of the small boats and moved to a nearby ice floe for handling, sampling and tagging. Captured seals were sedated using benzodiazepine intravenously or intramuscularly (diazepam 0.2mg/kg IV, or Midazolam 0.15 mg/kg IV or IM). IV dosing provided 20-30 minutes of adequate sedation. IM administration of midazolam was the preferred method, providing about 70 minutes of sedation. Heart rates (60-90 beats per min) and respiration rates (10 breaths per min) were normal throughout the procedure in all seals. Sedation was reversed with flumazenil at 0.01 mg/kg IV or IM.

The sedated seals were removed from the net, measured and weighed. Samples of their blood and skin were collected to establish baseline blood parameters and for DNA studies. Each seal was then instrumented with two SDRs: a SPOT tag (Figure 3), attached to the inter-digital webbing of a rear flipper, and one of two variants of a Mk10 tag (Figure 4; i.e., Mk10-A or Mk10-AF), glued to the hair on the seals’ head (all SDRs are manufactured by Wildlife Computers, Redmond, WA, USA). The SPOT tag recorded information on haul-out timing and, when transmitting the data to an overhead satellite, also provided the seals location. To conserve power, the tags were programmed to only transmit every 6 days from February through July and on the 1st and 15th of each month from August through January. This duty cycle was expected to enable the SPOT tags to transmit for up to 3 years, but also limited the frequency of location data. The Mk10 tags provided the same information as the SPOT tag and also recorded data on the timing and depth of the animal’s dives. Seals captured in 2009 were tagged with a

Mk10-AF. These SDRs utilized an experimental GPS antenna designed to provide additional locations of high accuracy at periodic intervals. Unfortunately, the additional data generated by the GPS utilized bandwidth that otherwise would have been available for transmitting dive and haul-out data. As such, the datasets reported by the Mk10-AF SDRs had significant periods of time with no data. Bearded seals captured in subsequent years were tagged with MK10-A tags and so had many fewer data gaps. Mk10 transmissions were not restricted by a specific duty cycle and so were expected to provide multiple locations each day until the tag fell off during the annual molt the following spring. Once the glue on the Mk10 tag had cured, sedation was reversed and the seal was released into the water near where it was captured.

Figure 3. Close up of a SPOT tag attached to the rear flipper of a captured bearded seal

Figure 4. An adult male bearded seal instrumented with a Mk10-AF tag.

In 2010, the field effort was repeated and also expanded to incorporate the North Slope Borough (NSB). Consultations with subsistence hunters in Wainwright and Barrow, and with NSB wildlife scientists, suggested that Wainwright (rather than Barrow) would be the best place to start the capture work given the relatively lower hunting pressure in that village. Sparse sea ice conditions near Wainwright in June 2010, however, precluded us from working there, and the decision was made to move the project to Peard Bay, located about halfway between Wainwright and Barrow along the coast. Unfortunately, the sea ice conditions at Peard Bay were so dense that the field team spent much of their time unable even to launch their boats. Eventually, the project was moved north again to Barrow, but no seals were captured. Barrow residents indicated that some adult bearded seals use sandbars near Barrow for hauling out in the fall, so a second field effort was mounted in October 2010. Weather, sea ice conditions, short daylight hours, and low numbers of seal sightings led us to rule out the fall as a productive time for tagging adult bearded seals.

The sea ice conditions near Wainwright and Peard Bay in 2011 were again so poor and unpredictable that the decision was made to abandon these locations and focus on Barrow for live-capturing adult bearded seals. With the respective cooperation of the North Slope Borough Wildlife Department and the Kotzebue IRA, springtime field efforts were again mounted in Barrow and Kotzebue in 2011. In 2012, spring sea ice conditions allowed the NSB field team, for the first time, to operate out of Wainwright while a second effort was staged out of Kotzebue.

Objective 1: Describe seasonal movements and dive behavior

Locations of the tagged seals were determined by the Argos satellite network (CLS America, Inc., Largo, MD), which also relayed dive and behavior data that were recorded by the tags. These data were processed through Wildlife Computers' DAP software and all data were uploaded to an enterprise Oracle database for additional processing and long-term archival.

Seasonal movements

Monthly locations were plotted in ArcGIS over a base layer containing the Alaskan and Russian coastlines and bathymetry of the Bering, Chukchi and Beaufort Seas. Each monthly plot also included a shapefile from NOAA's National Ice Center (NIC) depicting the extent and concentration of sea ice in the region during the month of interest. In the spring of 2011, the Argos algorithm for estimating tag locations was updated to a more robust and accurate system. All location data received prior to the upgrade were retroactively re-processed for full compatibility.

Dive behavior

The Mk10 SDRs were programmed to sample the pressure transducer every 10 seconds for a change in depth and to summarize the diving behavior into histograms for 'maximum dive depth', 'total dive duration', and 'time at given depth bins' (Table 1). Each day began at 03:00 GMT and was divided into four 6-hour periods over which the dive summaries were calculated and reported. We then summarized the dive data by averaging it across histogram type, individual, 6-hour period and season (summer =June-September; fall=October-December; and winter=January-April). Data were pooled across years.

Table 1. Histogram bin ranges for the three types of dive data summarized and reported by the Mk10 SDRs.

Histogram type	Bin 1	Bin 2	Bin 3	Bin 4	Bin 5	Bin 6	Bin 7	Bin 8	Bin 9	Bin 10	Bin 11	Bin 12	Bin 13	Bin 14
Max depth (m)	10	30	50	70	90	100	150	200	250	300	400	500	600	>600
Dive Duration (min)	1	2	3	4	6	8	10	12	16	20	30	40	50	>50
Time at depth (m)	4	10	30	50	70	90	100	150	200	250	300	400	500	>500

The pressure transducers on the three MK10-AF tags deployed in 2009 are known to have issues with corrupt depth values. After consulting with Wildlife Computers, we implemented a filtering algorithm to determine whether the dive data were corrupt based on information provided within the status messages. The status messages provide information on the current parameter values for 'zerodepthoffset' as well as the 'depth' reading at the time of status message transmission. Wildlife Computers advised us to average these two values and remove any values that are not close to zero. Status messages are sent at a lower frequency than the dive data messages and there are some deployment days with transmitted dive data but no status messages. For these analyses, we have chosen to remove any dive records for any day that reports a status message with an average filter value greater than 5. For any day without a transmitted status message, the filter value determined for the previous day is used.

Objective 2: Identify specific marine habitats in the Chukchi Sea Planning Area

Multi-state movement and behavior modeling

As an initial step toward describing and quantifying habitat use by bearded seals, we fit the movement and diving data from the seals tagged in 2009 and 2011 to a multi-state random walk model. The model allows for transitions between states of movement behavior (e.g., foraging, traveling, resting) as animals are affected by their internal and external environmental conditions. We utilized both location and dive summary data to characterize movement behavior as resting (*R*), foraging (*F*), or transit (*T*). Because our dive summary data were for 6hr intervals, but locations were obtained opportunistically at irregular time intervals, we estimated positions at the endpoints of each of these 6hr intervals and fit a discrete-time, multi-state movement model to both the predicted tracks and dive summary data. This state-space formulation consisted of two components: an observation process model for the temporally-irregular locations and a discrete-time, multi-state movement process model based on the (temporally-regular) predicted locations and dive summary data (McClintock et al. *In Press*).

For our discrete-time, multi-state movement process model, movement behavior state $z_{n,t} \in \{R, F, T\}$ was estimated based on step length ($s_{n,t}$), bearing $\left(\phi_{n,t}\right)$, and dive activity data $\left(\omega_{n,t}\right)$ for each 6hr time step t = 1, ..., T_n and individual n = 1, ..., 7. Dive activity data pertain to the proportion of each 6hr interval spent diving > 4m below the surface during time period t.

We assume step length $\left[s_{n,t} \mid z_{n,t} = i\right] \sim \text{Weibull}(a_{n,i}, b_{n,i})$:

$$f\left(s_{n,t} \mid z_{n,t} = i\right) = \frac{b_{n,i}}{a_{n,i}} \left(\frac{s_{n,t}}{a_{n,i}}\right)^{b_{n,i}-1} \exp\left[-\left(s_{n,t} / a_{n,i}\right)^{b_{n,i}}\right]$$

for state-specific scale parameter $a_{n,i} > 0$ and shape parameter $b_{n,i} > 0$. We assume bearing $\left[\phi_{n,t} \mid z_{n,t} = i\right] \sim \text{wCauchy}\left(\phi_{n,t-1}, \rho_{n,i}\right)$:

$$f\left(\phi_{n,t} \mid z_{n,t} = i\right) = \frac{1}{2\pi} \frac{1-\rho_{n,i}^2}{1+\rho_{n,i}^2 - 2\rho_{n,i}\cos\left(\phi_{n,t} - \phi_{n,t-1}\right)}$$

with bearing $0 \le \phi_{n,t} < 2\pi$ and state-specific mean vector length $0 \le \rho_{n,i} < 1$. We might expect average step length to be smaller for resting and largest for transit, and directional persistence to be largest for transit (i.e., $\rho_{n,R}, \rho_{n,F} \le \rho_{n,T}$). Reflecting these expectations at a maximum sustainable speed of 2m/s, we constrained the means for the state-dependent Weibull distributions for step length:

$$0 < a_{n,R}\Gamma\left(1 + \frac{1}{b_{n,R}}\right) < 3000$$

$$0 < a_{n,F}\Gamma\left(1 + \frac{1}{b_{n,F}}\right) < a_{n,T}\Gamma\left(1 + \frac{1}{b_{n,T}}\right)$$

$$a_{n,F}\Gamma\left(1+\frac{1}{b_{n,F}}\right) < a_{n,T}\Gamma\left(1+\frac{1}{b_{n,T}}\right) < 43200.$$

We also constrained directional persistence such that

$$\rho_{n,R} \sim \text{Unif}\left(0,1\right)$$

$$\rho_{n,F} \sim \text{Unif}\left(0,\rho_{n,T}\right)$$

$$\rho_{n,T} \sim \text{Unif}\left(0.75,1\right).$$

We incorporate memory into the state transition probabilities ($\boldsymbol{\psi}_n$) as a first-order Markov process. Hence, for switches between behavior states, we assign a first-order Markov categorical distribution, $\left[z_{n,t} \mid \boldsymbol{\psi}_n, z_{n,t-1}=k\right] \sim \text{Categorical}(\psi_{n,k,R},\psi_{n,k,F},\psi_{n,k,T})$, for $k=\{R,F,T\}$ where $\psi_{n,k,i}$ is the probability of switching from state *k* at time *t* – 1 to state *i* at time *t*, and $\sum_j \psi_{n,k,j}=1.$

Although movement behavior state could be assigned solely based on these movement characteristics (Morales et al. 2004, McClintock et al. 2012), we wished to incorporate the additional information about behavior states provided by the dive summary data. Assuming independence between step length and bearing, we incorporated $\omega_{n,t}$ into a joint conditional likelihood:

$$f\left(\boldsymbol{s}_n,\boldsymbol{\phi}_n,\boldsymbol{\omega}_n,\boldsymbol{z}_n \mid \boldsymbol{\theta}\right)=\prod_{t=1}^{T} f\left(s_{n,t} \mid \boldsymbol{\theta}, z_{n,t}\right) f\left(\phi_{n,t} \mid \boldsymbol{\theta}, z_{n,t}\right) f\left(\omega_{n,t} \mid \boldsymbol{\theta}, z_{n,t}\right) f\left(z_{n,t} \mid \boldsymbol{\theta}, z_{n,t-1}\right),$$

where $\boldsymbol{\theta}$ denotes the set of all model parameters. We assume *a priori* that any missing dive activity data are equally likely to have arisen from the resting, foraging, or transit states. As described earlier, some dive data were missing from the records of seals tagged with a Mk10-AF SDR in 2009. The duty cycle of the GPS component in these SDRs was not related to seal behavior, so we believe this assumption is valid. We further assume *a priori* that diving activity is equally likely to have arisen from the foraging or transit states:

$$f\left(\omega_{n,t} \mid \boldsymbol{\upsilon}_n, \boldsymbol{\delta}_n, z_{n,t}=i\right) \sim \text{Beta}\left(\upsilon_{n,i},\delta_{n,i}\right)$$

for $i = R, F, T$, where $\upsilon_{n,F} = \upsilon_{n,T}$ and $\delta_{n,F} = \delta_{n,T}$. Time spent < 4m below the surface is assumed to be indicative of the resting state, and time spent > 4m below the surface is assumed to be indicative of the foraging and transit states (Figure 5). We therefore assigned the priors

$$\upsilon_{n,R} \sim \text{Unif}\left(0, \delta_{n,R}\right)$$

$$\upsilon_{n,F} \sim \text{Unif}\left(\delta_{n,F}, 10\right)$$

$$\delta_{n,R} \sim \text{Unif}\left(\upsilon_{n,R}, 10\right)$$

$$\delta_{n,F} \sim \text{Unif}\left(0, \upsilon_{n,F}\right)$$

where $\upsilon_{n,T} = \upsilon_{n,F}$ and $\delta_{n,T} = \delta_{n,F}$.

For the observation process model, the location data consisted of the observed locations $\left(x_{n,t,i}, y_{n,t,i}\right)$ for individual $n = 1, \ldots, 7,$ time step $t = 1, \ldots, T_n,$ and observation $i = 1, \ldots, k_{n,t}$ (where time steps with $k_{n,t} = 0$ have no observed locations). Similar to Jonsen et al. (2005) and McClintock et al. (2012), we assumed that individuals travel in a straight line between times $t-1$ and t. The observed locations $\left(x_{n,t,i}, y_{n,t,i}\right)$ were then related to the temporally-regular and true locations $\left(X_{n,t}, Y_{n,t}\right)$ via:

$$\begin{pmatrix} x_{n,t,i} \\ y_{n,t,i} \end{pmatrix} \sim N\left(\boldsymbol{\mu}_{n,t,i}, \Sigma_{n,t,i}\right),$$

where

$$\boldsymbol{\mu}_{n,t,i} = \begin{pmatrix} \left(1 - j_{n,t,i}\right) X_{n,t-1} + j_{n,t,i} X_{n,t} \\ \left(1 - j_{n,t,i}\right) Y_{n,t-1} + j_{n,t,i} Y_{n,t} \end{pmatrix}$$

$$\Sigma_{n,t,i} = \begin{pmatrix} \sigma^2_{x,n,i} + \gamma^2_{x,n} & \dfrac{\sigma^2_{xy,n,i}}{\left(\sigma^2_{x,n,i} + \gamma^2_{x,n}\right)\left(\sigma^2_{y,n,i} + \gamma^2_{y,n}\right)} \\ \dfrac{\sigma^2_{xy,n,i}}{\left(\sigma^2_{x,n,i} + \gamma^2_{x,n}\right)\left(\sigma^2_{y,n,i} + \gamma^2_{y,n}\right)} & \sigma^2_{y,n,i} + \gamma^2_{y,n} \end{pmatrix},$$

$\gamma^2_{x,n} \sim \Gamma^{-1}(0.01, 0.01)$, $\gamma^2_{y,n} \sim \Gamma^{-1}(0.01, 0.01)$, and $j_{n,t,i} \in (0,1]$ is the proportion of the time interval between predicted locations $(X_{n,t-1}, Y_{n,t-1})$ and $(X_{n,t}, Y_{n,t})$ at which the *i*th observation between times $t-1$ and *t* was obtained. The observed location error terms $(\sigma^2_{x,n,i}, \sigma^2_{y,n,i}, \text{ and } \sigma^2_{xy,n,i})$ were derived from the Argos location error ellipse (Drs. R. Lopez and J. P. Malardé, Collecte Localisation Satellites (CLS), January 15, 2013, pers. comm.). Time intervals with no observations (i.e., $k_{n,t} = 0$) do not contribute to the observation model likelihood. The state-space model conditional likelihood for the observation and movement processes is therefore

$$f\left(\boldsymbol{x}_n, \boldsymbol{y}_n, \boldsymbol{\sigma}^2_{x,n}, \boldsymbol{\sigma}^2_{y,n}, \boldsymbol{\sigma}^2_{xy,n}, \boldsymbol{s}_n, \boldsymbol{\phi}_n, \boldsymbol{\omega}_n, \boldsymbol{z}_n \mid \boldsymbol{\theta}\right) = \prod_{t=1}^{T_n} f\left(s_{n,t} \mid \boldsymbol{\theta}, z_{n,t}\right) f\left(\phi_{n,t} \mid \boldsymbol{\theta}, z_{n,t}\right) f\left(\omega_{n,t} \mid \boldsymbol{\theta}, z_{n,t}\right) f\left(z_{n,t} \mid \boldsymbol{\theta}, z_{n,t-1}\right)$$
$$\times \prod_{i=1}^{k_{n,t}} f\left(x_{n,t,i}, y_{n,t,i}, \sigma^2_{x,n,i}, \sigma^2_{y,n,i}, \sigma^2_{xy,n,i} \mid \boldsymbol{\theta}\right),$$

where $\boldsymbol{\theta}$ again denotes the set of all model parameters (including $\boldsymbol{X}_n$ and $\boldsymbol{Y}_n$).

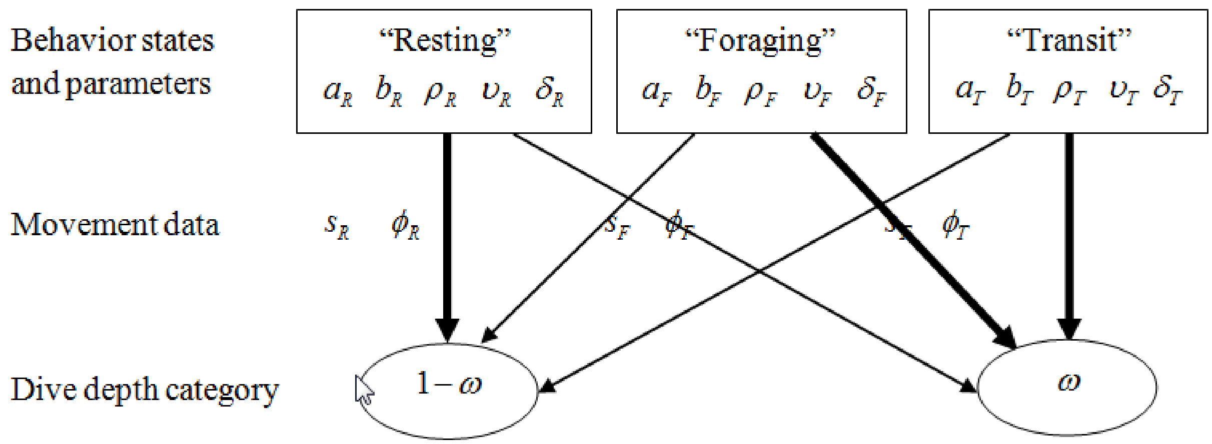

Figure 5. Characterization of three latent behavior states, "resting" (*R*), "foraging" (*F*), and "transit" (*T*), for bearded seals based on movement direction (ϕ), step length (s), and dive activity data.

The dive activity data consist of the proportion of each 6hr time step spent 4m below the surface, where dives below 4m are more strongly associated with foraging and transit. For each behavior state, arrow widths are proportional to the expected time spent in each dive depth category (= diving, = not diving). The Beta model parameters reflect these expected relationships between dive depth category and behavior state. Figure reproduced from McClintock et al. (In Press).

We fit the full state-space model to each individual by adopting a Bayesian perspective and using a Markov chain Monte Carlo (MCMC) algorithm written in the C programming language. Any missing dive activity data were imputed within the MCMC algorithm. After initial pilot tuning and burn-in, a single chain of 200,000 iterations was independently attained for posterior summaries of each individual.

Winter site fidelity

The home ranges during the months of January – April, which we termed winter, were approximated by simple convex polygons around the locations received from both the head-mounted and flipper-mounted transmitters. The low duty cycle and infrequent locations obtained from flipper-mounted tags rendered those locations unfit for interpolation by a movement model such as the one used above. The main object of our examination of winter sites was to evaluate whether bearded seals return to the same sites in successive winters, which we evaluated simply by qualitative, graphical analysis of the convex polygons.

Objective 3: Develop a haul-out correction factor for aerial surveys

Data on haul-out timing from both the head-mounted Mk10 tags and the flipper-borne SPOT tags were used to develop a haul-out correction factor for aerial surveys. As expected, the MK10 tags fell off with the annual molt in the spring following tagging, and so only Mk10 data collected prior to April were used in the analyses. Similarly, while data from the SPOT tags were available for a much longer period after tagging, the SPOT data exhibits signs of drift--perhaps as a result of bio-fouling--of their conductivity sensors. For the analyses presented therefore, we also restricted the SPOT tag dataset to dates prior to April.

We estimated haul-out probabilities for adult bearded seals as a function of day of year and hour using a generalized linear model with a logit link and Bernoulli distribution. For each hour, satellite tags provided an estimate of the proportion of time a tag is dry. To prepare these data for analysis, we transformed these records into binary (zero/one) responses. Let $H_{i,j,k}$ denote the hourly response for animal *i* on the *k*th day-of-year and *j*th hour-of-day. If a tag was <50% dry for a given hour it was given a $H_{i,j,k} = 0$ response, otherwise it received a $H_{i,j,k} = 1$ response. We then modeled

$H_{i,j,k} \sim \mathrm{Bernoulli}(v_{i,j,k})$, where

$v_{i,j,k} = (1 + \exp(-\eta_{i,j,k}))^{-1}$.

The expected value of the linear predictor ($\eta_{i,j,k}$) was modeled using a categorical effect for hour (24 levels), a cubic model for continuous day-of year-effects, as well as all interactions between hour and day-of year effects. We also included a random effect for individual seals. We fit this model using a generalized linear mixed modeling framework that allowed for temporal autocorrelation, as described in Ver Hoef et al. (2010), and implemented in the package “glmmLDTS” in the R statistical programming environment (R Core Development Team 2012).

Coefficients of variation were derived using mixed model theory on variances of fitted and random effects (Littell et al. 1996). In particular, let **Δ** be a diagonal matrix with diagonal elements ∂ν/∂η and let **A** be a diagonal matrix with the variance, in terms of the fit, on the diagonal; i.e., $A_{i,i} = \exp(\eta_i)/(1 + \exp(\eta_i))^2$, where $\mathbf{A}^{1/2}$ has diagonal elements that are the square root of the diagonal of **A**. Let **R** be an temporal autocorrelation matrix with an autocorrelation function with elements $r(t_{i,k},t_{i',k'}) = \exp(-|t_{i,k} - t_{i',k'}|/\rho)$ if i = i’ and zero otherwise. Now, let $\hat{\mathbf{G}} = \hat{\psi}^2\mathbf{I}$ be the covariance matrix of the random effects, and let **Z** be the design matrix for the random effects. Then, on the logit scale, the covariance matrix for the observations is modeled by

$$\mathbf{V} = \mathbf{\Delta}^{-1}\mathbf{A}^{1/2}\mathbf{R}\mathbf{A}^{1/2}\mathbf{\Delta}^{-1} + \mathbf{Z}\mathbf{G}\mathbf{Z}'.$$

Then the covariance matrix of the estimated fixed effects $\boldsymbol{\alpha}$ on the logit scale is

$$\mathbf{C}_{\alpha} = \mathbf{X}\mathbf{V}^{-1}\mathbf{X}',$$

where **X** is the design matrix for the fixed effects.

For developing a haul-out prediction map, we used various covariate predictions applied to $\boldsymbol{\alpha}$. Let the covariate values for each prediction be contained as columns in the matrix **L**; i.e., each row in **L** is a prediction. Then a set of fits is the vector $\boldsymbol{£} = \mathbf{L}\boldsymbol{\alpha}$ and the covariance matrix of all predictions, on the logit scale, is Var($\boldsymbol{£}$)= $\mathbf{L}\mathbf{C}_{\alpha}\mathbf{L}'$. To get predictions on the probability (real) scale as opposed to the logit scale, we took exp($\boldsymbol{£}$)/(1 + exp($\boldsymbol{£}$)) and used the delta method (Dorfman 1938, Ver Hoef 2012) to get the covariance matrix on the probability scale as well.

RESULTS

Field research and capture activities

Capture efforts were undertaken in Kotzebue Sound in 2009 (17 June - 1 July), 2010 (25 June – 2 July), 2011 (7 June – 24 June) and 2012 (17 June – 8 July). Field efforts were also conducted near Barrow/Peard Bay in 2010 (27 June – 24 June) and 2011 (30 June – 15 July) as well as Wainwright in 2012 (21 June – 6 July).

One adult and two sub-adult male bearded seals, ranging in weight from 184 to 253 kg (406 - 558 lb), were captured and released with SDRs during the first field effort, in 2009 (Table 2). Unfortunately, no bearded seals were captured at either Kotzebue or the NSB region in the spring of 2010. Based on reports from Barrow residents, of bearded seals using sand bars east of Barrow for hauling out in the autumn, a small field team returned to Barrow in October, 2010, with the objective of evaluating this as an alternative or supplemental capture and tagging scenario. No seals were captured during this late season field effort. In 2011, two females and one male were captured, instrumented with SDRs, and released in Kotzebue Sound (Table 2). Based on their size and dentition, we estimated that one of the females was a yearling (young sub-adult) and the other female and the male were 2-3 years old (sub-adults; see Table 2) at the time of tagging. The field team operating out of Kotzebue in 2012 captured and released a female bearded seal that we estimated to be a 4-year old (i.e., young adult) based on length (Quakenbush et al. 2011) and weight (Table 2). Unfortunately, no seals were captured in the Barrow or Wainwright regions in 2011 or 2012.

Table 2. Morphometric and SDR deployment information for bearded seals captured between 2009 and 2012 in Kotzebue Sound, Alaska

Year	Specimen Number	Capture Location	Capture Time (GMT)	Deployment Days*	Sex	Age	Standard Length (cm)	Weight (kg)
2009	EB2009_3000	66.388 °N 162.42	6/23/2009 00:30	1091	M	SUBADULT	182	184
2009	EB2009_3001	66.562 °N 162.69	6/25/2009 01:38	1034	M	ADULT	216	253
2009	EB2009_3002	66.611 °N 162.89	6/26/2009 04:15	1057	M	SUBADULT	195	197
2011	EB2011_3000	66.687 °N 163.08	6/16/2011 00:50	425	F	SUBADULT	186	161
2011	EB2011_3001	66.643 °N 162.98	6/17/2011 01:15	355	F	SUBADULT	159	115
2011	EB2011_3002	66.644 °N 162.97	6/18/2011 01:15	546	M	SUBADULT	176	158
2012	EB2012_3003	66.554 °N 163.03	7/04/2012 02:30	195	F	ADULT	198	213

* as of January 15, 2013

Objective 1: Describe seasonal movements and dive behavior

Movements of seals tagged in 2009

Upon release, the three male bearded seals tagged in 2009 moved out of Kotzebue Sound and followed the Alaska coastline north (Figure 6). From June through October, all three seals stayed primarily within 50 nmi of shore, remained in these relatively ice-free waters, and as is typical for this species in Alaska, did not haul out on land. One sub-adult occupied the region between Point Hope and Point Lay, the other between Point Lay and Wainwright. The adult moved farther west to an area near Prudhoe Bay making occasional brief trips north to deeper, ice-covered waters.

Throughout much of the winter and early-spring, all three seals occupied fairly distinct and localized areas Figure 6.8 - Figure 6.11. One sub-adult foraged to the south and east of St. Matthew Island while the other sub-adult and the adult selected Norton Sound. As expected, the glue-on, head-mounted Mk10 tags fell off as the seals began to molt in March, 2010.

The flipper-mounted SPOT tags provided very few locations between June and November, 2010 (likely in part due to duty-cycling the SPOT tags to conserve battery strength), though the adult did transmit occasionally from Kotzebue Sound in June. Interestingly, in January – April of 2011, all three seals were again occupying the very same locations in the Bering Sea they had occupied the previous year, and by the end of June 2011 all had returned north through the Bering Strait into Kotzebue Sound. No locations were received from the seals during July – December, 2011. In January – April of 2012, however, all three seals were again located in the same small regions they had occupied during the previous two winters, clearly documenting a strong tendency for winter site fidelity, at least among male bearded seals of the Bering Sea.

Movements of seals tagged in 2011

The initial movement pattern of the male sub-adult tagged in 2011 was very similar to the patterns displayed by the two sub-adult males tagged in 2009; moving north, close to the coast and then focusing on a region between Point Hope and Barrow (Figure 6.16 - Figure 6.19). In contrast, the two females traveled much farther from the coast, preferring to occupy the central Chukchi Sea north of 70°N, with less restricted foraging areas. In the fall, all seals began moving south with the advancing ice and by December all had passed into the Bering Sea, where they spent the winter and early-Spring of 2012 (Figure 6.20 - Figure 6.25). The wintering areas of these seals were all different from those used by the seals tagged in 2009, but the areas were similarly restricted to small regions. By summer, 2012, all had returned north through the Bering Strait into the Chukchi Sea.

Movements of seal tagged in 2012

Shortly after being released, the adult female left Kotzebue Sound and headed north close to the coastline (Figure 6.29) . She continued north and east along the coast to an area near Kaktovik, AK (Figure 6.31). This is in stark contrast to the two sub-adult females tagged in 2011 which, upon reaching Point Hope, left the coast for the central Chukchi Sea. It is also farther east than the area used by the adult male tagged in 2009, near Prudhoe Bay. As the ice continued to form throughout the fall she moved south into the Bering Sea in November and by January was restricting her movements to an area near Port Clarence (Figure 6.32 - Figure 6.35). As of January 15, 2013, her SDRs continued to operate properly.

Figure 6. Monthly maps of the sea ice distribution and seasonal movements of bearded seals captured and tagged in Kotzebue Sound

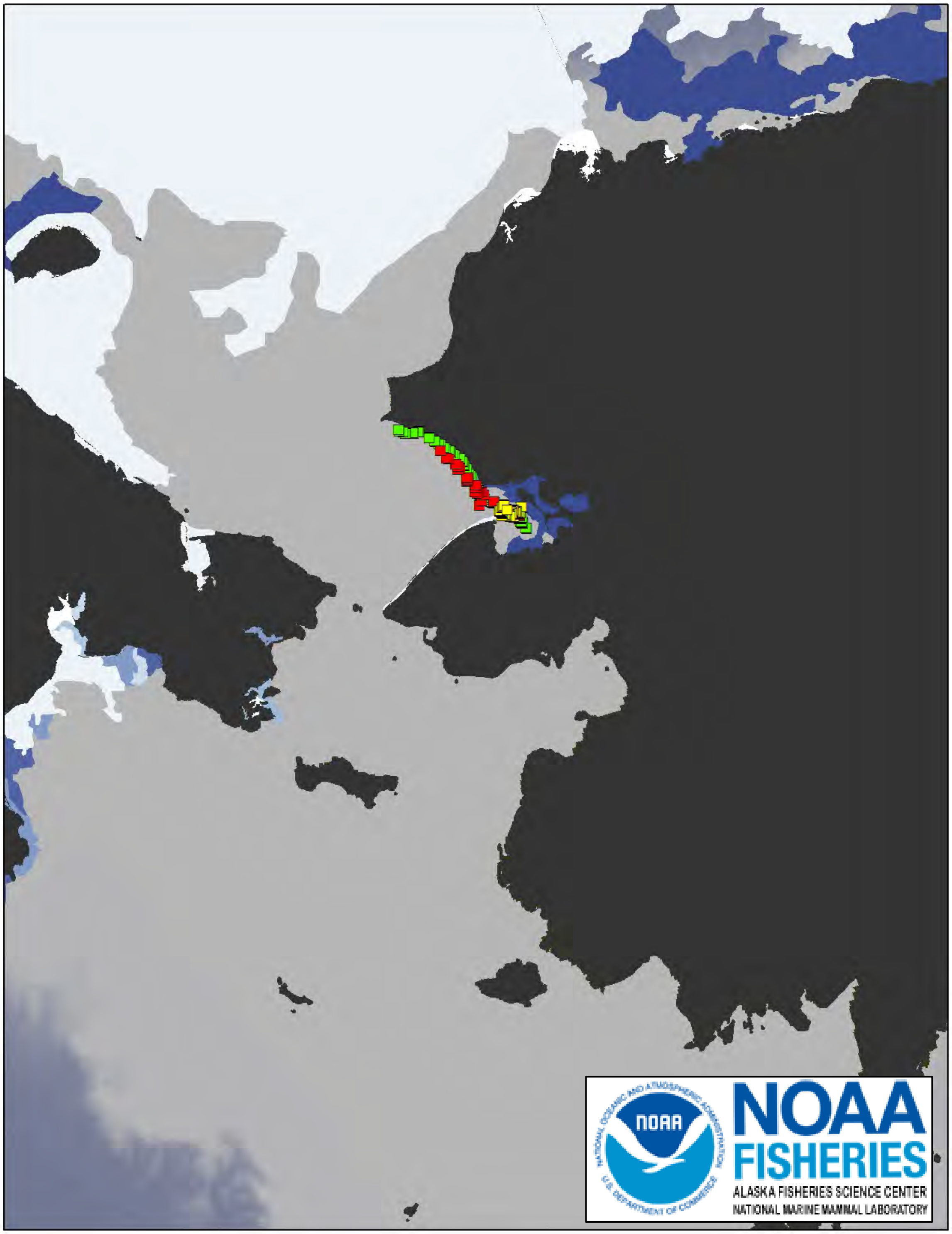

Figure 6.1. Map of the sea ice distribution and seasonal movements in late-June 2009 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

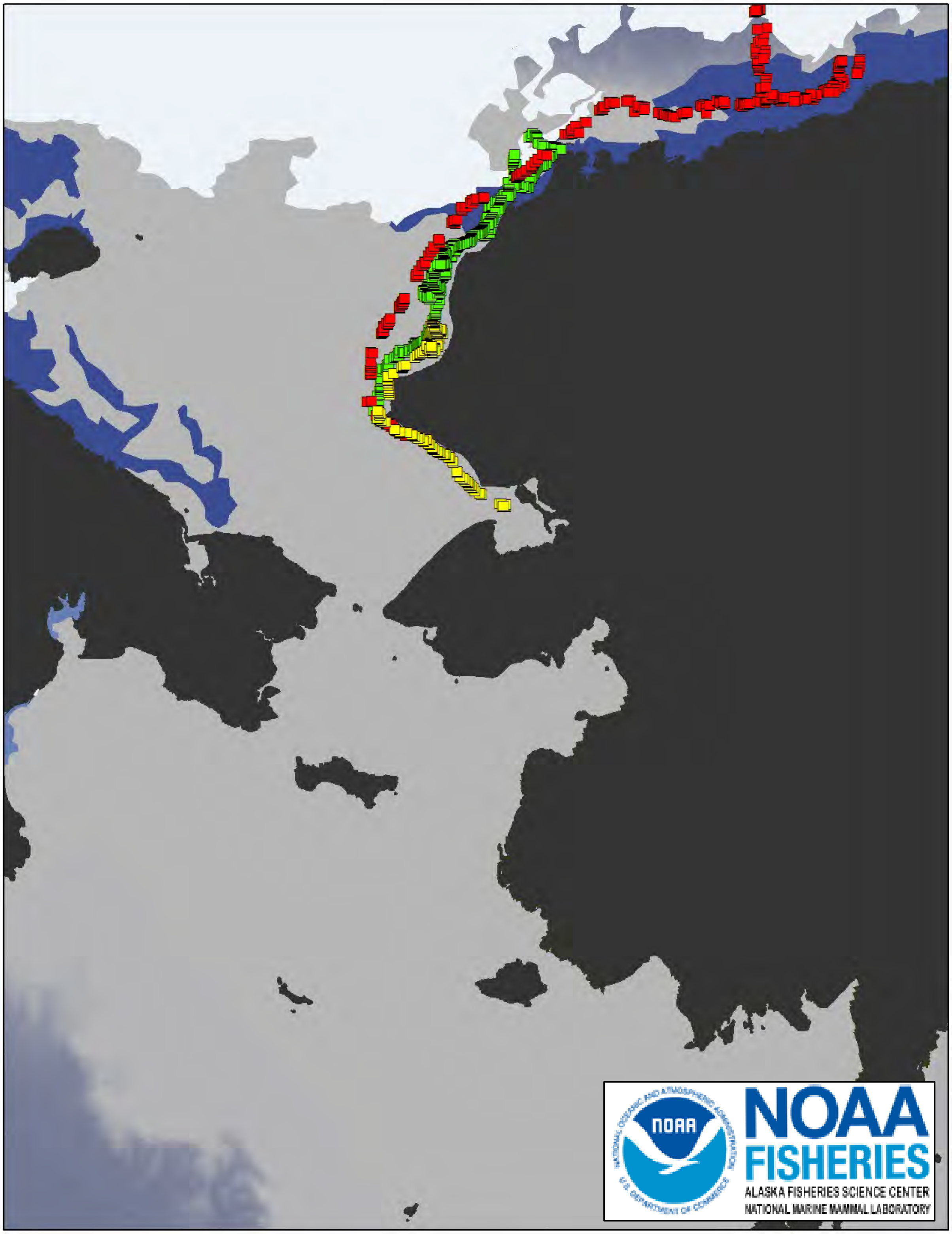

Figure 6.2. Map of the sea ice distribution and seasonal movements in July 2009 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

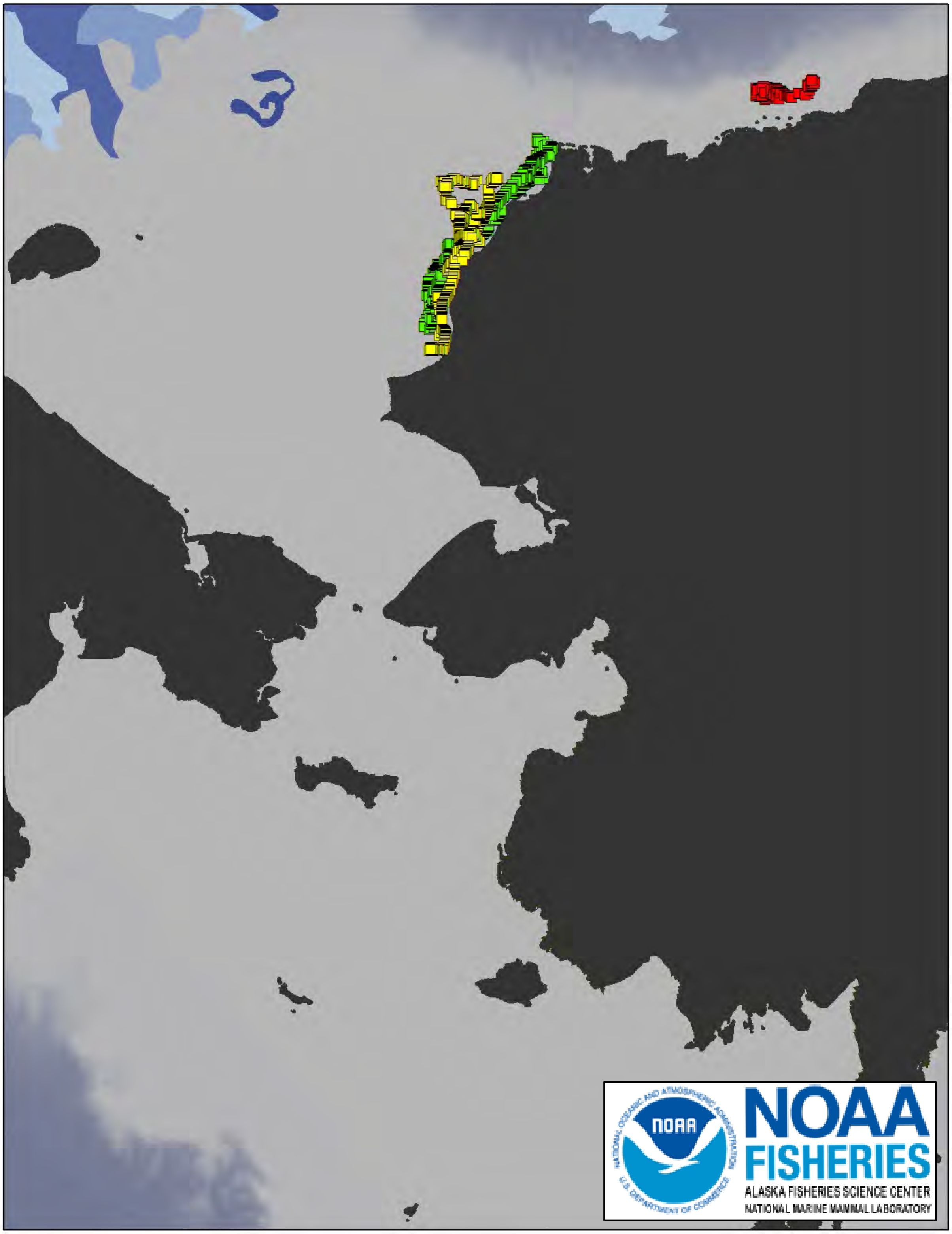

Figure 6.3. Map of the sea ice distribution and seasonal movements in August 2009 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

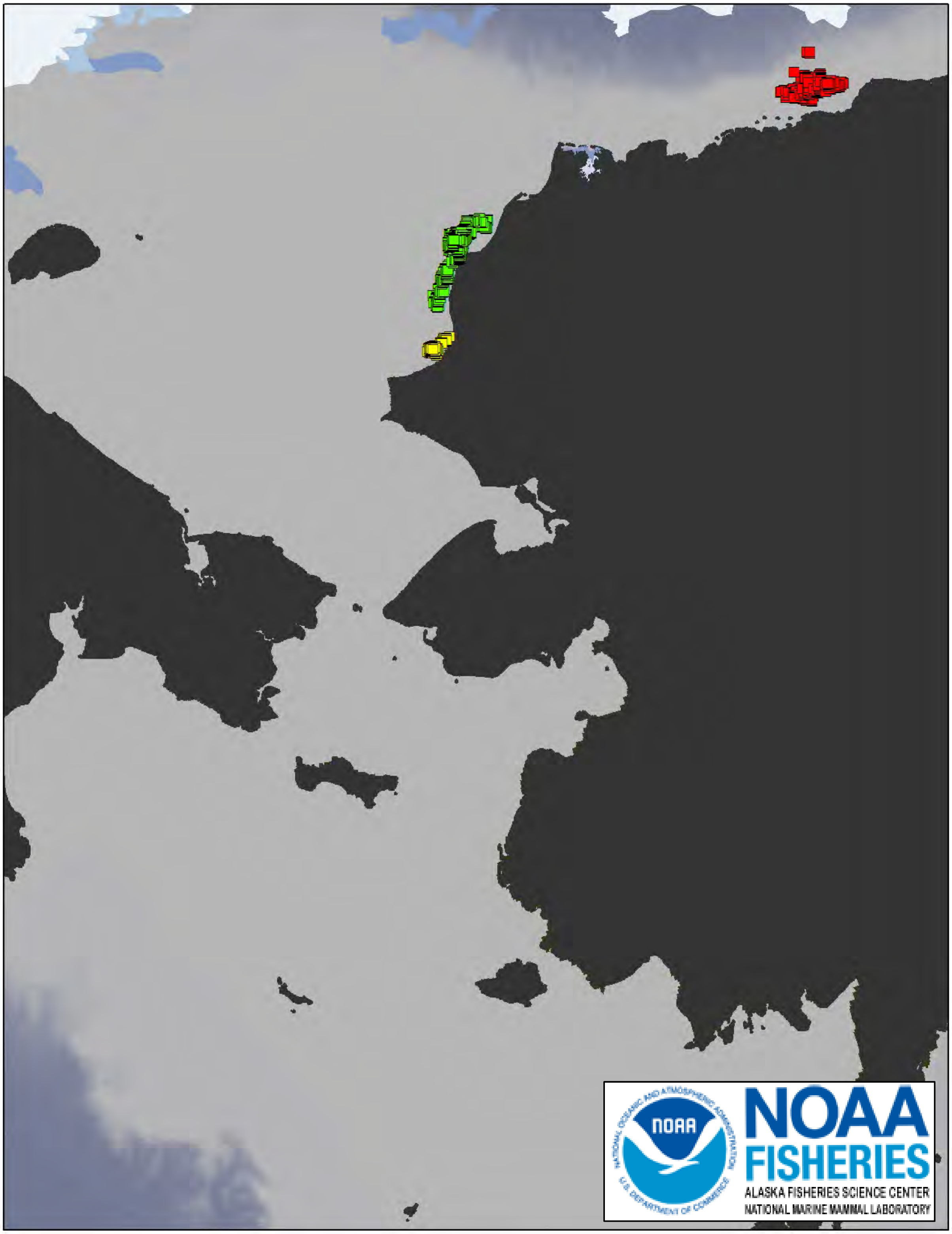

Figure 6.4. Map of the sea ice distribution and seasonal movements in September 2009 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

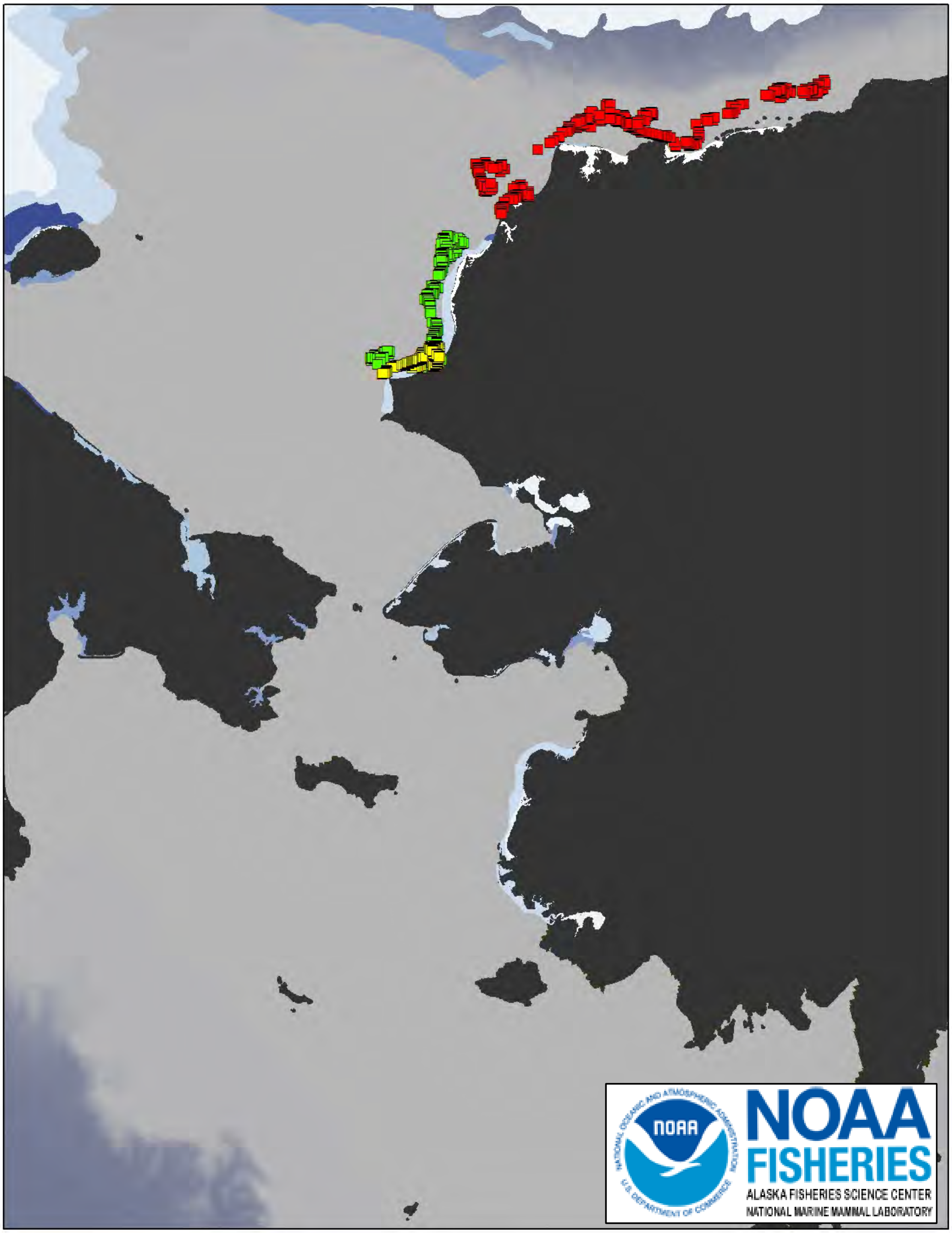

Figure 6.5. Map of the sea ice distribution and seasonal movements in October 2009 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

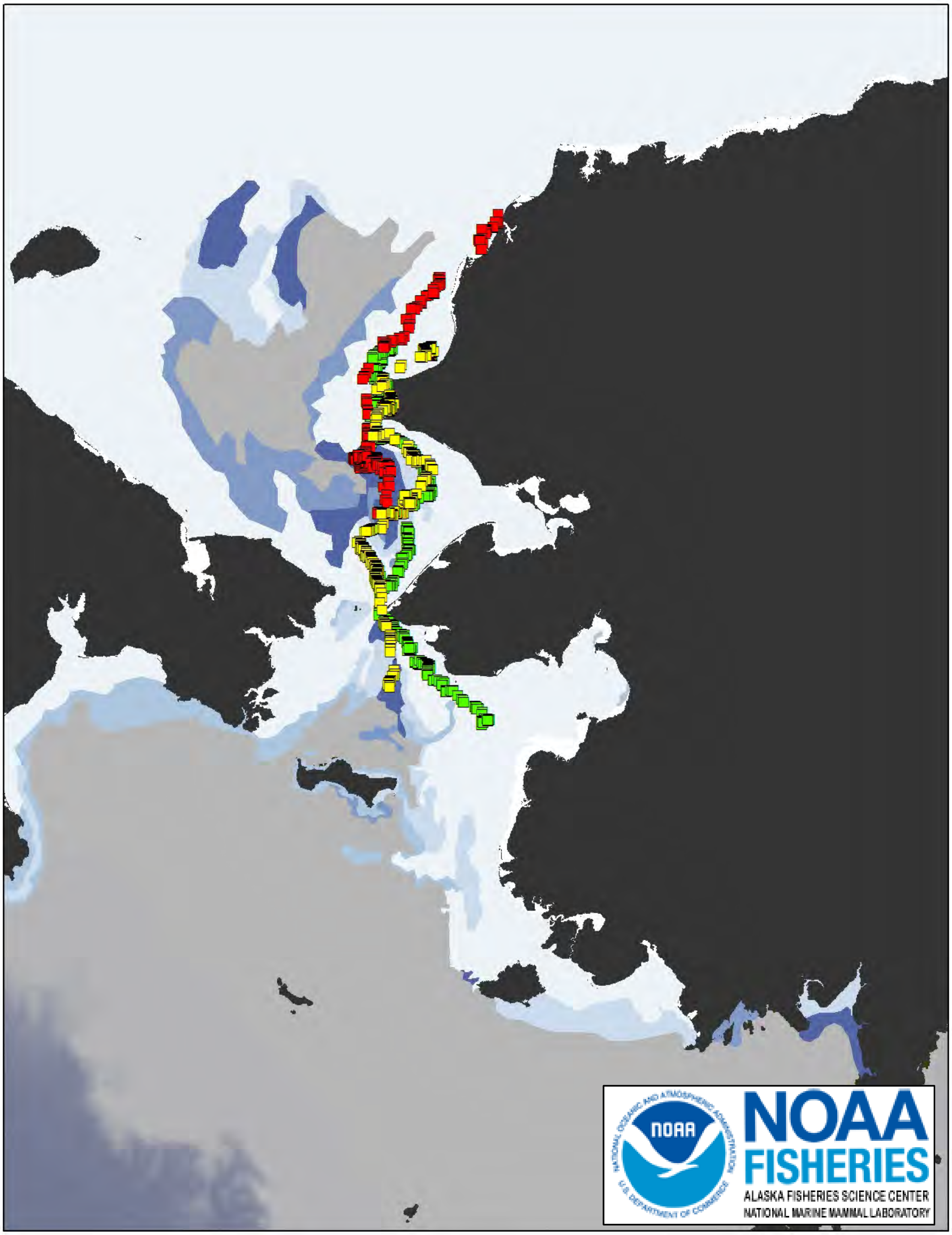

Figure 6.6. Map of the sea ice distribution and seasonal movements in November 2009 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

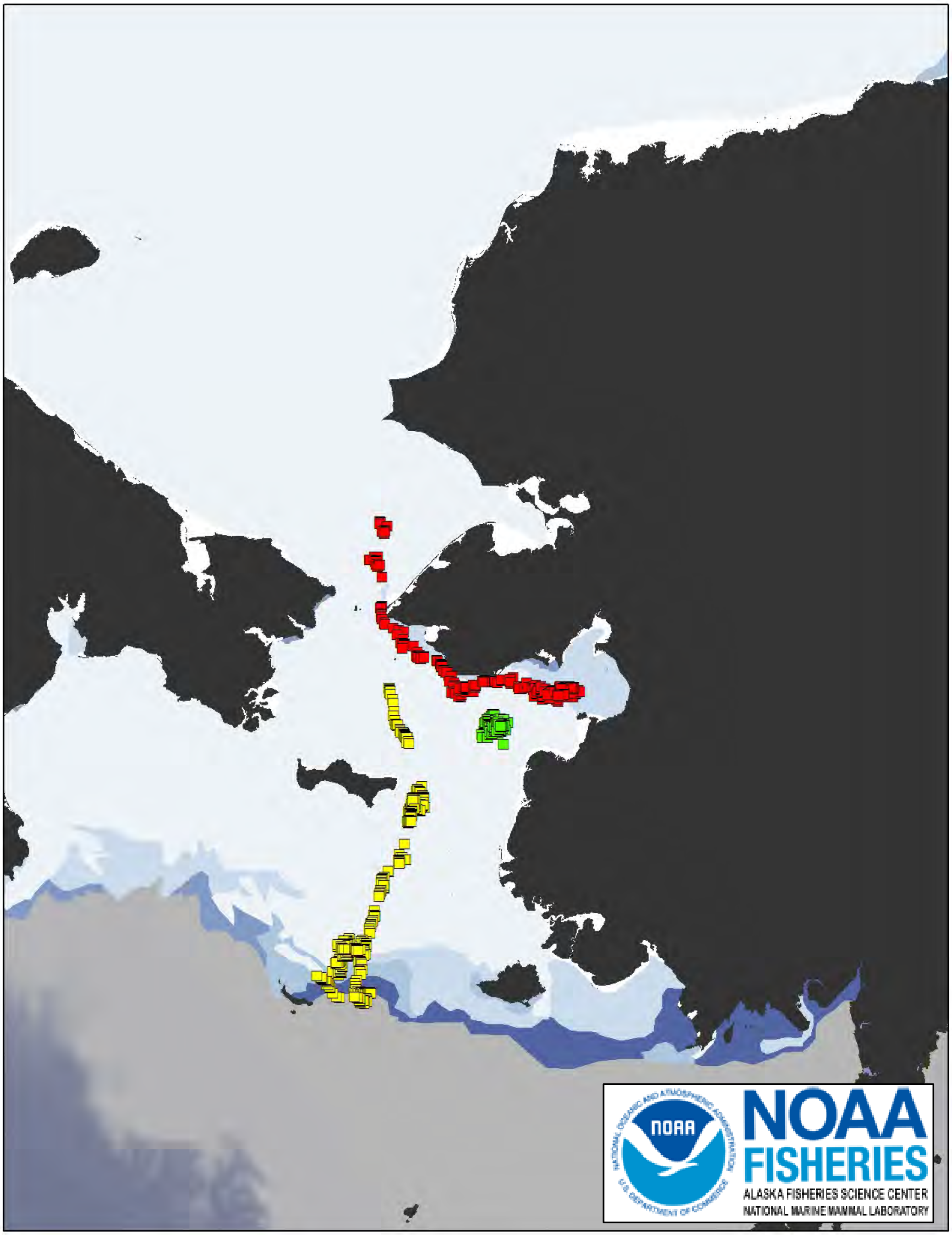

Figure 6.7. Map of the sea ice distribution and seasonal movements in December 2009 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

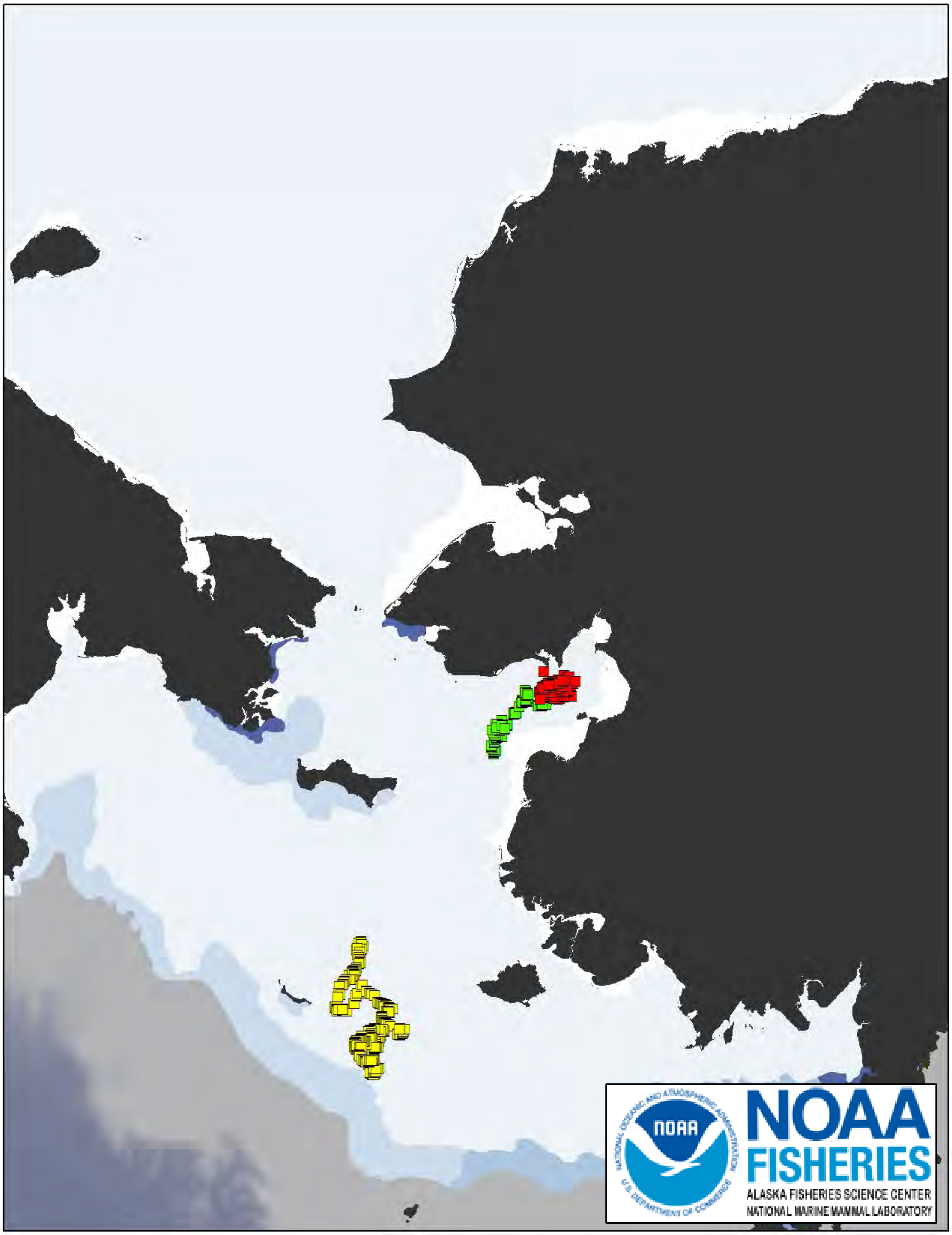

Figure 6.8. Map of the sea ice distribution and seasonal movements in January 2010 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

Figure 6.9. Map of the sea ice distribution and seasonal movements in February 2010 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

Figure 6.10. Map of the sea ice distribution and seasonal movements in March 2010 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

Figure 6.11. Map of the sea ice distribution and seasonal movements in April 2010 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

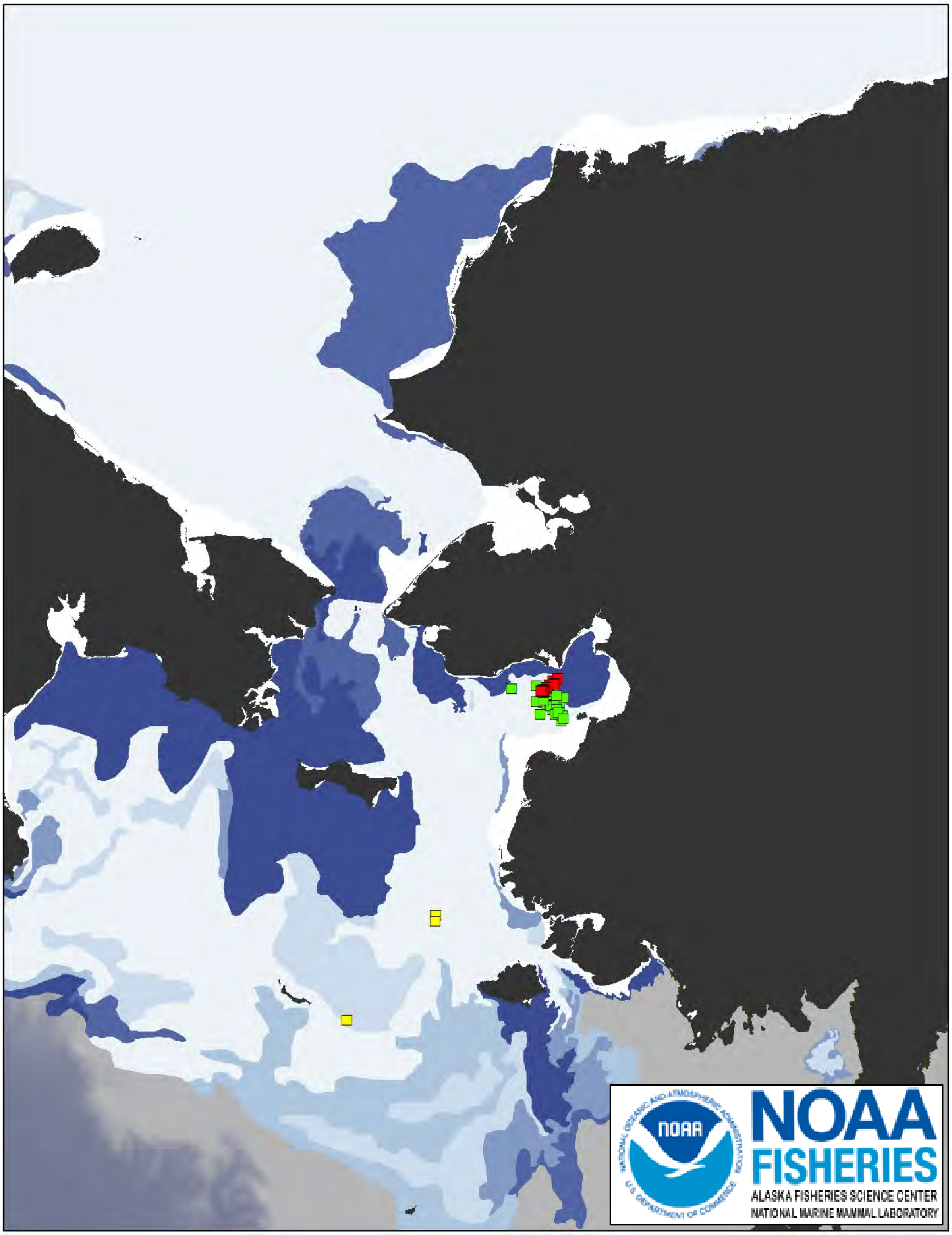

Figure 6.12. Map of the sea ice distribution and seasonal movements in May 2010 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

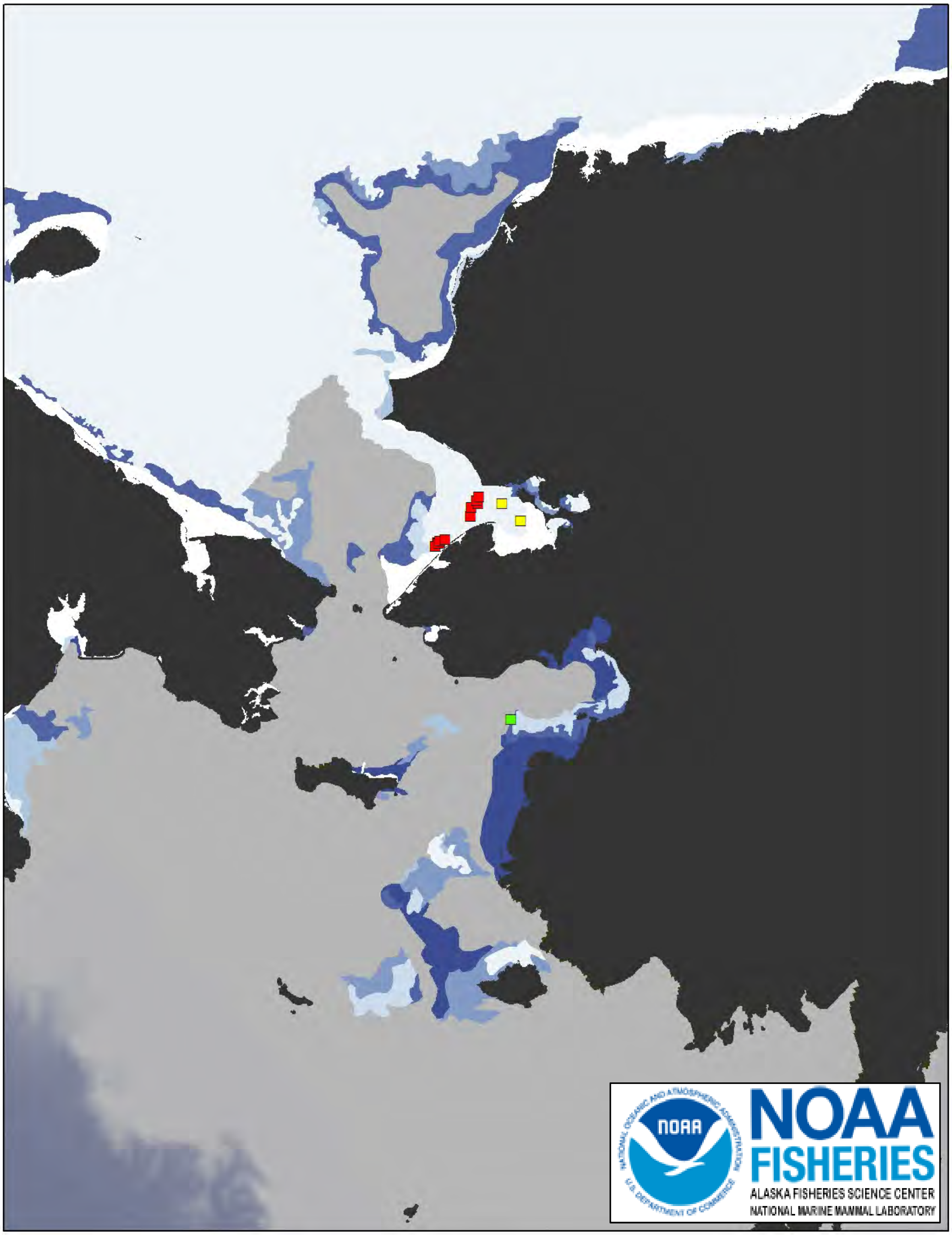

Figure 6.13. Map of the sea ice distribution and seasonal movements in June 2010 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

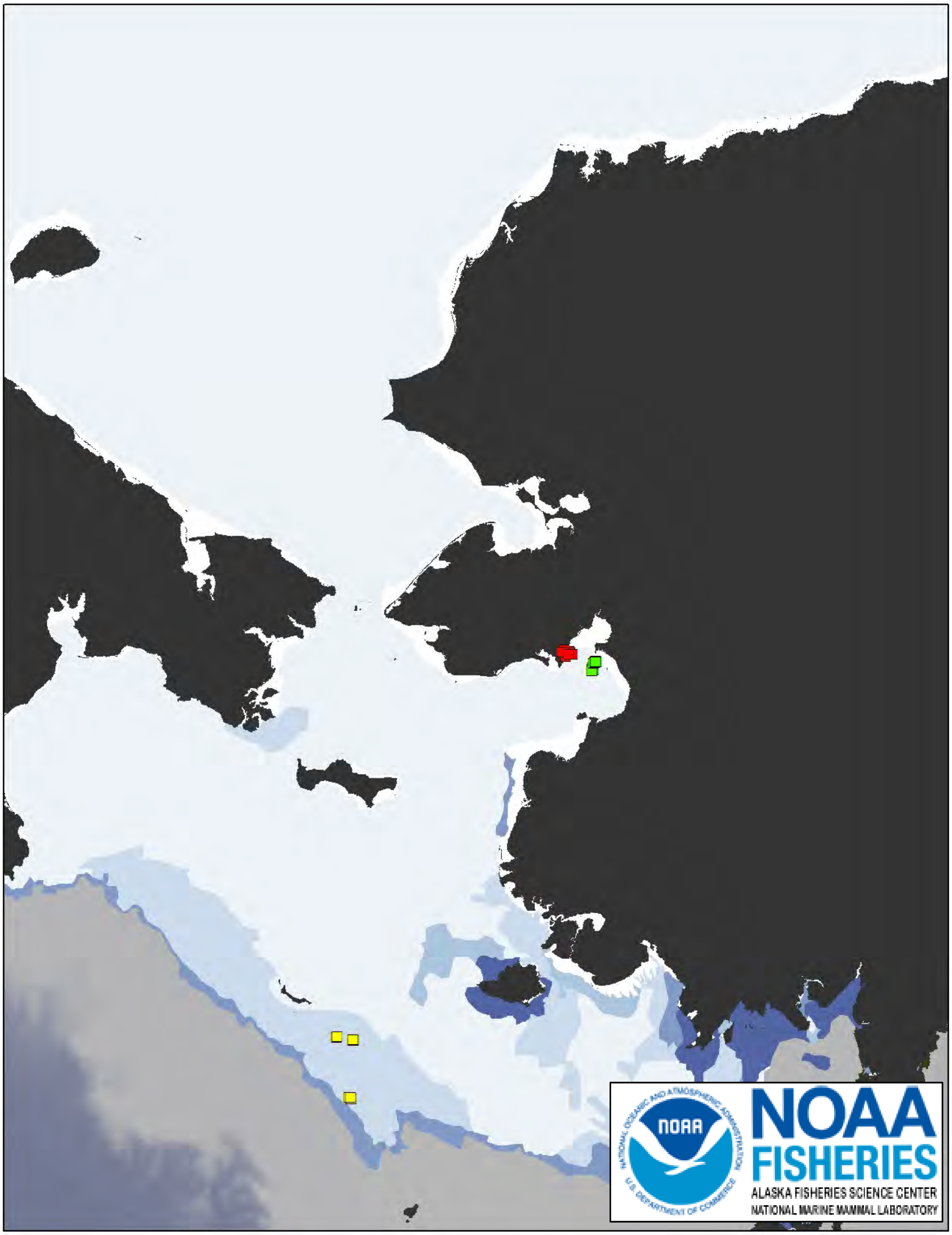

Figure 6.14. Map of the sea ice distribution and seasonal movements in February, March and April 2011 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

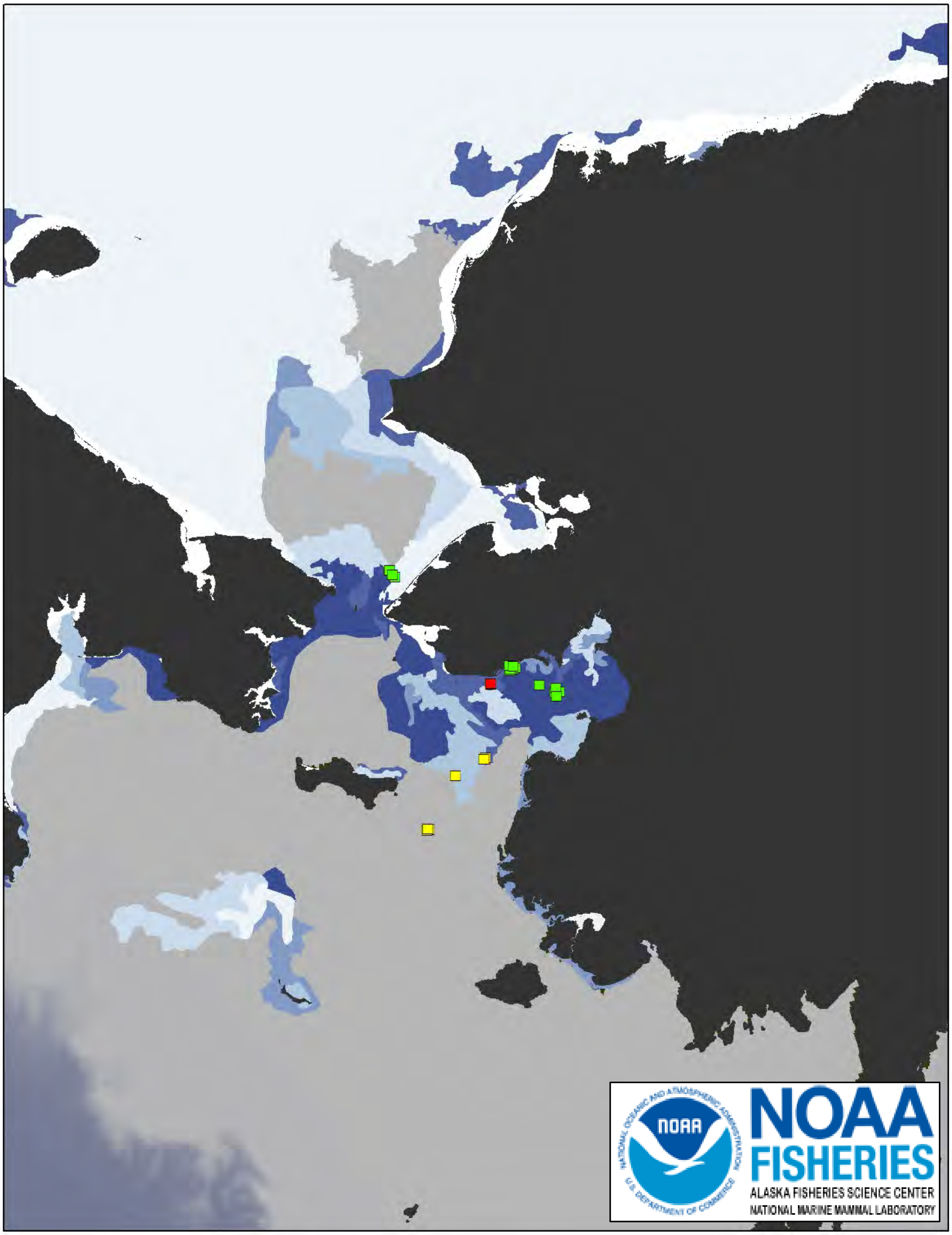

Figure 6.15. Map of the sea ice distribution and seasonal movements in May 2011 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002.

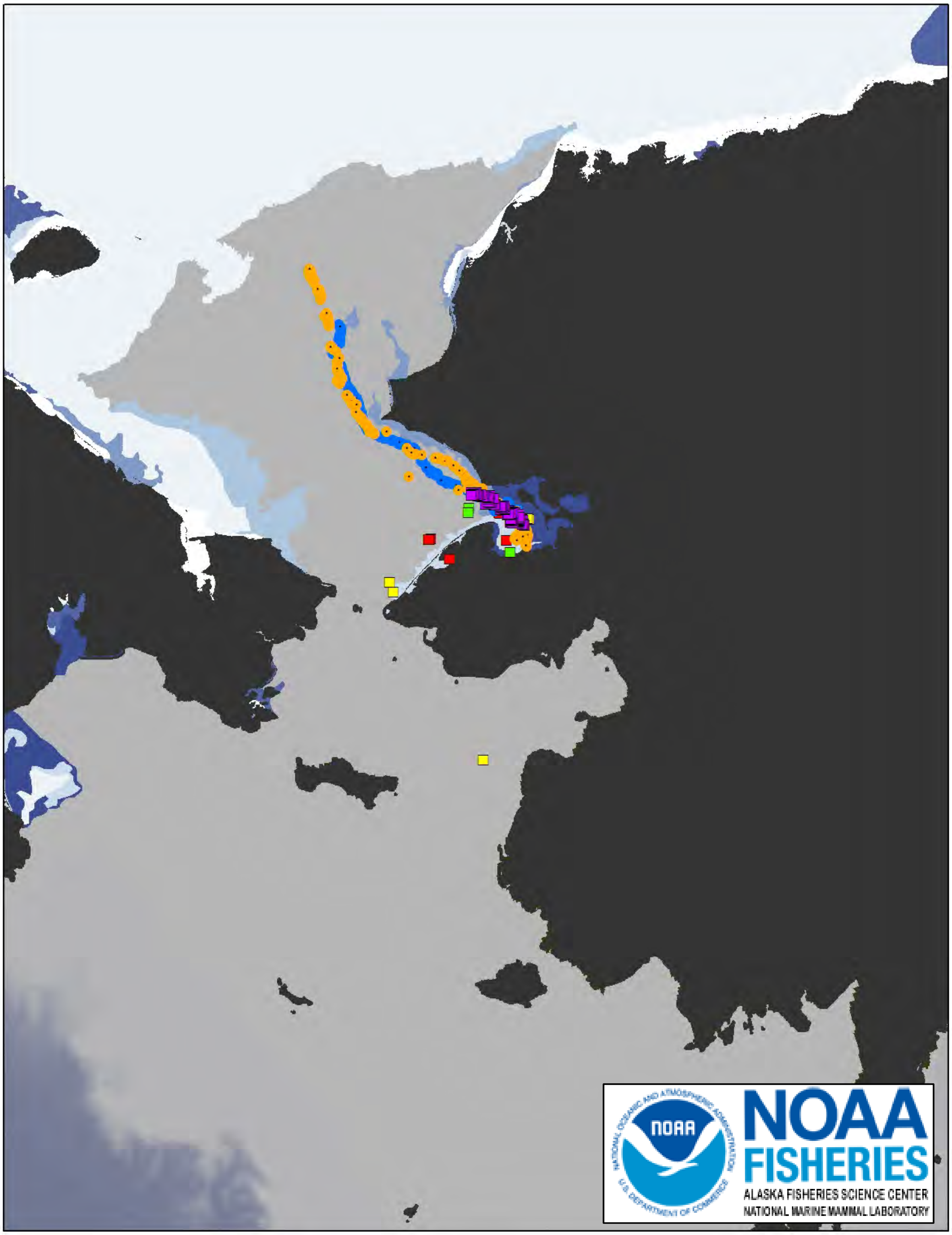

Figure 6.16. Map of the sea ice distribution and seasonal movements in June 2011 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

Figure 6.17. Map of the sea ice distribution and seasonal movements in July 2011 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

Figure 6.18. Map of the sea ice distribution and seasonal movements in August 2011 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

Figure 6.19. Map of the sea ice distribution and seasonal movements in September 2011 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

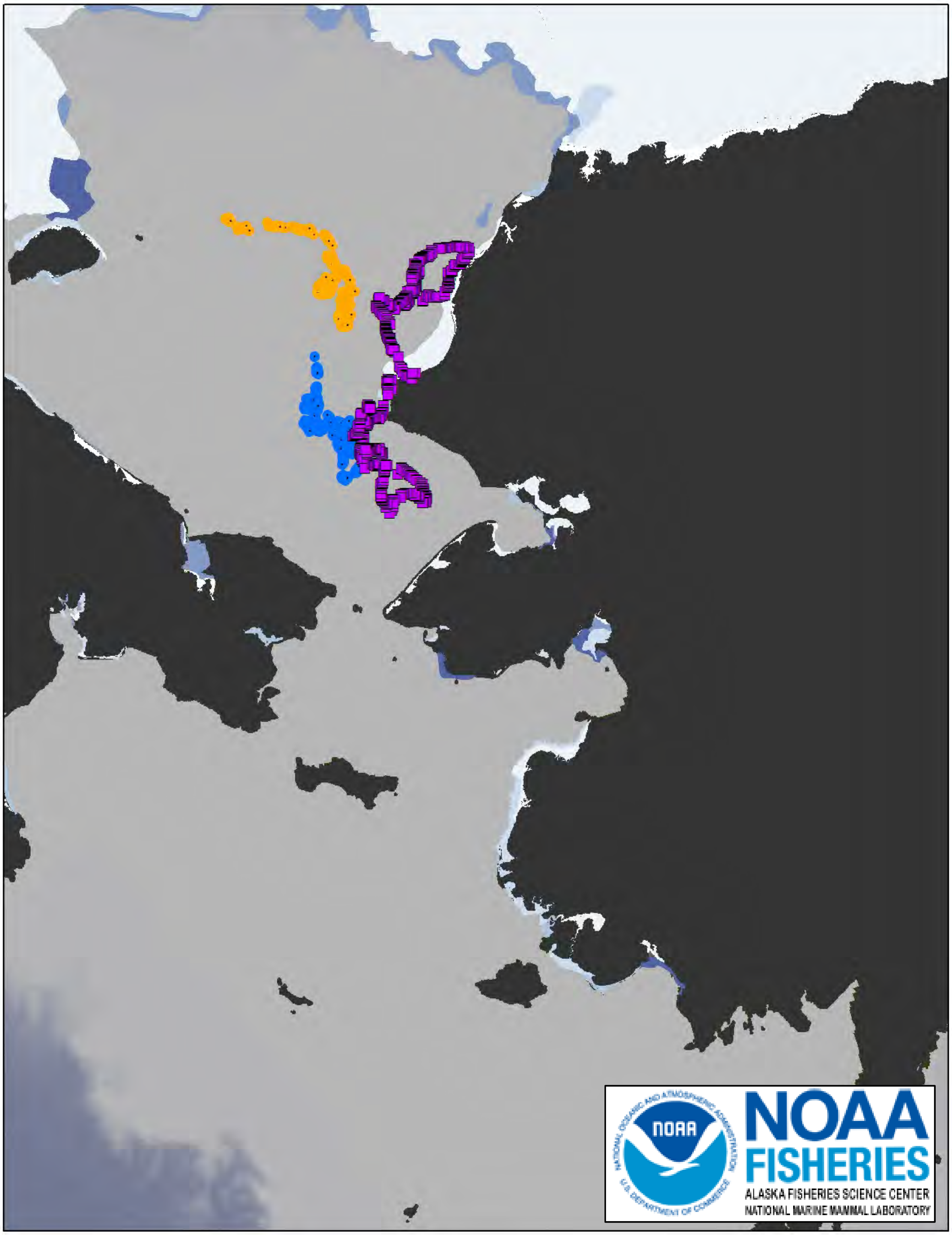

Figure 6.20. Map of the sea ice distribution and seasonal movements in October 2011 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

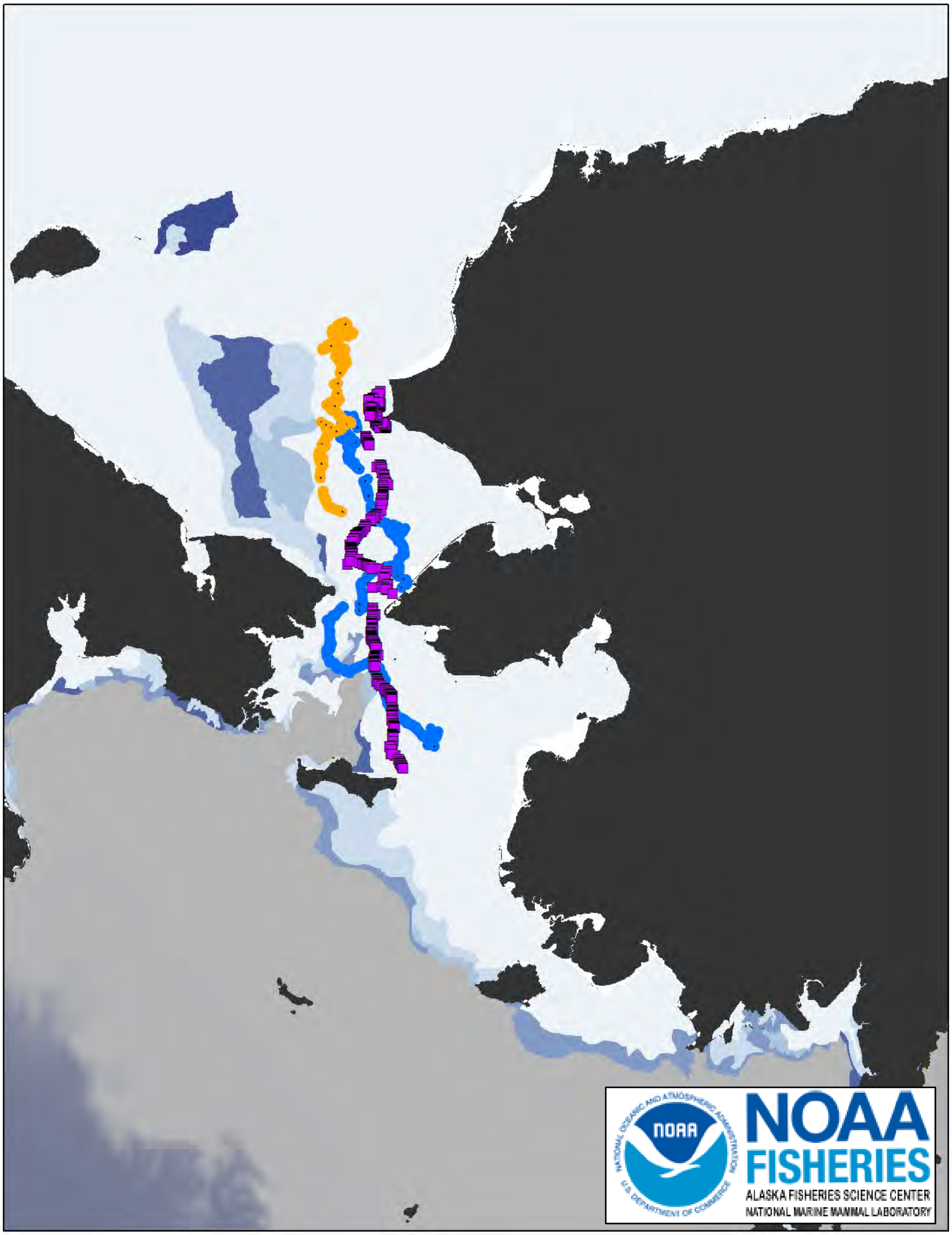

Figure 6.21. Map of the sea ice distribution and seasonal movements in November 2011 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

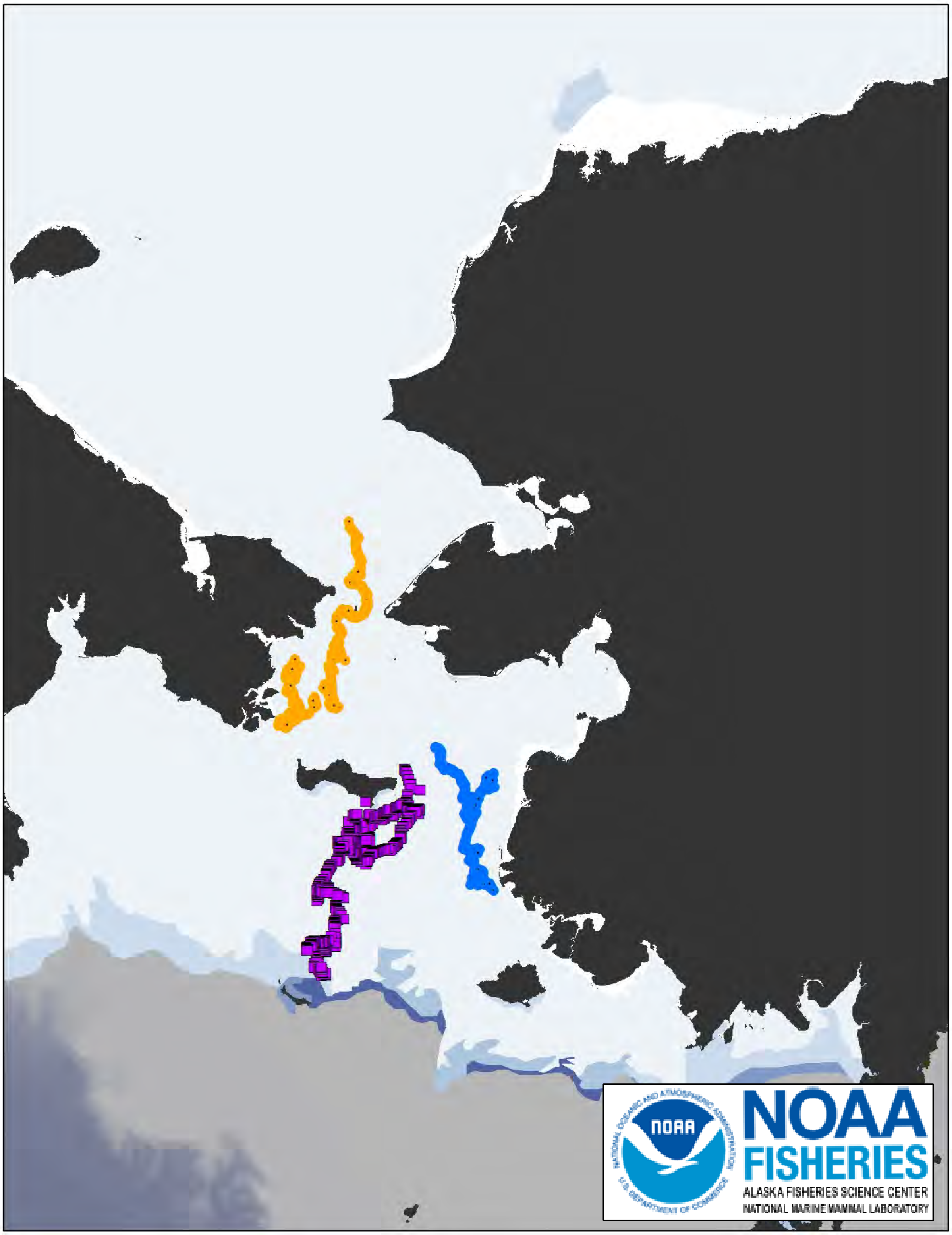

Figure 6.22. Map of the sea ice distribution and seasonal movements in December 2011 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

Figure 6.23. Map of the sea ice distribution and seasonal movements in January 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

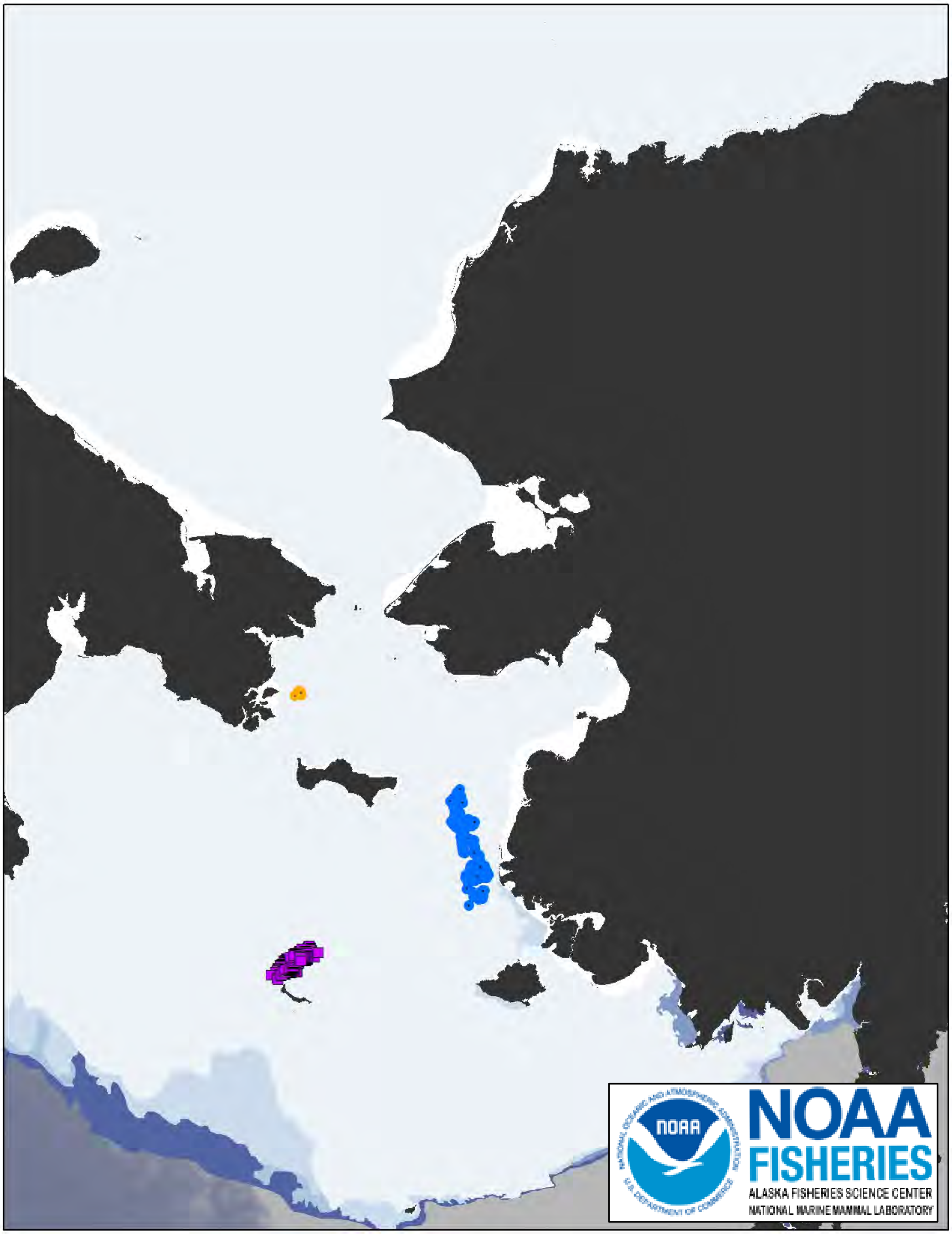

Figure 6.24. Map of the sea ice distribution and seasonal movements in February 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

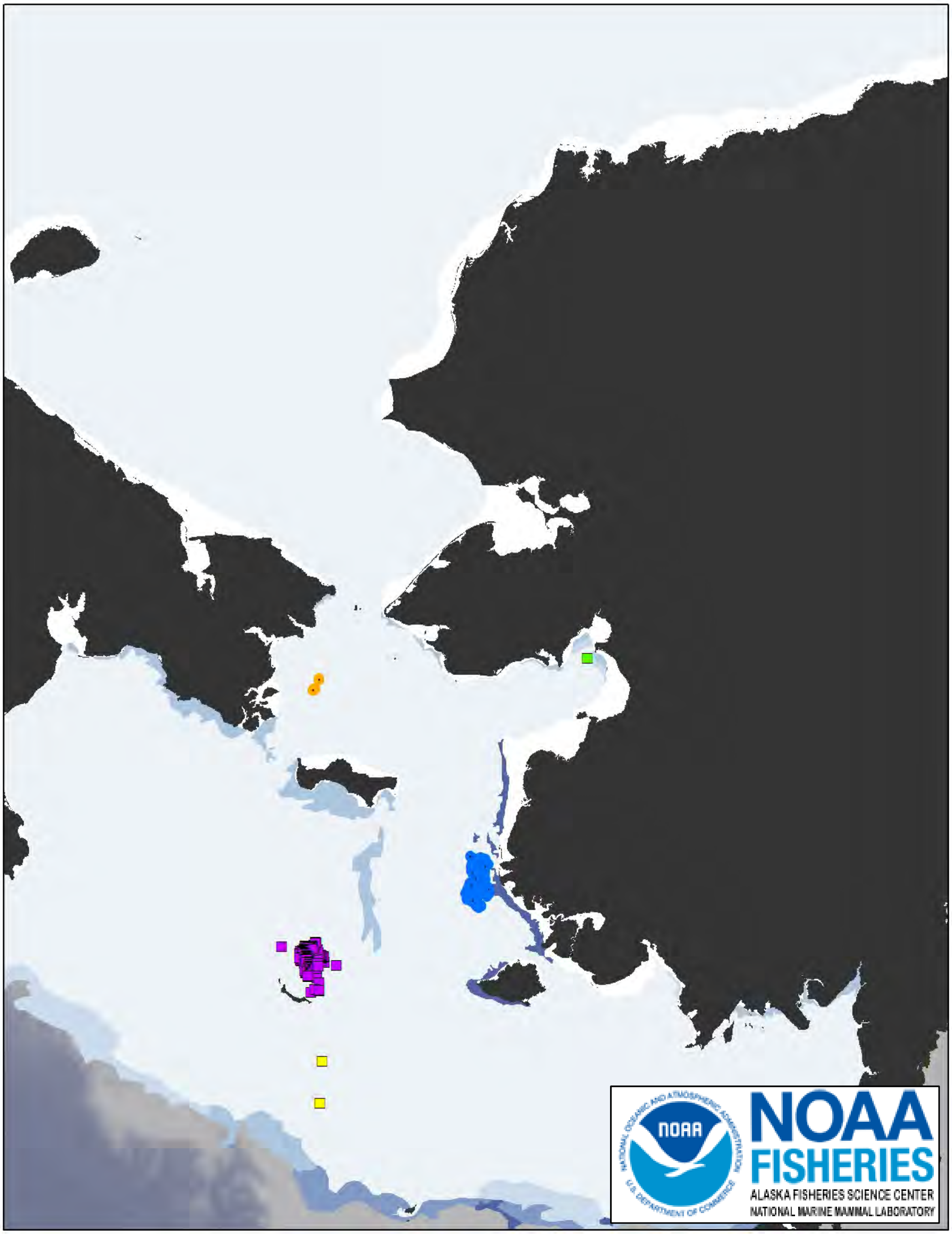

Figure 6.25. Map of the sea ice distribution and seasonal movements in March 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

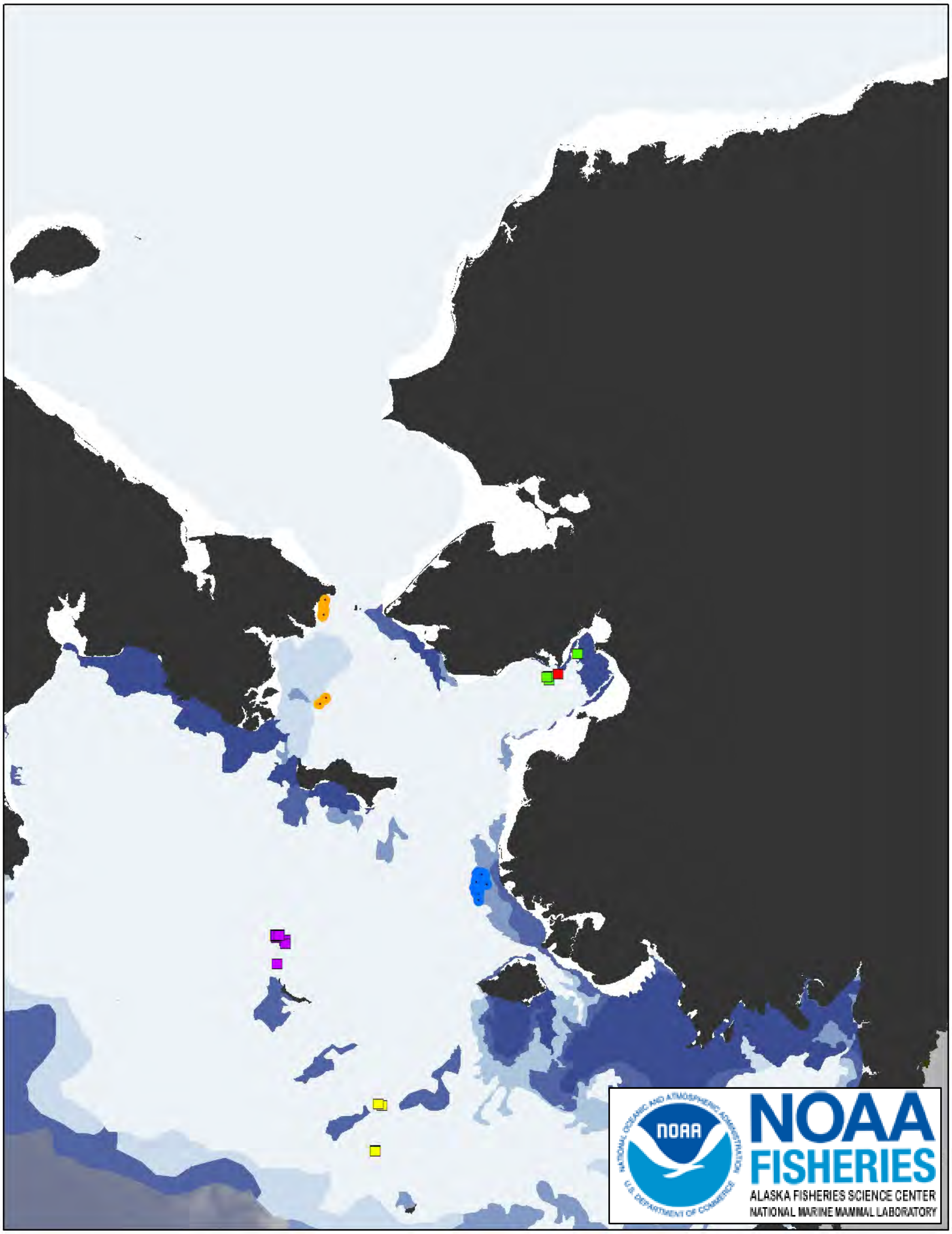

Figure 6.26. Map of the sea ice distribution and seasonal movements in April 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

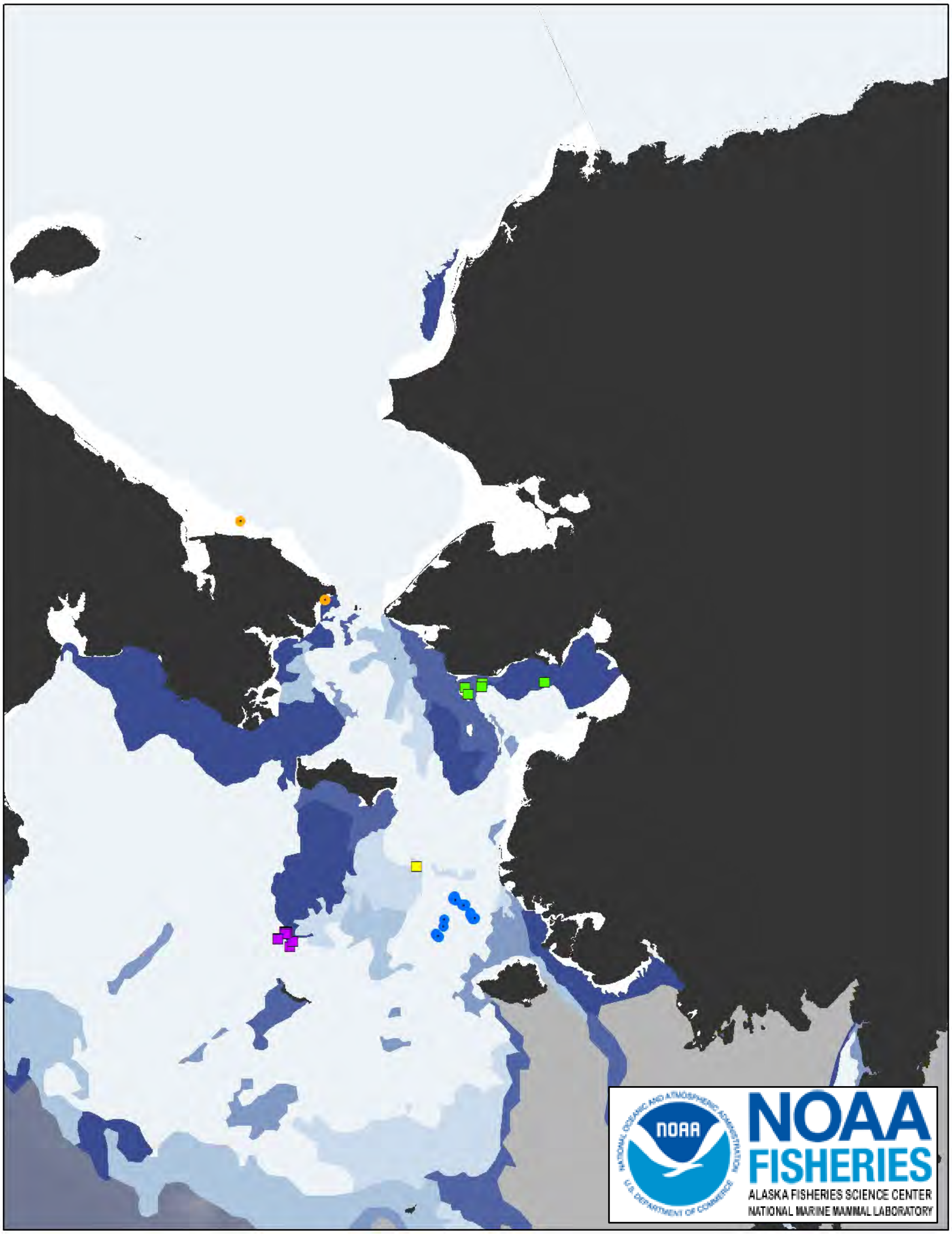

Figure 6.27. Map of the sea ice distribution and seasonal movements in May 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

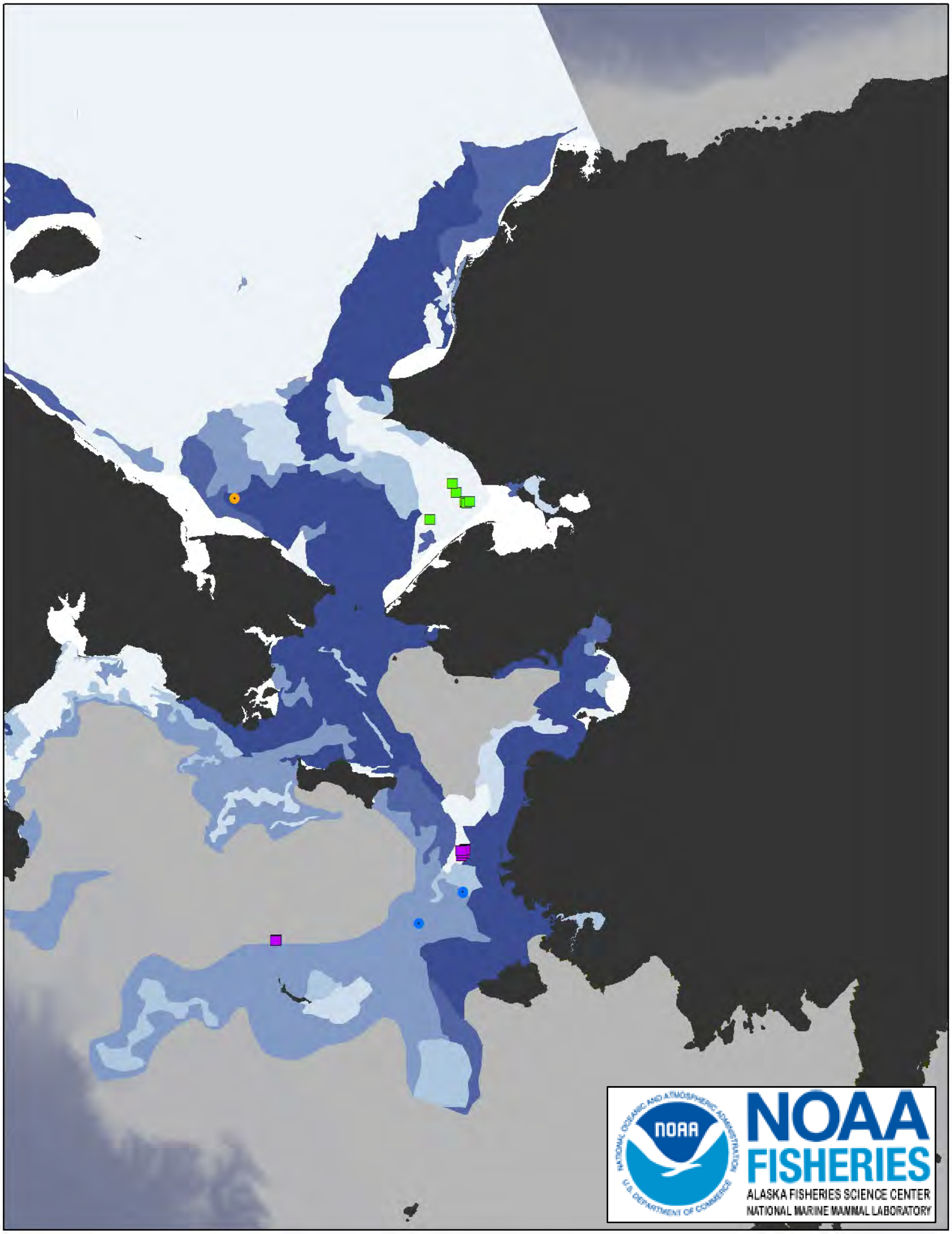

Figure 6.28. Map of the sea ice distribution and seasonal movements in June 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002.

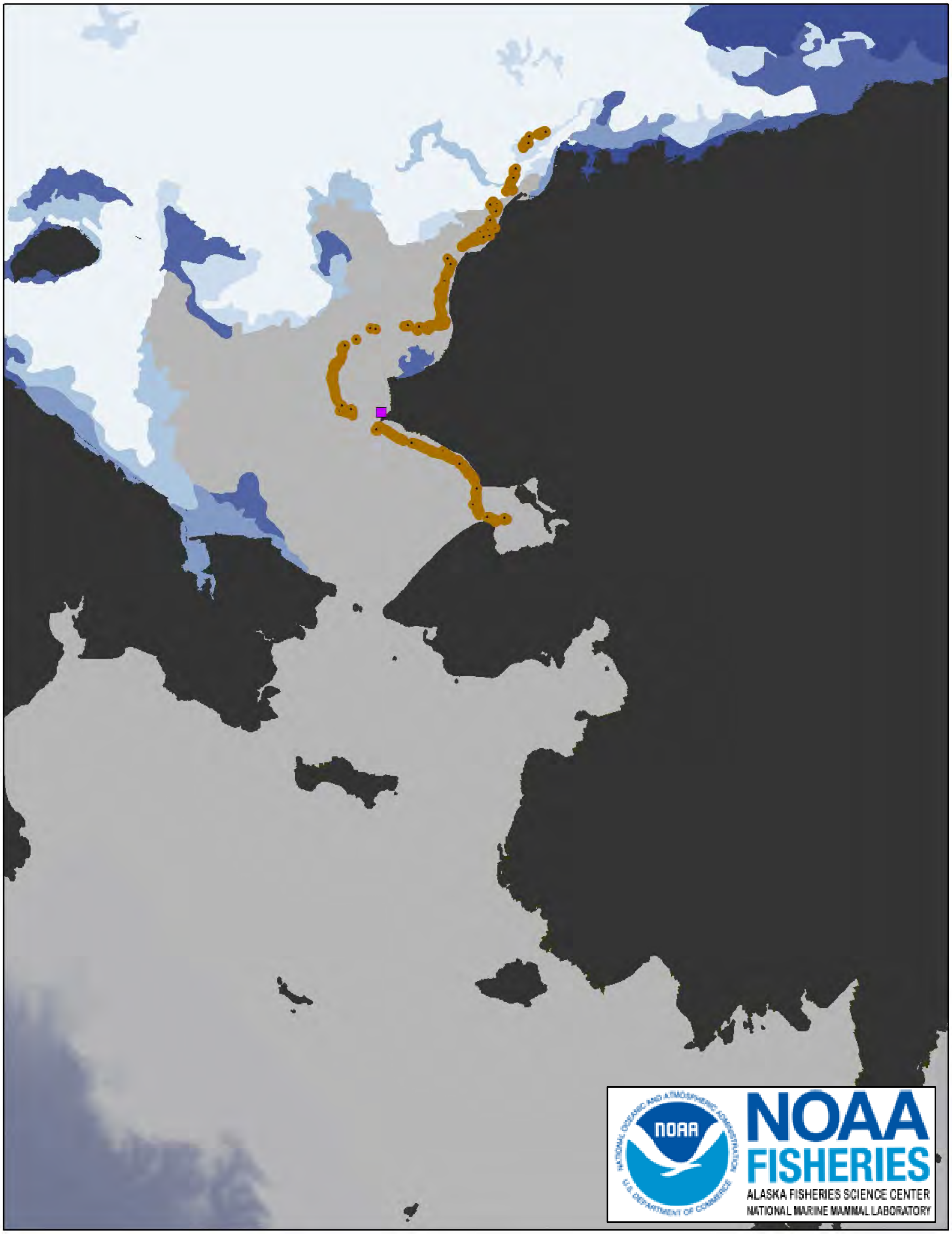

Figure 6.29. Map of the sea ice distribution and seasonal movements in July 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

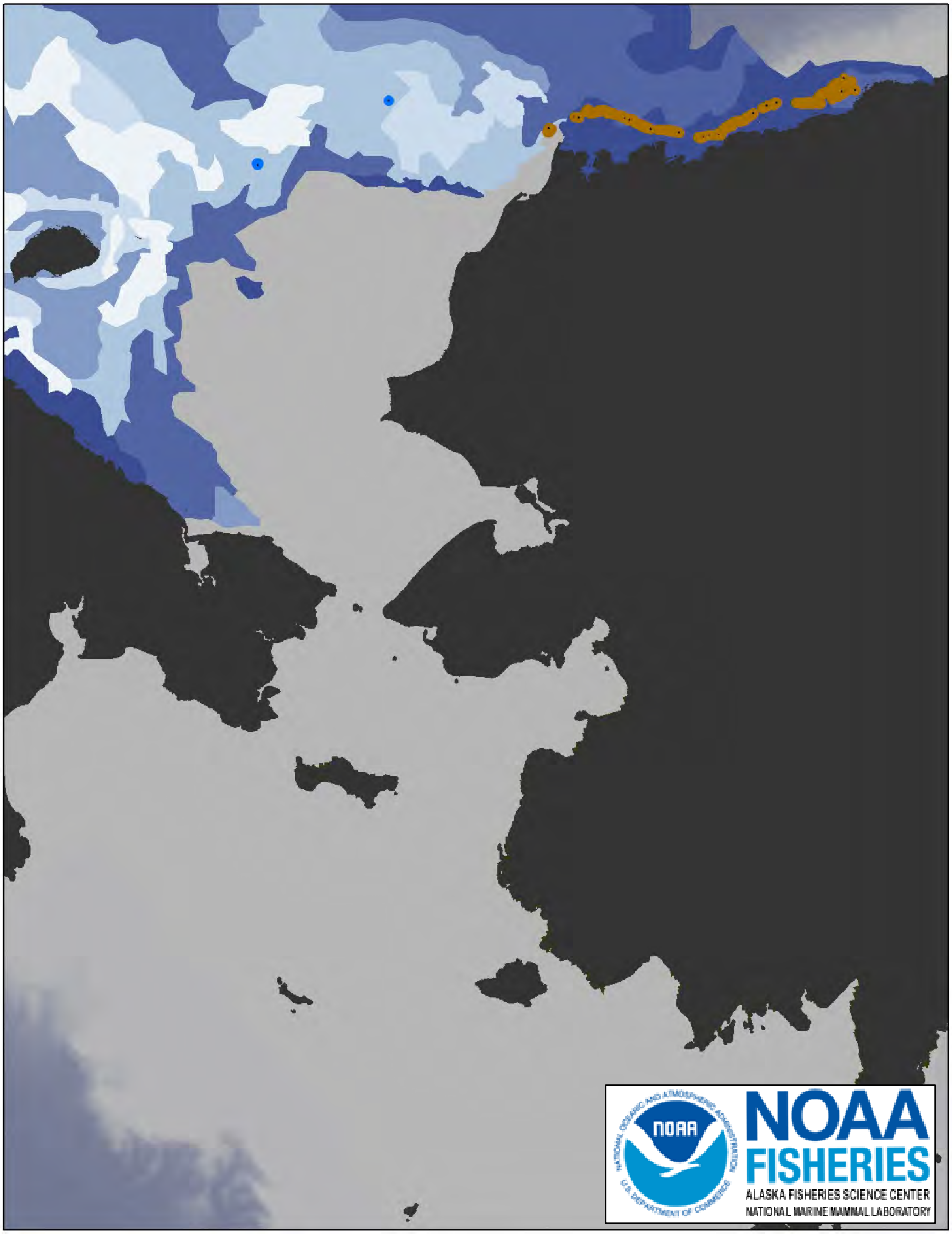

Figure 6.30. Map of the sea ice distribution and seasonal movements in August 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

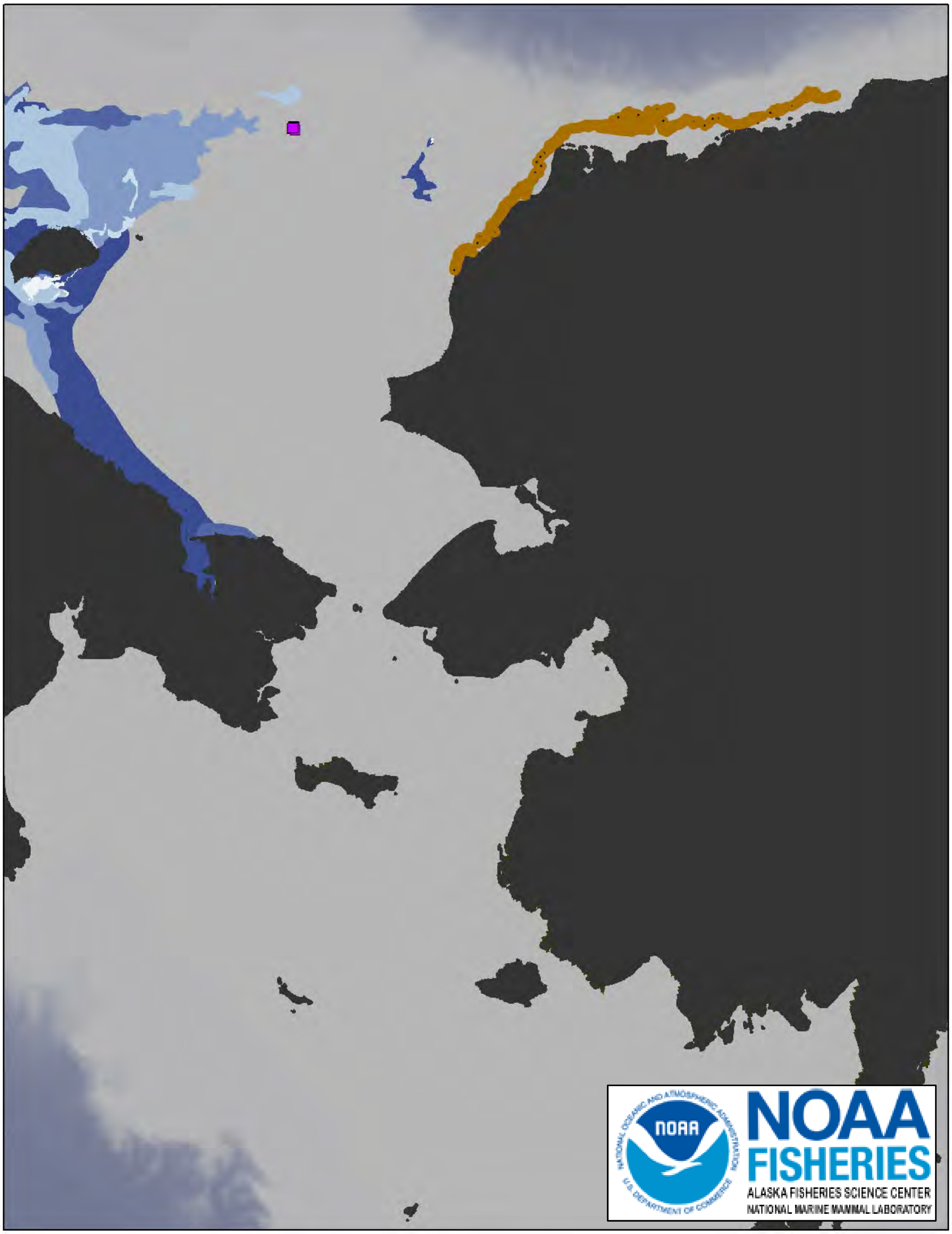

Figure 6.31. Map of the sea ice distribution and seasonal movements in September 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

Figure 6.32. Map of the sea ice distribution and seasonal movements in October 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

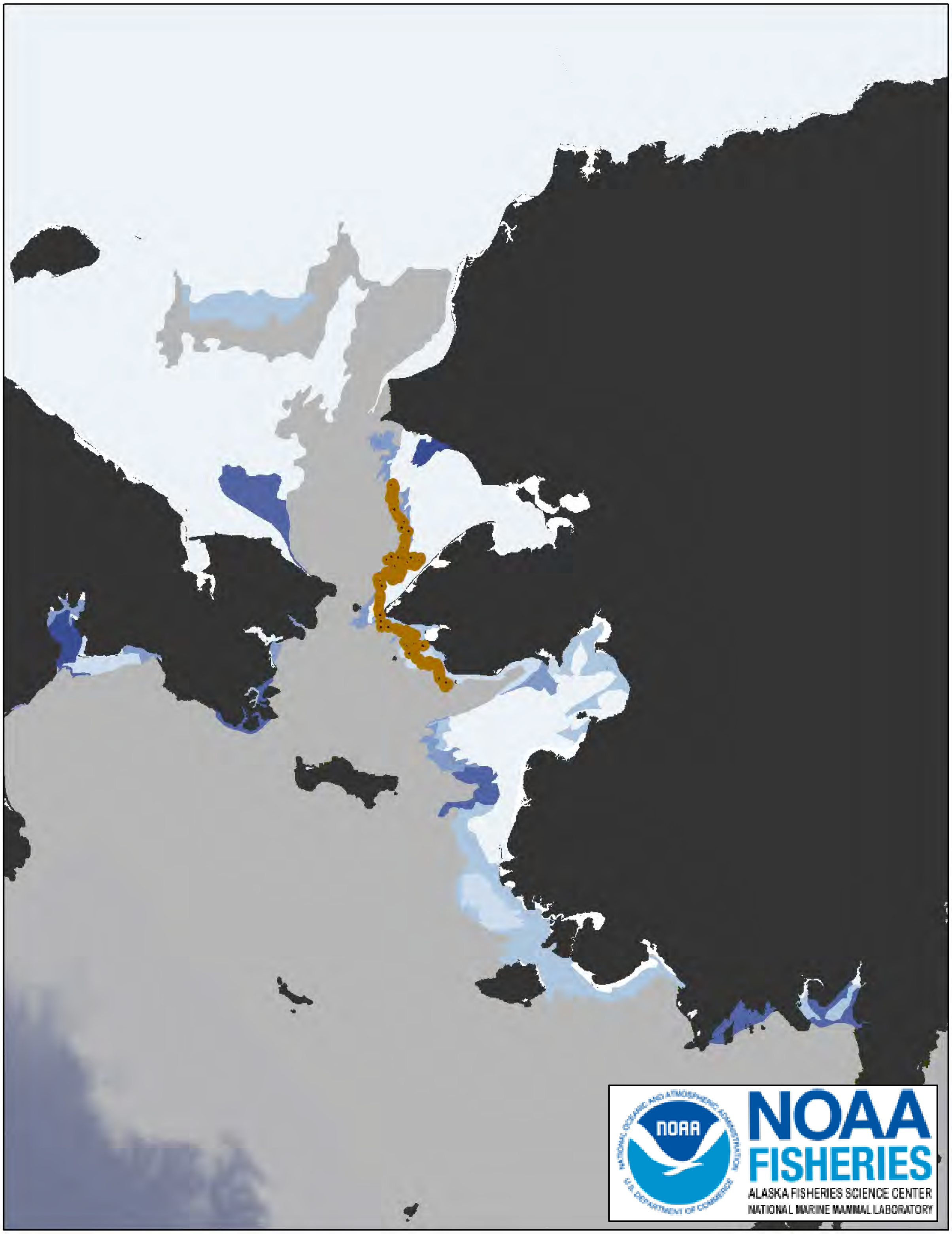

Figure 6.33. Map of the sea ice distribution and seasonal movements in November 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

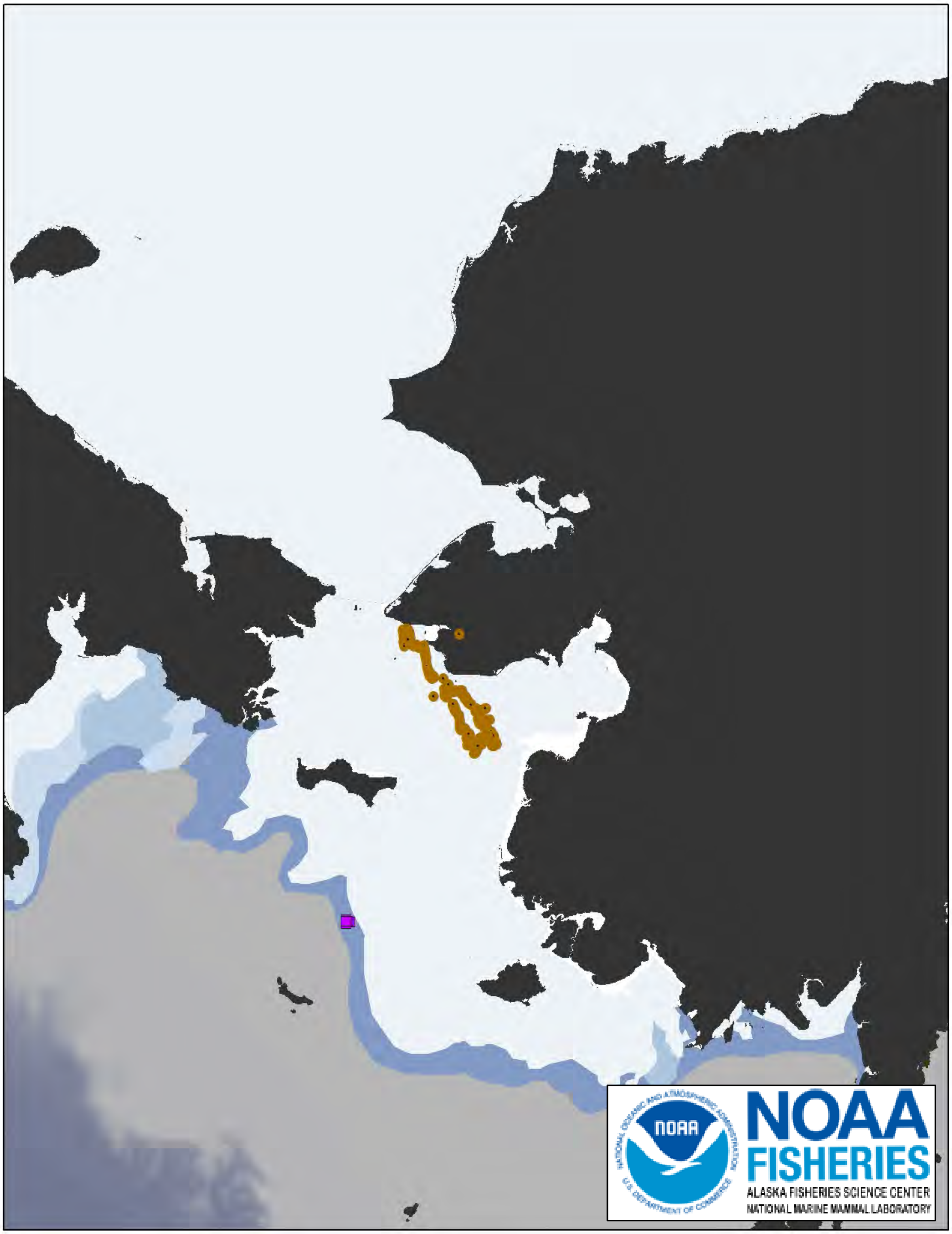

Figure 6.34. Map of the sea ice distribution and seasonal movements in December 2012 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

Figure 6.35. Map of the sea ice distribution and seasonal movements in early-January 2013 of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

Dive behavior

The vast majority of dives made by these 7 adult and sub-adult bearded seals were to depths less than 70 m throughout the seasons and times of day (Figure 7). There were a few records of dives deeper than 150m, made by individuals that were over canyons or the continental shelf break in the Beaufort and northern Chukchi seas.

There was remarkably little variation in the depth distributions of the seals' dives throughout the day (Figure 7). There were, however, clear differences between the depth distributions in summer, fall, and winter. In particular, winter dives tended to be shallower, with higher frequencies of dives in the 4 – 30 m range, than in summer and fall.

There was variability between individuals in their winter dive-depth distributions, likely reflecting the bathymetry of the relatively small areas in which they spent the winter months. For example, bearded seal EB2011_3002--which wintered in the relatively deep water just north of St. Matthew Island--made fewer, but deeper dives than EB2009_3001, which wintered in Norton Bay and upper Norton Sound (Figure 7, Figure 6.9, and Figure 6.25).

Most dives for all seals were 6-10 minutes long, though the adult male, EB2009_3001, made a few longer dives of roughly 20 minutes. Dive duration appeared to be related to seafloor depth and dive depth. In autumn of 2011, the females tagged in that year occupied areas of deeper water (50-150 m) than the males (approx. 50 m), and their dives were of longer duration (8-16 vs. 6-10 minutes, respectively). In the winter however, when both sexes occupied water less than 50 m in depth, dive duration was about 6-10 minutes for all seals.

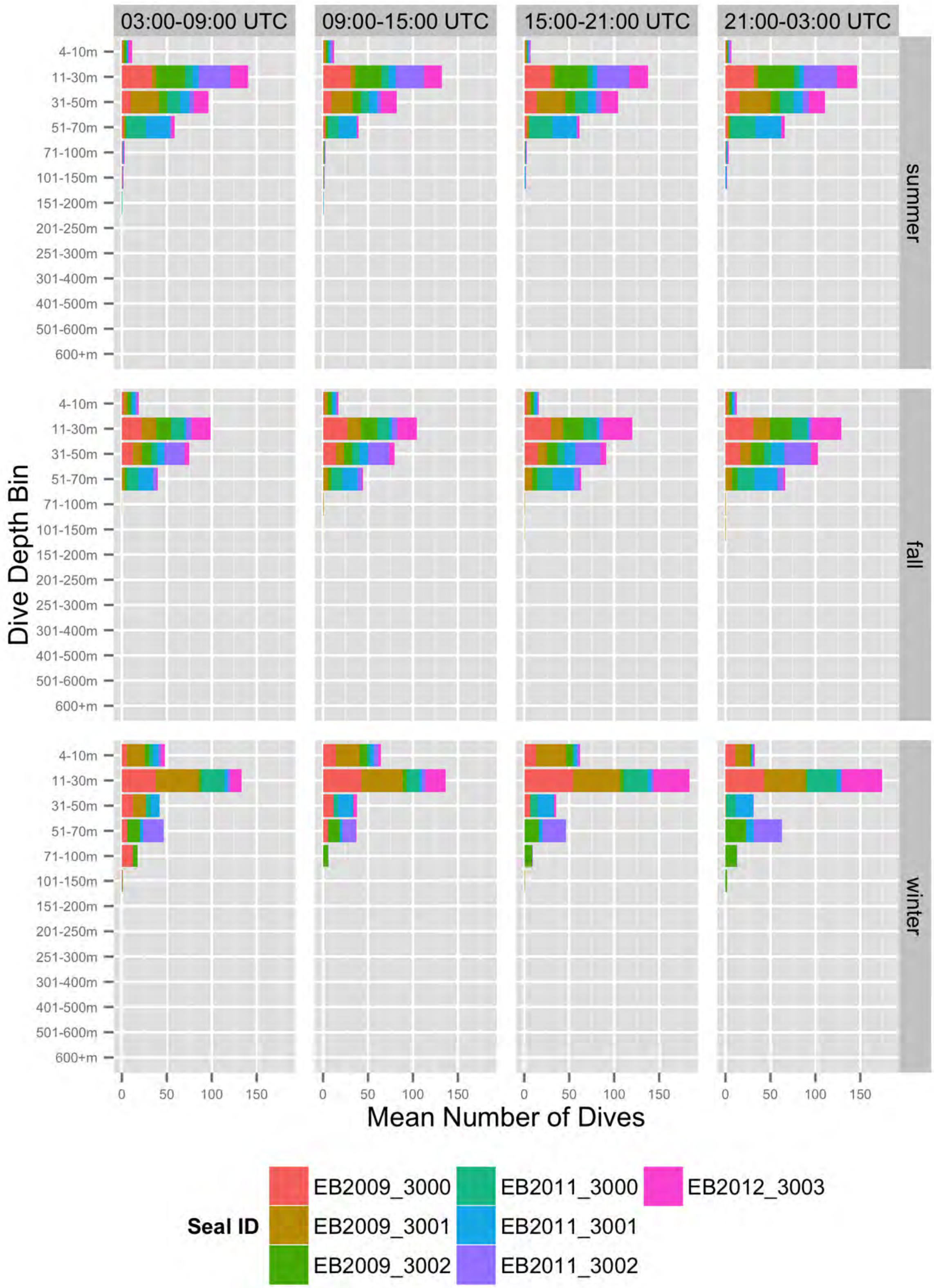

Figure 7. Dive Depths of bearded seals across daily and seasonal time periods (summer =June-September; fall=October-December; and winter=January-April)

Objective 2: Identify specific marine habitats in the Chukchi Sea Planning Area

Movements in Alaska Planning Areas

All seven of the bearded seals tracked in this study moved through the Chukchi Sea Planning Area (CSPA) and two of the seven also used the Beaufort Sea Planning Area (BSPA) (Figure 8). The tagged bearded seals' use of the habitat within the planning areas was a mix of transit, foraging, and resting, as determined by the multi-state movement and behavior modeling (see next section). The majority of the locations in the planning areas were in a corridor relatively near the Alaska coast (Figure 9). Of all the locations obtained from bearded seals in the CSPA, 70.8% were within 50 km of the coast. In the BSPA, 96.5% of the locations obtained were within 50 km of the coast. Small numbers of locations were obtained from the narrow region between the coast and the boundaries of the CSPA and BSPA; these composed only 3.2% and 0.6% of the total locations within and coast-ward of the CSPA and BSPA, respectively. The CSPA can be characterized as mostly shelf (i.e., shallow water) habitat while the seafloor is much deeper across most of the BSPA. As such, it is perhaps not surprising that bearded seals in the latter are more likely to be found near the coast than those in the former. The lease sale blocks are all in shallow water and so bearded seals in the BSPA are also more likely to be found in close proximity to a lease sale area than those in the CSPA (Figure 10). Of all the locations obtained from bearded seals in the CSPA, 21.8% were within 50 km of a lease sale area (and 5.5% were within 10 km). In the BSPA, 75.0% of the locations obtained were within 50 km of a lease sale area (and 53.0% were within 10 km).

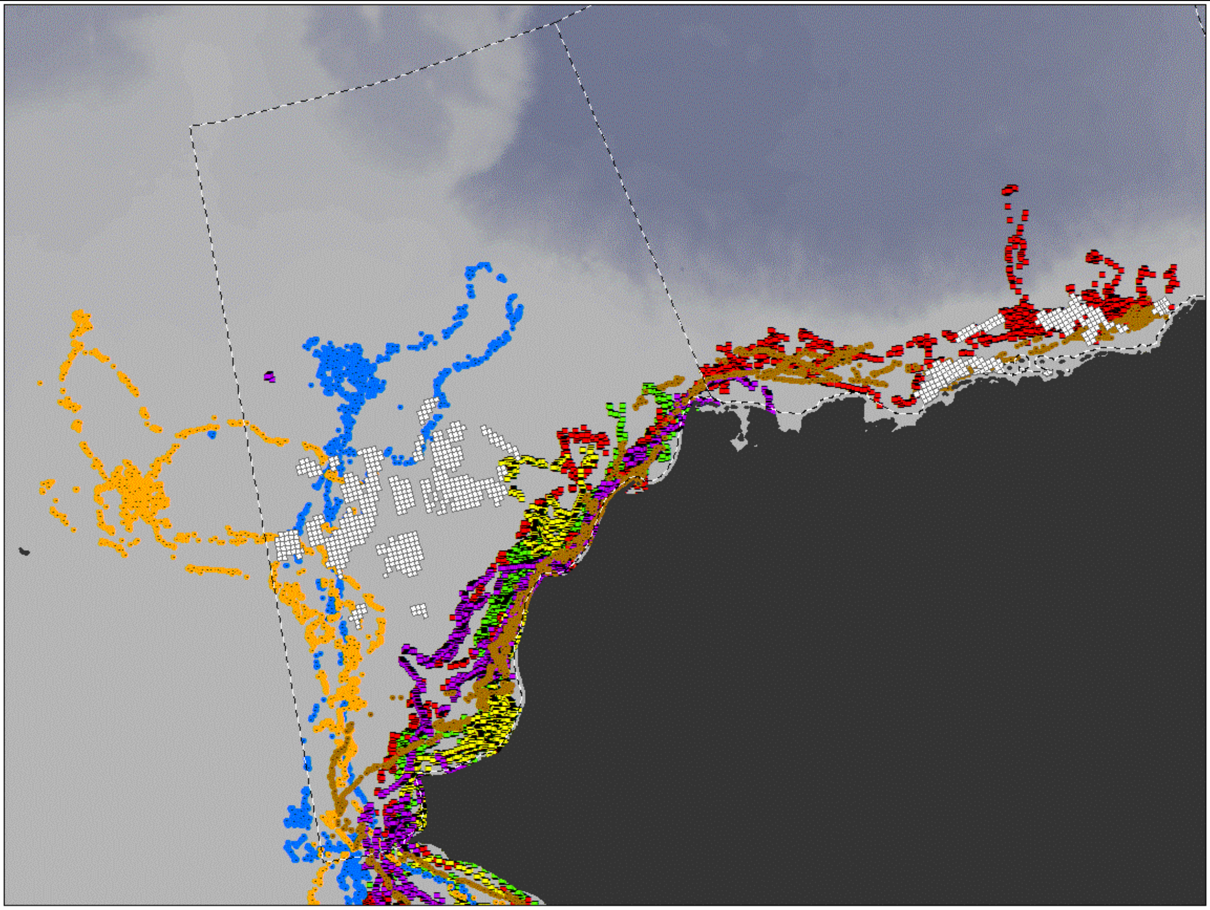

Figure 8. Locations and movements of bearded seals in relation to the Chukchi and Beaufort Planning Areas (dashed lines) and the lease blocks. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

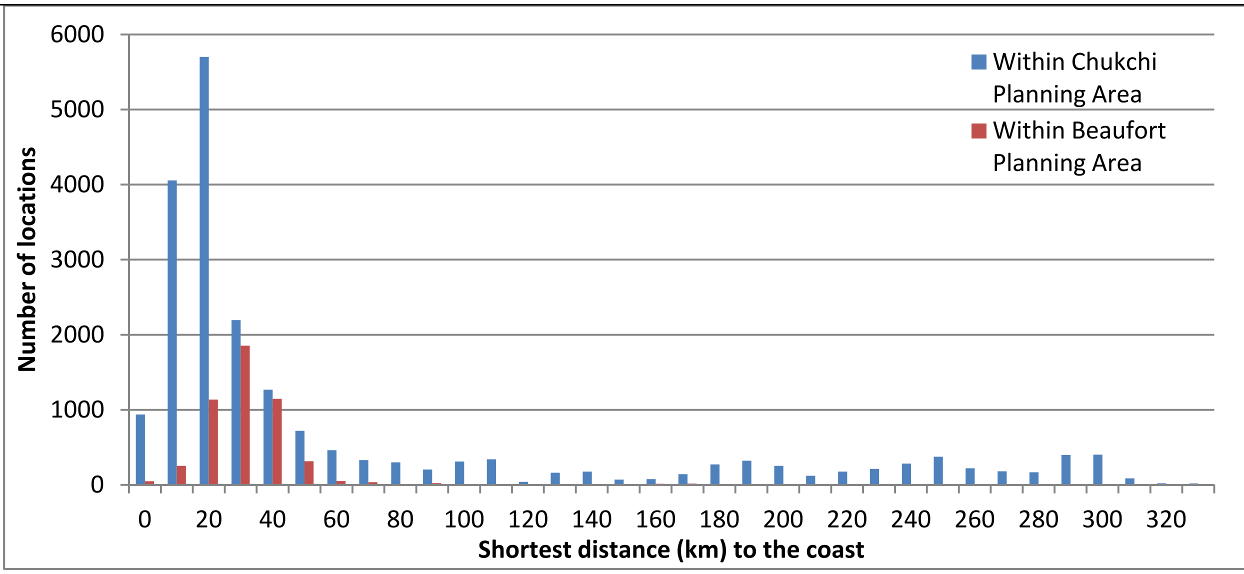

Figure 9. Distributions of distances to the coastline as measured from all Mk10 locations within the given planning area

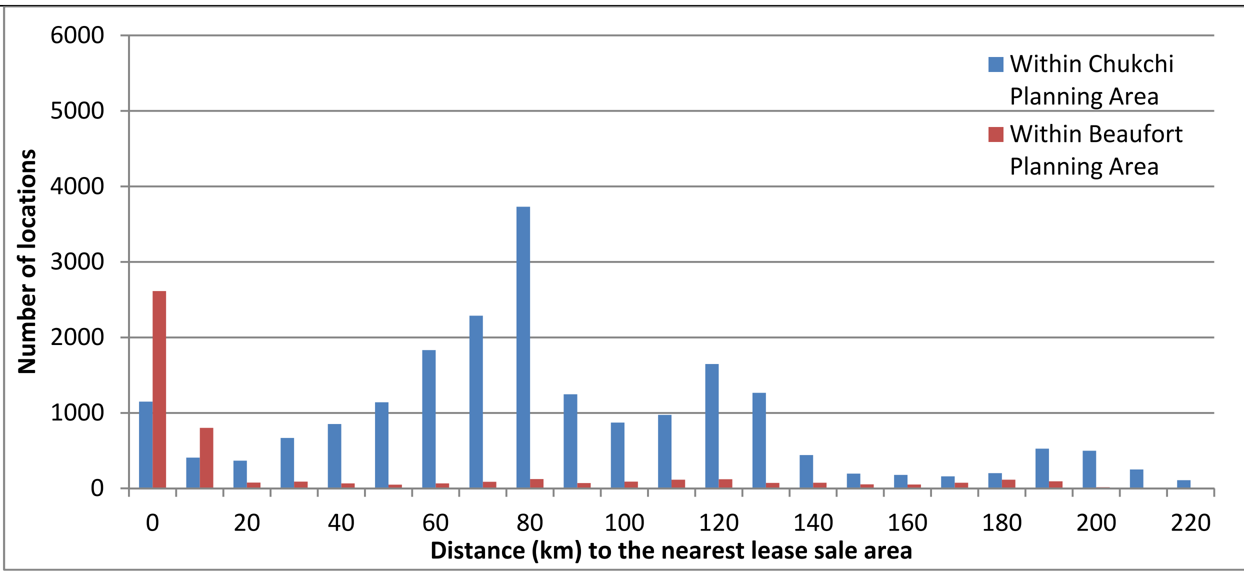

Figure 10. Distributions of distances to the nearest lease sale as measured from all Mk10 locations within the given planning area

Multi-state movement and behavior modeling

During the summer period, all seven individuals remained north of Kotzebue Sound, in either the Chukchi or Beaufort Sea (Figure 11). Five of the seven individuals remained within about 50 km of the shore on their summer transits through the Chukchi and/or Beaufort Seas. The remaining two followed the same route to about Point Hope, then diverged and moved into the north-central Chukchi Sea. The model results indicated that summer, northward movement from Cape Krusenstern at the northern mouth of Kotzebue Sound, past Kivalina, Point Hope, and Cape Lisburne was almost solely transit type behavior, with very little foraging or resting (Figure 11). A second region in which the modeled behavior state was primarily transit rather than foraging or resting was along the Beaufort Sea coast between Point Barrow and Oliktok Point. There were, however, at least two regions used extensively by multiple individuals for summer foraging. These occurred along the Chukchi Sea coast between Cape Beaufort and Barrow, and along the Beaufort Sea coast from Oliktok Point to Kaktovik. The two individuals that used the north-central Chukchi Sea apparently foraged intensively in selected areas, but there was little overlap between the two, so it is less clear whether these may represent areas that could be potentially important to the population at large. In all the areas where the foraging behavior state was frequent, the resting state was also frequent, indicating that bearded seals typically intersperse foraging with resting on a daily basis, rather than making long (say, > 1 day) bouts of one behavior or the other.

The fall period was characterized by southward migrations to the Bering Sea as the ice advanced during autumn. The southward migration was slower than the northward (summer) migration, and included more time spent foraging and resting than the northward migration. None of the individuals returned to Kotzebue Sound on the southward migration, instead remaining in the central Chukchi Sea as they passed from the Pt. Hope area to Bering Strait.

In winter, the restricted distributions of locations were conspicuously different from the migratory distributions of summer and fall. A large portion of the winter time was allocated to foraging. Still, there was a mix of behaviors--including a substantial portion of time spent in transit--apparent in the winter modeling results.

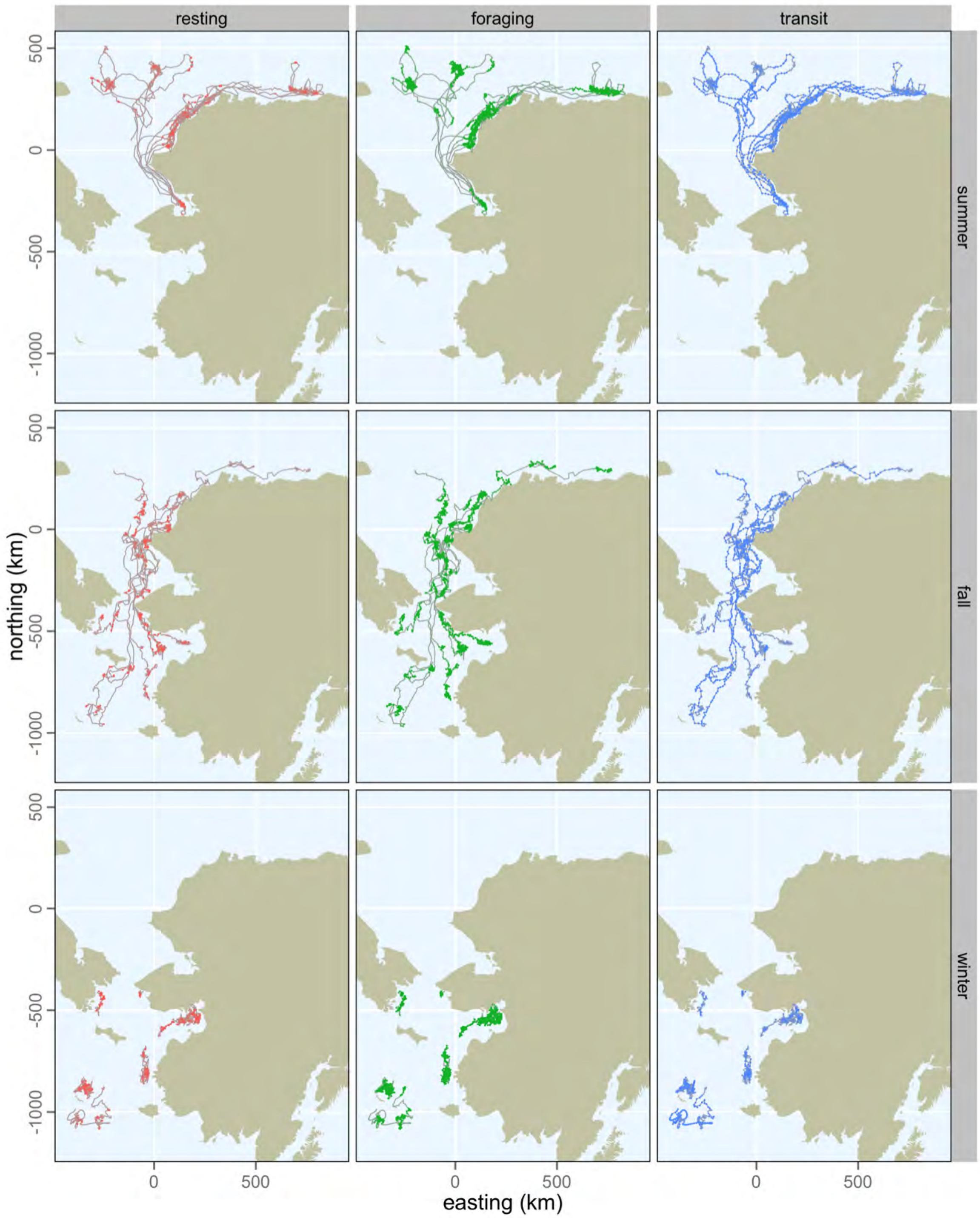

Figure 11. Modeled tracks of bearded seals tagged with SDRs, in the summer (June-September), fall (October-December), and winter (January-April). The behavior states (resting, foraging and transit) were estimated from reported locations and maximum dive depths using a multi-state random walk model that allows for transitions between behavior states as the seals are affected by their internal and environmental conditions.

Winter site fidelity

As shown in Figure 6, bearded seals tagged during June and July in Kotzebue Sound, Alaska move south into, and reside amidst the Bering Sea pack ice in winter (January-May). A plot of all winter locations reported by ARGOS from both the Mk10 and SPOT SDRs is presented in Figure 12 and a plot of the minimum convex polygons encompassing these points is shown in Figure 13. SPOT tags are attached to a flipper and so provide location data for multiple winters (although the seal must be hauled out of the water). As such, these plots include SPOT tag derived locations for all successive winters after tagging (e.g., winters in 2010, 2011 and 2012 for seals tagged in 2009). The relatively small area of the minimum convex polygons suggests that bearded seals do indeed exhibit fidelity to a specific location in winter year-after-year. Figure 14, shows the minimum convex polygons of only the SPOT tag derived winter locations of the three males tagged in 2009 by individual and season. Each seal returned, year-after-year to a small but distinct area. Two individuals occupied regions in close proximity to one another in eastern Norton Sound, while the third inhabited a small area east-southeast of St. Matthew Island. To investigate the importance of habitat, we plotted the polygons from Figure 13 onto a map (Figure 15) showing the April sea ice concentration of the Bering Sea averaged over all years from 1979 to 2012 (Stroeve 2003). The minimum convex polygons of most individuals overlap with areas of historically lower ice concentrations relative to other areas nearby.

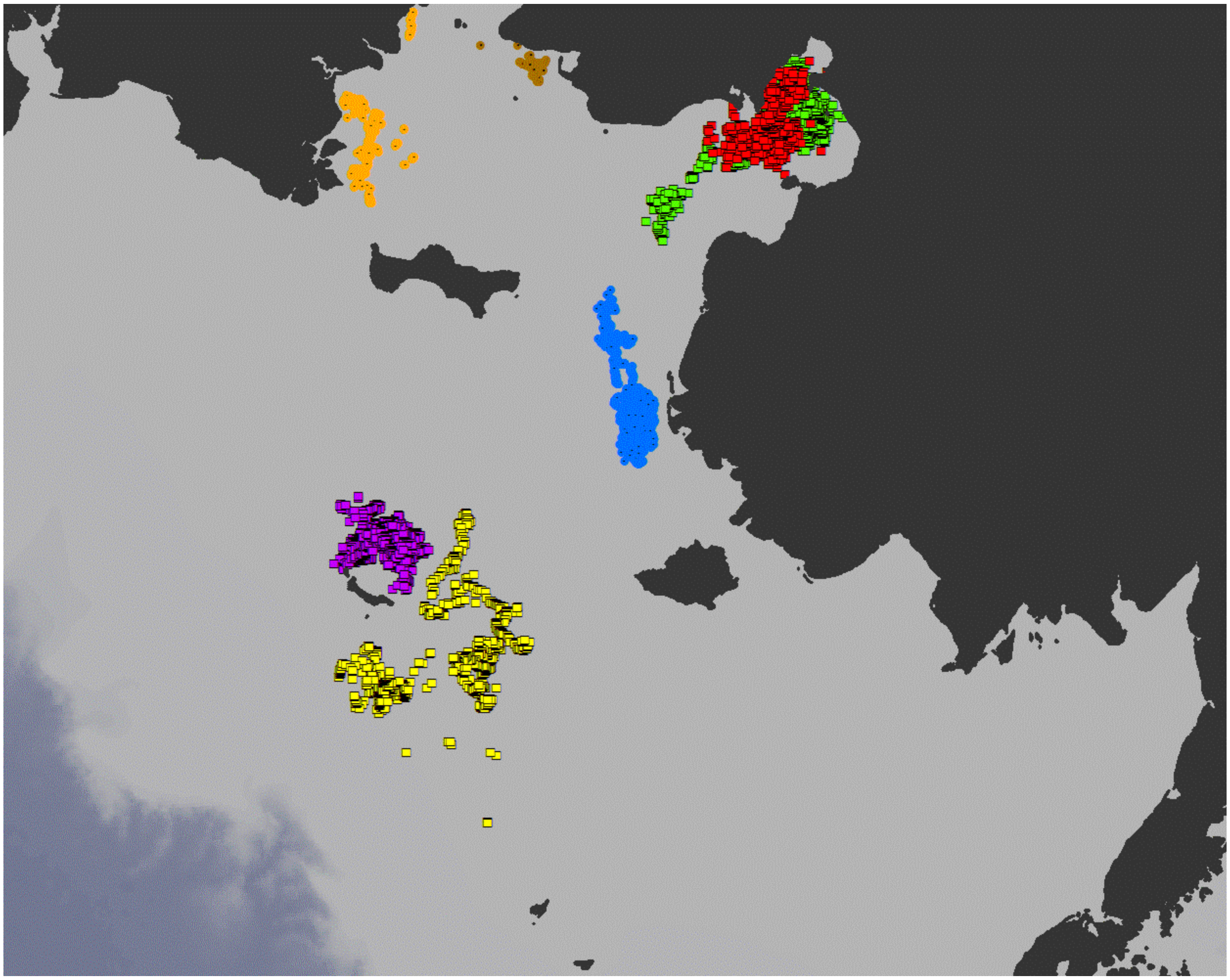

Figure 12. Map of the 2010, 2011 and 2012 winter (January-April) locations of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

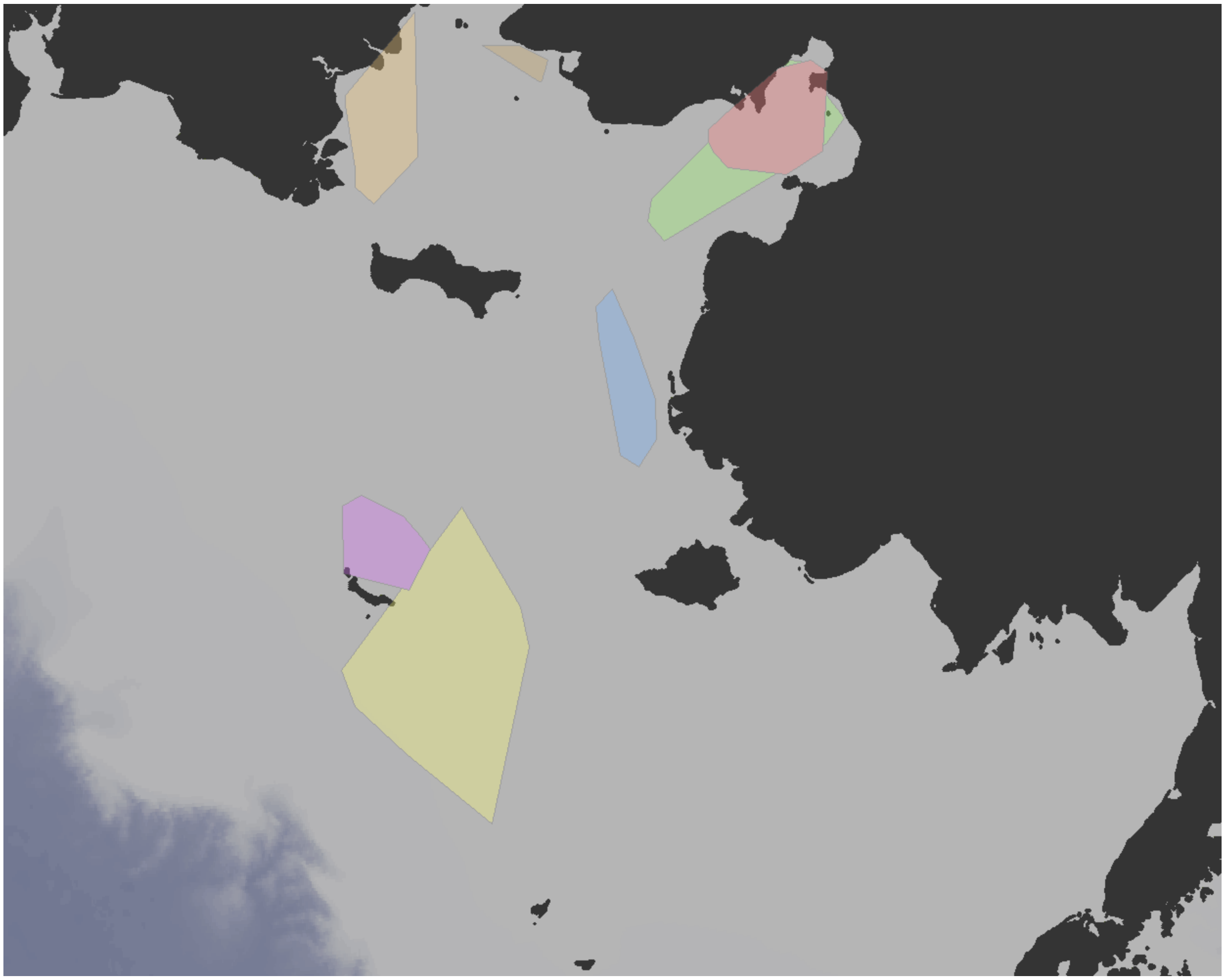

Figure 13. Map of the minimum convex polygons encompassing the 2010, 2011 and 2012 winter (January-April) locations of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003.

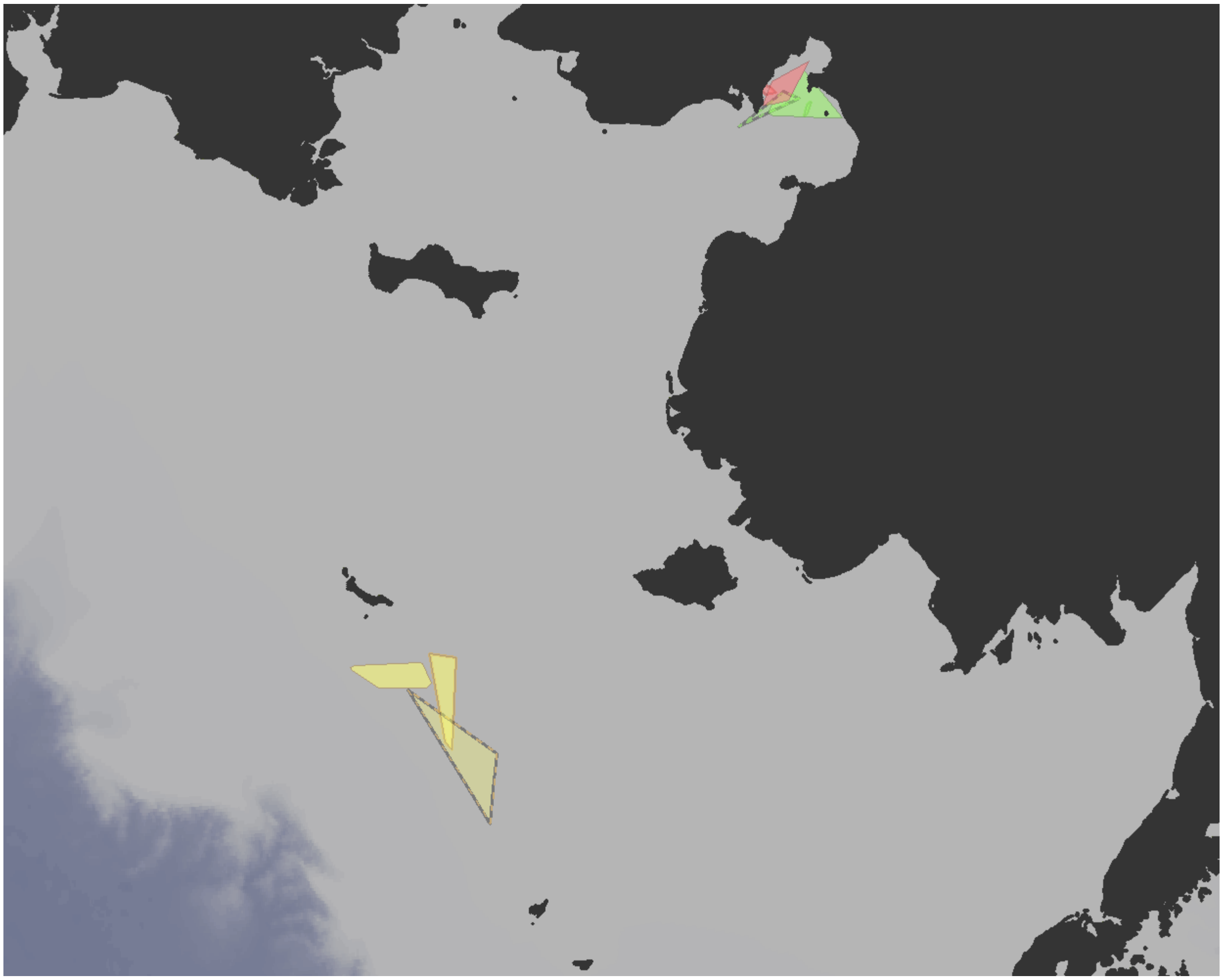

Figure 14. Map of the minimum convex polygons encompassing the successive winter (January-April) locations in 2010 – 2012 of bearded seals captured and tagged during 2009 in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002. Only locations from flipper-mounted SPOT tags were used to derive the polygons and their border (i.e., thin, thick or dashed outline) indicates the year (i.e., 2010, 2011 and 2012 respectively).

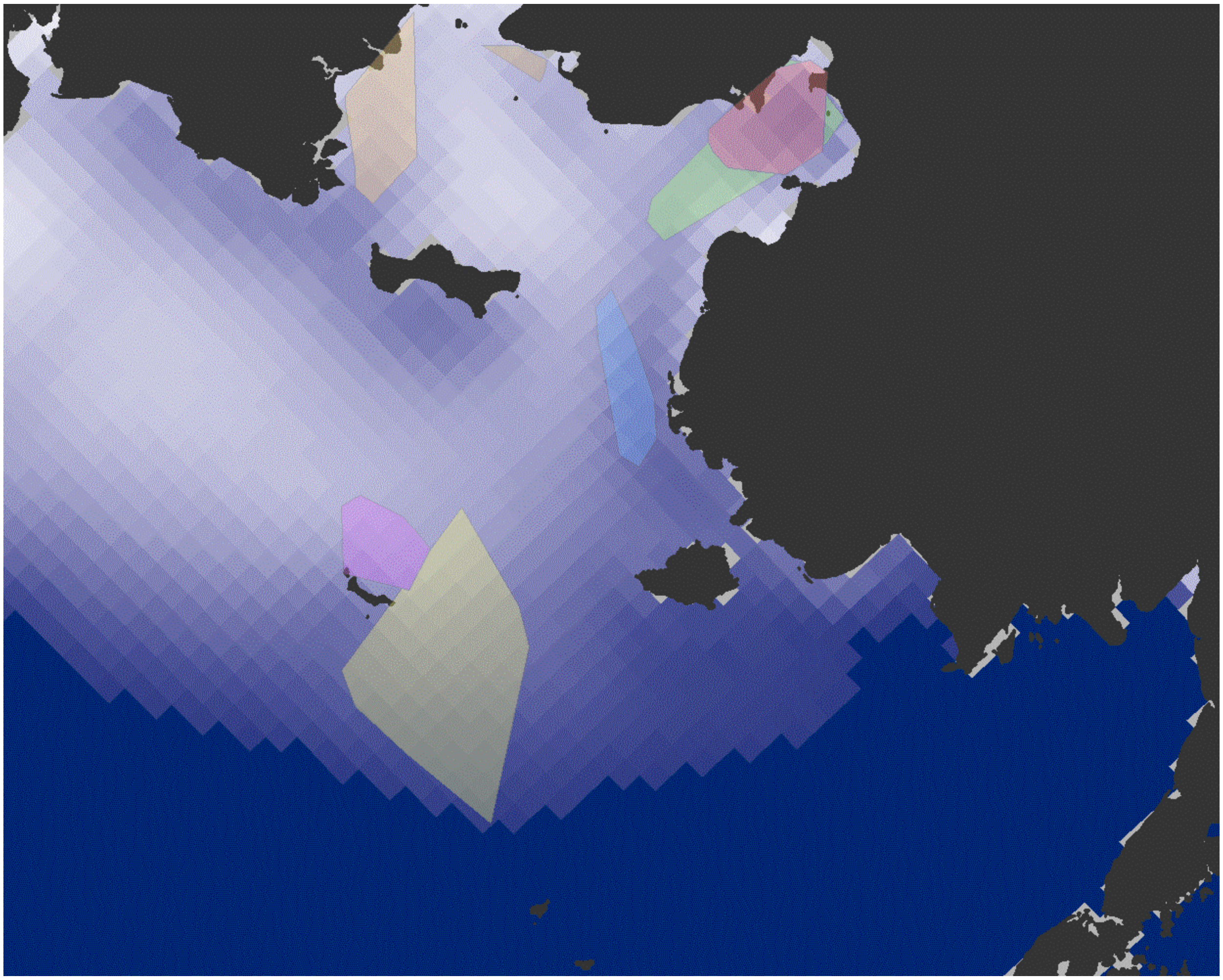

Figure 15. Map of the minimum convex polygons encompassing the 2010, 2011 and 2012 winter (January-April) locations of bearded seals captured and tagged in Kotzebue Sound, AK. Green=EB2009_3000; Red=EB2009_3001; Yellow=EB2009_3002; Blue=EB2011_3000; Orange=EB2011_3001; Purple=EB2011_3002; Brown=EB2012_3003. The polygons are overlaid on a map depicting the average sea ice concentration in April from 1979 to 2012 (white grid cells denote areas with 100% sea ice concentration and dark blue indicates open water).

Objective 3: Develop a haul-out correction factor for aerial surveys

The patterns in the timing of hauling out were similar for seals tagged in 2009 and 2011. When the seals occupied areas with sea ice in July, they hauled out for up to 38 hours, but in August – October they hauled out very little or not at all. Interestingly, even in areas of abundant sea ice in winter, the seals rarely hauled out, preferring instead to remain in the water, perhaps for foraging or thermoregulatory reasons. Comparison of the wet/dry time lines from the head mounted and the flipper mounted SDRs indicated that all seals tended to spend several hours in the late evenings, resting at the surface (i.e., with the head frequently exposed but the rear flippers submerged). Later, in winter and early spring, despite the presence of sea ice, haul-out bouts increased in frequency and duration, but it was still relatively rare for the seals to haul out onto the ice.

The fitted surface showing the hourly probabilities for an adult bearded seal (i.e., with a random effect of 0) to be hauled out of the water (i.e., available to be observed and counted in an abundance survey) from mid-June through March is shown in Figure 16, with a plot of uncertainty associated with these predictions shown in Figure 17. From July through November, adult bearded seals rarely haul out of the water. This is likely related to the paucity of a suitable platform, in the form of sea ice, over the shallow waters of the Bering and Chukchi Sea shelf during these months. As the ice returns to areas occupied by bearded seals in late-fall, bearded seals begin to haul out onto the ice in increasing numbers in the evening (note: local solar noon is at approximately 16:00 Hawaii/Aleutian time (UTC-10), perhaps reflective of preparations for whelping and nursing pups and for setting up breeding territories.

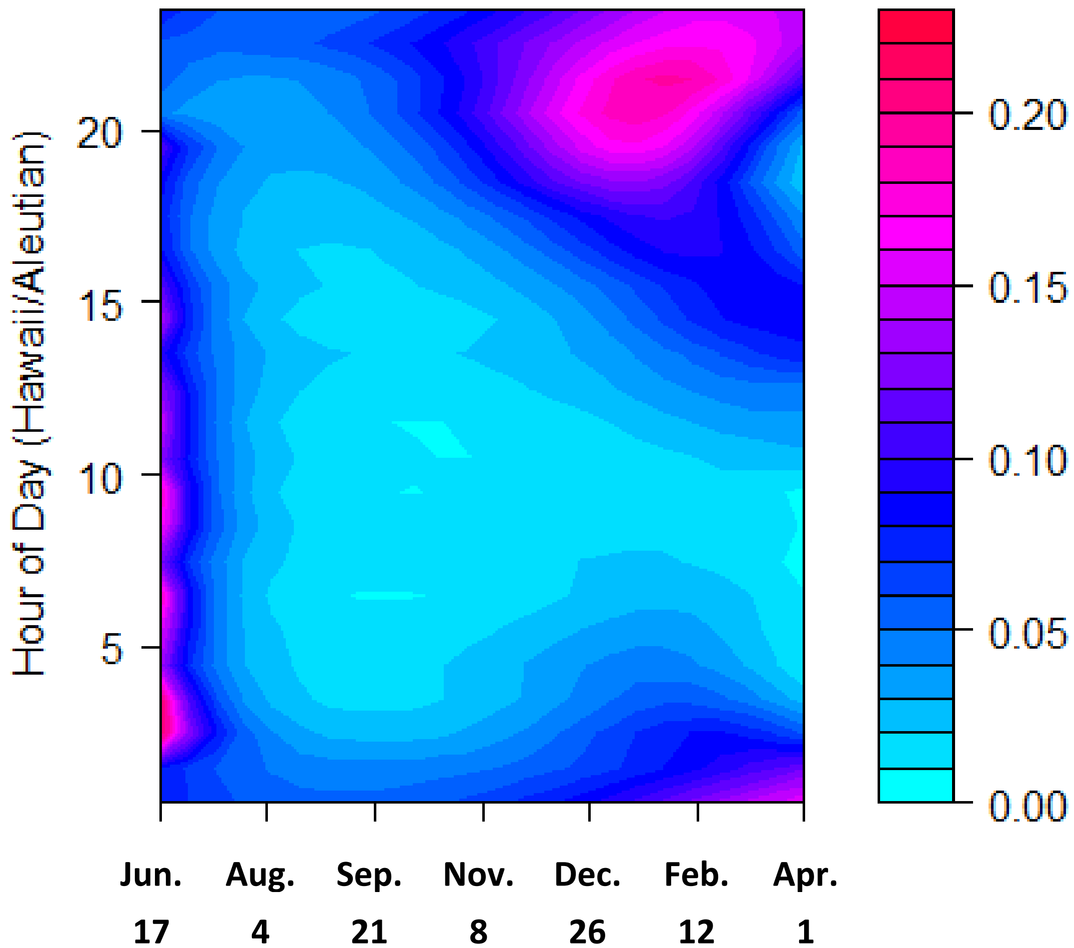

Figure 16. Estimated probability of haul-out (satellite transmitter dry for ≥ 50% of an hour) for adult bearded seals, as predicted from a generalized linear mixed model with temporal autocorrelation fitted to satellite telemetry records.

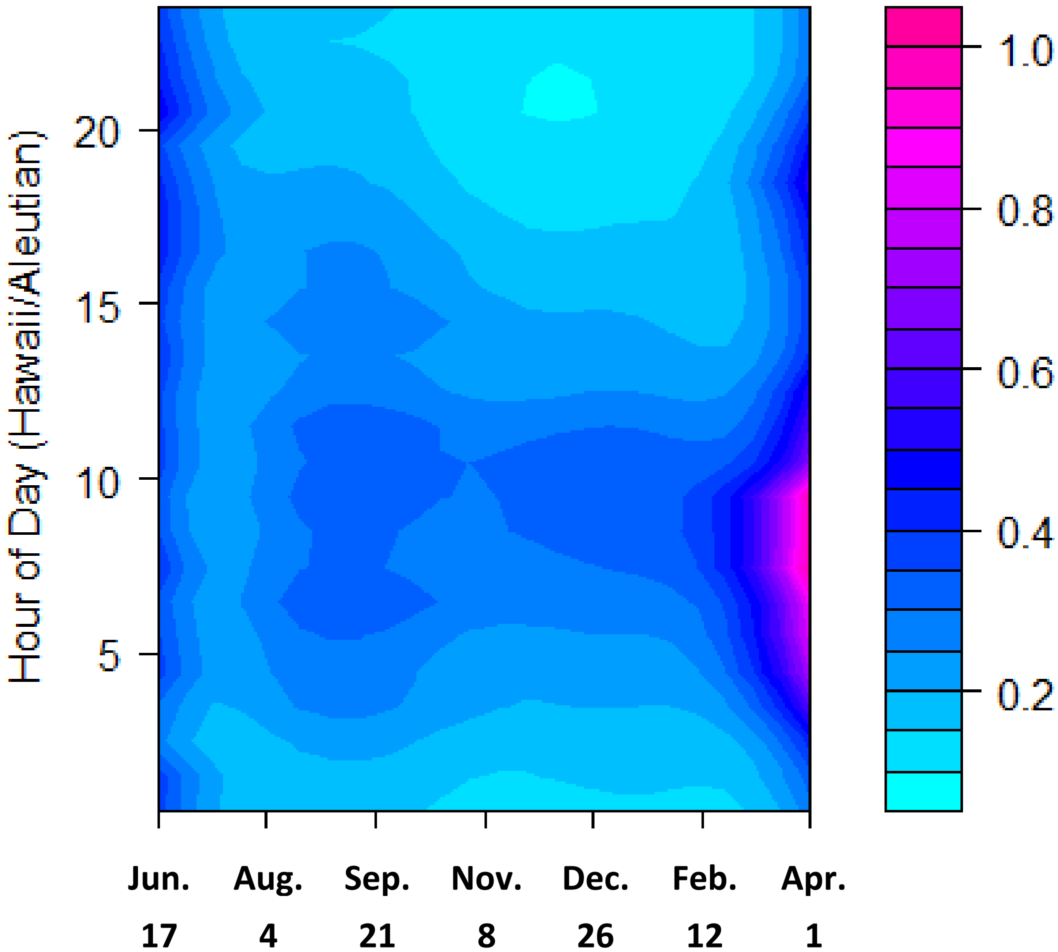

Figure 17. Coefficient of variation (CV=SE/Mean) for haul-out predictions of adult bearded seals as a function of day and hour.

DISCUSSION

Despite the relatively small number of seals tagged to date, several conclusions can be drawn, providing novel insights to the understanding of the ecology of bearded seals in the Chukchi, Beaufort, and Bering seas:

Objective 1: Describe seasonal movements and dive behavior

The bearded seals found in Kotzebue Sound during late June are 'Bering Sea' bearded seals, enroute to open-water summer foraging grounds in the Chukchi and Beaufort seas. In other words, these are bearded seals associated with a population or sub-population that winters and breeds in the Bering Sea, but makes extensive seasonal use of the Arctic seas to the north. Aerial surveys and recent, preliminary abundance estimates for Bering Sea bearded seals (NMML unpublished data) indicate that this population may compose a large and significant fraction of the bearded seals found in Alaska waters. These observations illustrate important linkages between the ecology of the Bering, Chukchi, and Beaufort Seas. The status and fate of the species in a changing and increasingly developed Arctic depend upon the well being of both the sub-Arctic Bering Sea ecosystem and the Arctic Chukchi and Beaufort ecosystems. Accordingly, the nutritional and cultural well being of the communities that harvest bearded seals are also inextricably linked; what happens in the Arctic is important to Bering Sea communities, and vice-versa.

Bearded seals are viable subjects for long-term satellite telemetry studies using flipper-mounted transmitters. Our records of more than 1000 days duration are the longest of which we are aware for any pinniped. Although the data from flipper mounted tags are of coarse temporal resolution, they can be very revealing for certain aspects of ecology and behavior, such as the winter site fidelity documented here. We are continuing to investigate the reason(s) for the failure of the conductivity (i.e., haul-out) sensors of these instruments to reliably discern the submerged state after several months of deployment. Long-term haul-out records to accompany the seasonal movement and site fidelity results would be extremely valuable for assessment of population abundance and monitoring of responses to a diminishing sea-icescape from disruption of the climate.

Recognizing that a study of bearded seal vocalizations captured by acoustic recorders could be useful as context for interpreting the results of this and future satellite telemetry studies on bearded seals, some of the funds from this grant were used to support a study of acoustic recordings of bearded seas in the

Bering, Chukchi and Beaufort Seas. The full peer-reviewed and published article (MacIntyre et al. 2013), describing this project is included in Appendix 1.

Objective 2: Identify specific marine habitats in the Chukchi Sea Planning Area

Multi-state movement and behavior modeling

Bearded seals from the Bering Sea make extensive use of the shallow waters of the Chukchi Sea in summer, not only along the coast but offshore, as well. Analysis of patterns in the diving behavior recorded by our satellite tags will help to document the areas that appear to be most important. Integration of these data with biological and oceanographic data related to bearded seal prey will help to determine the factors that are most important in defining bearded seal habitat. A larger sample of individuals, and a sample that includes bearded seals from the portion that winters and breeds in the Chukchi and Beaufort seas, will be needed for more comprehensive identification of important summer and autumn foraging habitats and to make general inference about the population as a whole. In the interim, however, areas that were heavily used by the bearded seals tagged in this study should be considered as a minimum representation of the habitat that is likely to be important for the population as a whole.

Winter site-fidelity

Bering Sea bearded seal males exhibit strong winter site fidelity, apparently establishing their preferred sites even as sub-adults. The two sub-adult males tagged in 2009 were, in the winter of 2012 after nearly three years had elapsed, likely to be full adults. Their lengths (prone, nose to tail) at tagging were 182 cm (EB2009_3000) and 195 cm (EB2009_3002). Quakenbush et al. (2010) found that Alaska bearded seals collected in recent decades were, on average, in this length range when they were 2 - 4 years of age. Therefore, the ages of these two seals at the end of our study were likely in the range of 5 - 7 years. Quakenbush et al. (2010) found that the average age of maturation for females is about 4 years; males were not analyzed for maturity, but they probably mature about 1 - 2 years later than females (McLaren 1958, Tikhomirov 1966, Burns 1967, Burns and Frost 1979, Andersen et al. 1999). Taken together, our results indicate that the winter sites occupied by sub-adult male bearded seals persist into adulthood.

Site fidelity of male bearded seals was suggested to occur based on consistent patterns in vocalizations observed in more than one year at the same sites in the eastern Beaufort Sea (Cleator et al. 1989). Examination of a series of recordings made near Barrow, Alaska between 1985 and 2001 confirmed that some males have long-term fidelity to breeding sites; tenures covering the entire 16-year study period were observed (Van Parijs and Clark 2006). Our results corroborate the prevalence of site fidelity in male bearded seals, and extend the finding to the Bering Sea. They also confirm this behavior independently from vocalization studies, by following individual seals over multiple years.

The typical precision of Argos satellite geolocation by our SPOT5 flipper-mounted tags did not allow us to investigate whether male bearded seals in the Bering Sea exhibit both territorial and roaming behavior during the breeding season, as has been documented elsewhere (Van Parijs et al. 2003, Van Parijs and Clark 2006). Likewise, the size of the convex hulls we used to portray the wintering areas of our tagged seals cannot meaningfully be compared with the territory sizes that have been reported from more means of location used by (Van Parijs et al. 2003, Van Parijs and Clark 2006).

Because female bearded seals are not known to vocalize and to be included in the acoustic studies of breeding behavior, the degree to which they exhibit winter site fidelity is undetermined. The use of long-term satellite telemetry has the potential to resolve this. However, at the conclusion of our study, no 2013 winter locations had been received from the two females tagged in 2011 for confirmation of whether they also exhibited winter site fidelity similar to males. Similarly, the lone female tagged in 2012 will not provide evidence for female site fidelity until and unless locations are received from her during 2014 in the same area in which she spent the winter of 2013.

Fidelity to natal, breeding, and foraging sites can be extremely significant for many important ecological and demographical aspects such as geographic population structure, and individual fitness (e.g., Kelly et al. 2010, Authier et al. 2012, Hoffman and Forcada 2012). One important aspect for bearded seals in the Bering Sea that warrants further investigation is the degree to which strong breeding site fidelity may reduce the resilience of this species to rapid decreases in extent of sea ice, anticipated to occur from the ongoing climate disruption and warming.

The sample size achieved in this study, and the geographic limitation of the tagging sites to Kotzebue Sound, must be considered for inference about wintering areas for the bearded seal population as a whole. We note that none of the tagged seals have wintered in an area southwest of St. Lawrence Island that was observed to be a major concentration of bearded seals during aerial surveys in April – May of 2007 and 2008 (Cameron and Boveng 2007, Cameron et al. 2008). The wintering areas of the 7 bearded seals tagged in this study were distributed throughout most other regions of the Bering Sea that are characteristically covered with broken, drifting ice of moderate concentration during the winter months.

That none of the tagged individuals were associated with the area southwest of St. Lawrence Island may simply be a matter of the limited sample size. Clearly, our results leave open the question of whether bearded seals that winter and breed north of Bering Strait are different from Bering Sea bearded seals in the ecology of their summer and autumn use of the Chukchi and Beaufort seas. This should be a high priority for future research on bearded seals in Alaska waters.

Objective 3: Develop a haul-out correction factor for aerial surveys

The apparent bio-fouling or drift of the SPOT tag conductivity sensors has not been observed in SDR records from other seal species; further investigation of this phenomenon and a possible solution is under way. Discussions with the tag manufacturer indicate that the problem may be resolved, either by selection of different materials for the conductivity sensors or modifying the tag software to adaptively adjust the conductivity threshold to changes in the surface properties of the sensors. Assuming that this problem can be overcome, bearded seal haul-out data, for ecological studies and population assessment, could be collected over long time intervals to provide insight into the longitudinal (i.e., within individual) variability in haul-out patterns and time budgets.

Lacking reliable haul-out data from the SPOT tags, we were limited to analysis of data from the head-mounted SDRs, which mostly ceased providing data just prior to the normal seasonal period in which aerial surveys should be conducted for bearded seals (approximately mid-April through May). The extent to which the results from these head-mounted tags can be extrapolated to the aerial survey period will be investigated by comparing the diel pattern in the haul-out data from April with diel patterns in bearded seal detections from aerial surveys conducted in April - May. Differences in these patterns would suggest that the haul-out data may not be applicable for aerial survey correction; similarity in the patterns would suggest that the haul-out data are useful at least for reducing variability in survey counts from time-of-day effects, though it would not necessarily confirm applicability of the average magnitude of correction. Acquisition of reliable haul-out data for bearded seals remains a high priority for research and monitoring.

ACKNOWLEDGMENTS

In addition to the investigators and project coordinators with the Kotzebue IRA and North Slope Borough, we would like to acknowledge the field assistance of Gavin Brady, Shawn Dahle, John Jansen and Heather Ziel from the NMML; James Adams, Jeff Barger, David Barr, Wendell Booth, Frank Garfield, Henry Goodwin, Pearl Goodwin, Brett Kirk, Noah Naylor, Virgil Naylor Jr., Virgil Naylor Sr., Allen Stone and Randy Toshavik from Kotzebue, Alaska; Billy Adams, Mary-Ellen Ahmaogak, James Aiken, Tim Aiken, Howard Kittick, Gilbert Leavitt, Isaac Leavitt, J.R. Leavitt, Shawn Oktollik, Stacey Osborn, Fred Rexford, Bob Shears and Joe Skin from the North Slope borough, Alaska; James Bailey, Sarah Coburn and Scott Gende. The National Park Service, Noatak National Preserve Office also provided key logistical support by facilitating field team housing in Kotzebue, Alaska.

PRESENTATIONS, SIGNIFICANT MEETINGS, AND PUBLICATIONS

January 11-14, 2010 – Barrow and Wainwright, AK – The NMML met with Alaska Native subsistence hunters in Wainwright and Barrow, AK, and representatives from the North Slope Borough to discuss the possibility of initiating a tagging project near Barrow and/or Wainwright in late-June and early-July of 2010. The discussions were well received and they confirmed general support from the communities. The North Slope Fish and Game Management Committee voted to support the research and the North Slope Borough agreed to act as the local organizing group with responsibilities to administer funds, designate a Co-Investigator and Field Project Leader.

January 18-22, 2010 – Anchorage, AK - The NMML presented overviews of the research goals, details of the initial pilot study and preliminary results in a oral presentation titled "Seasonal movements, habitat selection, foraging and haul-out behavior of adult bearded seals" and a poster of preliminary results from bearded seal tissue analyses titled "Hemoglobin and packed-cell volume of ribbon, spotted and bearded seals in Alaska" at the Alaska Marine Science Symposium.

March 22-24, 2010 – Anchorage, AK –NMML presented a summary of the pilot study in an oral presentation at the NMFS Open Water Meeting.

June 7-9, 2010 – Barrow and Wainwright, AK – The NMML met with Alaska Native subsistence hunters and representatives from the North Slope Borough to finalize arrangements for the 2010 field season in the region.

November 16-18, 2010 – Anchorage, AK - The NMML presented a summary of the project's progress to date of in an oral presentation to the Alaska Native Ice Seal Committee.

January 18-19, 2011 – Anchorage, AK – The NMML met with representatives from the Native Village of Kotzebue and the North Slope Borough to discuss details of plans for field work during June-July, 2011.

July 11-14, 2011 – Fairbanks, AK – The NMML presented a summary of the project's progress to date of in an oral presentation to the Alaska Native Ice Seal Committee.

November 28-December 2, 2011 – Tampa Bay, FL – The NMML presented preliminary results of an analysis to estimate the abundances of seals in the Bering Sea titled "Abundances of three ice-associated seal species in the Eastern Bering Sea" at the Society of Marine Mammalogy's 19th Biennial

Conference. The analysis incorporated data on the timing of haul out that was collected by SDRs attached to bearded seals in 2009.

January 16-19, 2012 – Anchorage, AK - The NMML presented a poster titled “Seasonal migration of bearded seals between intensive foraging patches” at the Alaska Marine Science Symposium.

January 19-20, 2012 – The NMML presented a project update in an oral presentation to the Alaska Native Ice Seal Committee.

January 24-27, 2012 – Anchorage, AK – The NMML presented an overview of the project to the U.S. Marine Mammal Commission, 50th Annual Meeting.

January 21-25, 2013 – Anchorage, AK - The NMML made an oral presentation titled “Winter site fidelity of bearded seals in the Bering Sea” at the Alaska Marine Science Symposium.

January 24-25, 2013 – The NMML presented a project update in an oral presentation to the Alaska Native Ice Seal Committee.

February 12-13, 2013 – The NMML made an oral presentation titled “Winter site fidelity of bearded seals in the Bering Sea” to the Marine Mammal Hunters meetings in Savoonga and Gambell, Alaska.

March 21, 2013 – The NMML made an oral presentation titled “Winter site fidelity of bearded seals in the Bering Sea” to the Western Alaska Integrated Science Conference in Nome, Alaska.

In addition to these official presentations, NMML has regularly emailed a map of the recent movements of any instrumented bearded seals still transmitting to a growing distribution list since July 1, 2009.

Descriptions of the project, maps and other information are also reported on the following websites:

http://www.kotzebueira.org

http://www.afsc.noaa.gov/nmml/species/species_bearded.php

MacIntyre, K. Q., K. M. Stafford, C. L. Berchok, and P. L. Boveng. 2013. Year-round acoustic detection of bearded seals (*Erignathus barbatus*) in the Beaufort Sea relative to changing environmental conditions, 2008–2010. Polar Biology:1-13.

LITERATURE CITED

Andersen, M., A. M. Hjelset, I. Gjertz, C. Lydersen, and B. Gulliksen. 1999. Growth, age at sexual maturity and condition in bearded seals (*Erignathus barbatus*) from Svalbard, Norway. Polar Biology **21**:179-185.

Authier, M., I. Bentaleb, A. Ponchon, C. Martin, and C. Guinet. 2012. Foraging fidelity as a recipe for a long life: foraging strategy and longevity in male southern elephant seals. PLoS ONE **7**:e32026.

Bengtson, J. L., L. M. Hiruki-Raring, M. A. Simpkins, and P. L. Boveng. 2005. Ringed and bearded seal densities in the eastern Chukchi Sea, 1999-2000. Polar Biology **28**:833-845.

Benjaminsen, T. 1973. Age determination and the growth and age distribution from cementum growth layers of bearded seals at Svalbard. Fiskeridirektoratets Skrifter. Serie Havundersoekelser **16**:159-170.

Braham, H. W., J. Burns, J., G. A. Fedoseev, and B. D. Krogman. 1981. Distribution and density of ice-associated pinnipeds in the Bering Sea. to be published 1981/1982 as a book, NOAA, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, National Marine Mammal Laboratory, Seattle, WA.

Burns, J. J. 1967. The Pacific bearded seal. Alaska Department of Fish and Game, Juneau, AK.

Burns, J. J. 1981. Bearded seal *Erignatus barbatus* Erxleben, 1777. Pages 145-170 *in* S. H. Ridgway and R. J. Harrison, editors. Handbook of Marine Mammals Volume 2: Seals. Academic Press, New York, NY.

Burns, J. J. 2002. Arctic marine mammals. Pages 39-45 *in* W. F. Perrin, B. G. Wursig, and J. G. M. Thewissen, editors. Encyclopedia of Marine Mammals. Academic Press, San Diego, CA.

Burns, J. J. and K. J. Frost. 1979. The natural history and ecology of the bearded seal, *Erignathus barbatus*. Alaska Department of Fish and Game, Fairbanks, Alaska.

Burns, J. J. and S. J. Harbo. 1977. An aerial census of spotted seal, *Phoca vitulina largha*, and walruses, *Odobenus rosmarus*, in the ice front of Bering Sea. Pages 58-132 Environmental Assessment of the Alaskan Continental Shelf. Quarterly Reports of Principal Investigators April-June 1977. Volume 1. U.S. Department of Commerce, NOAA and the U.S. Department of Interior, Bureau of Land Management, Boulder, CO.

Cameron, M. and P. Boveng. 2007. Abundance and distribution surveys for ice seals aboard USCG *Healy* and the *Oscar Dyson,* April 10-June 18, 2007. Alaska Fisheries Science Center Quarterly Report, April-May-June 2007:12-14.

Cameron, M. and P. Boveng. 2009. Habitat use and seasonal movements of adult and sub-adult bearded seals. Alaska Fisheries Science Center Quarterly Report, October-November-December 2009:1-4.

Cameron, M., E. Moreland, and P. Boveng. 2008. Abundance and distribution surveys for ice seals conducted from the USCG icebreaker *Polar Sea,* April 6-April 27, 2008. Alaska Fisheries Science Center Quarterly Report, April-May-June 2008:20-21.

Cameron, M. F. 2005. Habitat use and seasonal movements of bearded seals in Kotzebue Sound, Alaska. Alaska Fisheries Science Center Quarterly Research Report, October-November-December 2004:18.

Cameron, M. F. 2006. Habitat use and seasonal movements of bearded seals in Kotzebue Sound, Alaska. Alaska Fisheries Science Center Quarterly Research Report, October-November-December 2005:18-19.

Chapskii, K. K. 1938. The bearded seal (*Erignathus barbatus* Fabr.) of the Kara and Barents seas. Pages 7-70 Game mammals of the Barents and Kara Seas. Arctic Institute Glavsevmorputi, Leningrad, USSR.

Chapskii, K. K. 1955. An attempt at revision of the systematics and diagnostics of seals in the subfamily Phocinae. Trudy Zoologicheskovo Instituta Akademii Nauk SSSR **17**:160-199.

Cleator, H. J., I. Stirling, and T. G. Smith. 1989. Underwater vocalizations of the bearded seal (*Erignathus barbatus*). Canadian Journal of Zoology **67**:1900-1910.

Dorfman, R. 1938. A note on the delta-method for finding variance formulae. The Biometric Bulletin **1**:129-137.

Fay, F. H. 1974. The role of ice in the ecology of marine mammals of the Bering Sea. Pages 383-399 *in* D. W. Hood and E. J. Kelley, editors. Oceanography of the Bering Sea. Institute of Marine Science, Hakodate, Japan.

Fedoseev, G. A. 1965. The ecology of the reproduction of seals on the northern part of the Sea of Okhotsk. Izvestiya TINRO **65**:212-216.

Fedoseev, G. A. 1984. Population structure, current status, and perspective for utilization of the ice-inhabiting forms of pinnipeds in the northern part of the Pacific Ocean Pages 130-146 *in* A. V. Yablokov, editor. Marine Mammals. Nauka, Moscow, Russia.

Fedoseev, G. A. 2000. Population biology of ice-associated forms of seals and their role in the northern Pacific ecosystems. Center for Russian Environmental Policy, Russian Marine Mammal Council, Moscow, Russia.

Feltz, E. T. and F. H. Fay. 1966. Thermal requirements in vitro of epidermal cells from seals. Cryobiology **3**:261-264.

Finley, K. J. and W. E. Renaud. 1980. Marine mammals inhabiting the Baffin Bay north water in winter. Arctic **33**:724-738.

Fiscus, C. H. and H. W. Braham. 1976. Baseline characterization: marine mammals.

Frost, K. J., M. F. Cameron, M. Simpkins, C. Schaeffer, and A. Whiting. 2005. Diving behavior, habitat use, and movements of bearded seal (*Erignathus barbatus*) pups in Kotzebue Sound and Chukchi Sea. Pages 98-99 Proceedings of the Sixteenth Biennial Conference on the Biology of Marine Mammals. Society for Marine Mammalogy, San Diego, CA.

Frost, K. J., A. Whiting, M. F. Cameron, and M. A. Simpkins. 2008. Habitat use, seasonal movements and stock structure of bearded seals in Kotzebue Sound, Alaska. Tribal Wildlife Grants Program, Fish and Wildlife Service, Achorage, AK.

Gjertz, I., K. M. Kovacs, C. Lydersen, and Ø. Wiig. 2000. Movements and diving of bearded seal (*Erignathus barbatus*) mothers and pups during lactation and post-weaning. Polar Biology **23**:559-566.

Heptner, L. V. G., K. K. Chapskii, V. A. Arsen'ev, and V. T. Sokolov. 1976. Bearded seal. *Erignathus barbatus* (Erxleben, 1777). Pages 166-217 *in* L. V. G. Heptner, N. P. Naumov, and J. Mead, editors. Mammals of the Soviet Union. Volume II, Part 3--Pinnipeds and Toothed Whales, Pinnipedia and Odontoceti. Vysshaya Shkola Publishers, Moscow, Russia.

Hoffman, J. I. and J. Forcada. 2012. Extreme natal philopatry in female Antarctic fur seals (*Arctocephalus gazella*). Mammalian Biology **77**:71-73.

Johnson, M. L., C. H. Fiscus, B. T. Ostenson, and M. L. Barbour. 1966. Marine mammals. Pages 877-924 *in* N. J. Wilimovsky and J. N. Wolfe, editors. Environment of the Cape Thompson Region, Alaska. U.S. Atomic Energy Commission, Oak Ridge, TN.

Jonsen, I. D., J. M. Flemming, and R. A. Myers. 2005. Robust state-space modeling of animal movement data. Ecology **86**:2874-2880.

Kelly, B. P. 1988. Bearded seal, *Erignathus barbatus*. Pages 77-94 *in* J. W. Lentifer, editor. Selected Marine Mammal Species of Alaska: Species Accounts with Research and Managment Recommendations. Marine Mammal Commission, Washington, D.C.

Kelly, B. P., O. H. Badajos, M. Kunnasranta, J. R. Moran, M. Martinez-Bakker, D. Wartzok, and P. Boveng. 2010. Seasonal home ranges and fidelity to breeding sites among ringed seals. Polar Biology **33**:1095-1109.

Kingsley, M. C. S., I. Stirling, and W. Calvert. 1985. The distribution and abundance of seals in the Canadian high Arctic, 1980-82. Canadian Journal of Fisheries and Aquatic Sciences **42**:1189-1210.

Kosygin, G. M. 1971. Feeding of the bearded seal *Erignathus barbatus nauticus* (Pallas) in the Bering Sea during the spring-summer period. Izvestiya TINRO **75**:144-151.

Kovacs, K. M. 2002. Bearded seal *Erignathus barbatus*. Pages 84-87 *in* W. F. Perrin, B. Würsig, and J. G. M. Thewissen, editors. Encyclopedia of Marine Mammals. Academic Press, San Diego, CA.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute Inc., Cary, NC.

Lydersen, C. and K. M. Kovacs. 1999. Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. Marine Ecology Progress Series **187**:265-281.

MacIntyre, K. Q., K. M. Stafford, C. L. Berchok, and P. L. Boveng. 2013. Year-round acoustic detection of bearded seals (*Erignathus barbatus*) in the Beaufort Sea relative to changing environmental conditions, 2008–2010. Polar Biology:1-13.

McClintock, B. T., R. King, L. Thomas, J. Matthiopoulos, B. J. McConnell, and J. M. Morales. 2012. A general discrete-time modeling framework for animal movement using multistate random walks. Ecological Monographs **82**:335-349.

McClintock, B. T., D. J. F. Russell, J. Matthiopoulos, and R. King. *In Press*. Combining individual animal movement and ancillary biotelemetry data to investigate population-level activity budgets. Ecology.

McLaren, I. A. 1958. Some aspects of growth and reproduction of the bearded seal, *Erignathus barbartus* (Erxleben). Journal of the Fisheries Research Board of Canada **15**:219-227.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsiner, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology **85**:2436-2445.

Nelson, R. K. 1981. Harvest of the sea: coastal subsistence in modern Wainwright. North Slope Borough, Coastal Management Program, North Slope Borough, Alaska.

Nelson, R. R., J. J. Burns, and K. J. Frost. 1984. The bearded seal (*Erignathus barbatus*). Pages 1-6 *in* J. J. Burns, editor. Marine Mammal Species Accounts, Wildlife Technical Bulletin No. 7. Alaska Department of Fish and Game, Juneau, AK.

Potelov, V. A. 1969. Distribution and migrations of bearded seals in the White, Barents and Kara seas. . Third All-Union Conference on Marine Mammals. Publishing House "Nauka".

Quakenbush, L., J. Citta, and J. Crawford. 2010. Biology of the bearded seal (*Erignathus barbatus*) in Alaska, 1962-2009. Arctic Marine Mammal Program, Alaska Department of Fish and Game, Fairbanks, AK.

Quakenbush, L., J. Citta, and J. Crawford. 2011. Biology of the bearded seal (*Erignathus barbatus*) in Alaska, 1961-2009. Arctic Marine Mammal Program, Alaska Department of Fish and Game, Fairbanks, AK.

R Core Development Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rice, D. W. 1998. Marine mammals of the world: systematics and distribution. Society for Marine Mammalogy, Lawrence, KS.

Rutilevskii, L. G. 1939. Game mammals of Chelyuskin Peninsula and Vil'kits Strait. National Research Institute of Polar Land Use.

Simpkins, M. A., L. M. Hiruki-Raring, G. Sheffield, J. M. Grebmeier, and J. L. Bengtson. 2003. Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska in March 2001. Polar Biology **26**:577-586.

Smirnov, N. 1927. Diagnostical remarks about some seals (Phocidae) of the Northern Hemisphere. Tromsø Museum Årshefte, Tromsø, Norway.

Smith, T. G. 1981. Notes on the bearded seal, *Erignathus barbatus*, in the Canadian Arctic. 0706-6457, Department of Fisheries and Oceans, Arctic Biological Station, Quebec, Canada.

Stirling, I., W. R. Archibald, and D. DeMaster. 1977. Distribution and abundance of seals in the eastern Beaufort Sea. Journal of the Fisheries Research Board of Canada **34**:976-988.

Stirling, I., M. Kingsley, and W. Calvert. 1982. The distribution and abundance of seals in the eastern Beaufort Sea, 1974-79. Environment Canada, Canadian Wildlife Service, Edmonton, Canada.

Stroeve, J. 2003. Sea Ice Trends and Climatologies from SMMR and SSM/I-SSMIS. National Snow and Ice Data Center, Boulder, Colorado USA.

Tarasevich, M. N. 1963. Biology of the bearded seal (*Erignathus barbatus*). Pages 223-225 Proceedings of the Institute of Oceanography. Akademiya nauk SSSR, USSR.

Tikhomirov, E. A. 1966. Reproduction of seals of the family Phocidae in the North Pacific. Zoologicheskii Zhurnal **45**:275-281.

Van Parijs, S. M. and C. W. Clark. 2006. Long-term mating tactics in an aquatic-mating pinniped, the bearded seal, *Erignathus barbatus*. Animal Behaviour **72**:1269-1277.

Van Parijs, S. M., C. Lydersen, and K. M. Kovacs. 2003. Vocalizations and movements suggest alternative mating tactics in male bearded seals. Animal Behaviour **65**:273-283.

Ver Hoef, J. M. 2012. Who invented the delta method? The American Statistician **66**:124-127.

Ver Hoef, J. M., M. F. Cameron, P. L. Boveng, J. M. London, and E. M. Moreland. 2013. A spatial hierarchical model for abundance of three ice-associated seal species in the Eastern Bering Sea. Statistical Methodology.

Ver Hoef, J. M., J. M. London, and P. L. Boveng. 2010. Fast computing of some generalized linear mixed pseudo-models with temporal autocorrelation. Computational Statistics **25**:39-55.

APPENDIX 1. - MacIntyre, et al. 2013. Year-round acoustic detection of bearded seals (Erignathus barbatus) in the Beaufort Sea relative to changing environmental conditions, 2008–2010. Polar Biology:1-13.

Polar Biol
DOI 10.1007/s00300-013-1337-1

ORIGINAL PAPER

Year-round acoustic detection of bearded seals (*Erignathus barbatus*) in the Beaufort Sea relative to changing environmental conditions, 2008–2010

Kalyn Q. MacIntyre · Kathleen M. Stafford · Catherine L. Berchok · Peter L. Boveng

Received: 19 November 2012 / Revised: 20 March 2013 / Accepted: 2 May 2013

Abstract Bearded seals (*Erignathus barbatus*) are pan-Arctic pinnipeds that are often seen in association with pack ice, and are known for their long, loud trills, produced underwater primarily in the spring. Acoustic recordings were collected from August 2008 to August 2010 at two locations and a single year (2008–2009) at a third location, in the western Beaufort Sea. Three recorders in 2008–2009 had a 30 % duty cycle and a bandwidth of 10–4,096 Hz. One recorder in 2009–2010 had a 45 % duty cycle and a bandwidth of 10–4,096 Hz and the second had a 20 % duty cycle and bandwidth of 10–8,192 Hz. Spectrograms of acoustic data were examined for characteristic patterns of bearded seal vocalizations. For each recorder, the number of hours per day with vocalizations was compared with in situ water temperature and satellite-derived daily sea ice concentrations. At all sites, bearded seals were vocally active year-round. Call activity escalated with the formation of pack ice in the winter and the peak occurred in the spring, coinciding with mating season and preceding breakup of the sea ice. There was a change in the timing of seasonal sea ice formation and retreat between the two consecutive years that was reflected in the timing of peak bearded seal call activity. This study provides new information on fall and winter bearded seal vocal behavior and the relationship between year-round vocal activity and changes in annual sea ice coverage and in situ water temperature.

Keywords Bearded seal · *Erignathus barbatus* · Beaufort Sea · Acoustics · Sea ice concentration

K. Q. MacIntyre (✉)
School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat St., Seattle, WA 98105, USA
e-mail: kalyn.macintyre@noaa.gov

K. Q. MacIntyre · C. L. Berchok · P. L. Boveng
National Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115, USA

K. M. Stafford
Applied Physics Laboratory, University of Washington, 1013 NE 40th St., Seattle, WA 98105, USA

Introduction

Climate disruption and warming of the Arctic is causing a rapid shift in environmental stability, especially at high latitudes (Walsh 2008; Maslanik et al. 2011; Timmermans et al. 2011; Woodgate et al. 2012). The increased variability caused by warming challenges the capacity of Arctic species to adapt to these changes (Moore and Huntington 2008). Ice-obligate species such as the polar bear (*Ursus maritimus*), walrus (*Odobenus rosmarus*), ringed seal (*Phoca hispida*), and bearded seal (*Erignathus barbatus)* will have more difficulty adapting to this change than temperate or seasonally migrant species that have the ability to extend their geographic range (Moore and Huntington 2008). Declining seasonal sea ice extent, delayed freeze-up, and accelerated spring breakup are likely to reduce the available habitat for resting, breeding, molting and hunting, posing the greatest threat to the survival of ice-obligate species (Moore and Huntington 2008). Due to the threats posed by diminishing sea ice, the National Oceanic and Atmospheric Administration (NOAA) has proposed that bearded seals and ringed seals be listed as *threatened* under the US Endangered Species Act of 1973 (73 FR 16617).

Bearded seals are a pan-Arctic pinniped widely distributed throughout the northern Bering, Chukchi, and Beaufort Seas (BCB) and are most abundant north of the ice edge zone and south of the Bering Strait (Burns 1981). They maintain a close association with sea ice for critical life history activities, such as reproduction and molting (Burns 1970, 1981; Nelson et al. 1984; Moore and Huntington 2008). In the spring, large numbers of bearded seals move north as the seasonal sea ice retreats and subsequently move south in the autumn/winter as sea ice forms (Potelov 1969; Burns 1981; Simpkins et al. 2003; Frost et al. 2008). Bearded seals occupy spring pack ice (Simpkins et al. 2003) and generally prefer to be near polynyas and other natural openings in sea ice for breathing, hauling out, and access to prey (Nelson et al. 1984; Stirling 1997). Their life histories are linked to seasonal changes in ice conditions; therefore, any extreme variation in their sea ice habitat may have a considerable effect on the persistence of the population. Variability in water temperature and climate patterns may also pose risks for bearded seal populations. The Alaska Coastal Current (ACC) runs along the northwestern Alaskan coast and is composed of warm water intrusions from the Bering and Chukchi Seas (Okkonen et al. 2009). Changes in climate patterns in the Chukchi Sea (e.g., wind) have been shown to influence water temperature flowing through the ACC off Barrow, AK in the summer months. The variability due to wind (storms) as well as water temperatures may impact the distribution of prey or affect the reproductive cycle of marine mammal species (Atkinson 1997; Ashjian et al. 2010).

Bearded seals are highly vocal and use elaborate underwater vocalizations to advertise breeding condition or establish aquatic territories (Van Parijs et al. 2004; Risch et al. 2007). They produce a series of frequency modulated (FM) calls that typically range in frequency from 130 to 4,800 Hz (Ray et al. 1969; Stirling et al. 1983). Captive studies have shown that males are the primary source of underwater vocalizations (Ray et al. 1969; Davies et al. 2006), producing reproductive displays consisting of long loud trills (Van Parijs and Clark 2006). Their predominant call type consists of several variations of a long FM trill in addition to moans and groans. A typical trill will propagate between 5 and 10 km, however, some can propagate more than 20 km and last as long as 3 min (Cleator et al. 1989). Bearded seal vocalizations have been studied in great detail during their reproductive season, which is thought to be roughly April to June (McLaren 1958). However, little information is available for vocalizations produced outside this period, particularly during autumn and winter, during which time bearded seals are believed to be vocally inactive (Van Parijs et al. 2001).

Previous passive acoustic research in the Beaufort Sea focused on the deployment of recorders during the spring months only. Due to increased interest in the Arctic and the effects of climate change on marine mammals in this region, the use of year-round passive acoustic recordings has increased providing long-term data on whale, seal, and human activity in the Bering, Chukchi, and Beaufort Seas (Delarue et al. 2009; Moore et al. 2012; Roth et al. 2012). Here, we present the first year-round recordings of bearded seals at three locations in the Beaufort Sea over a 2-year period and compare these to in situ water temperature and sea ice concentrations around each location. This study demonstrates a tight coupling between the presence of vocally active bearded seals and the condition of their surrounding sea ice habitat and provides new information on the year-round vocal activity of bearded seals in the Beaufort Sea.

Methods

Passive acoustic recorders (Aural-M2, http://www.MultiElectronique.com) were deployed on three subsurface oceanographic moorings (Fig. 1) in the Beaufort Sea over a 2-year period. These instruments recorded in the frequency range 10–4,096 Hz or 10–8,192 Hz (Table 1). Instrument packages were set to record for an entire year, and sampling rates were sufficient for recording a range of acoustic energy from low frequency baleen whale calls to some of the high frequency calls produced by toothed whales. During the first year, three recorders were deployed in August 2008 (A1, A2, A3). Each recorder in 2008–2009 was set to record on a 30 % duty cycle, where the first 9 min out of every 30 min period for each day (24 h) was recorded. All three instruments were recovered in 2009, and two of these were subsequently redeployed (Table 1). The instruments redeployed in August of 2009 were recovered 1 year later. One instrument deployed in 2009–2010 was set to record on a 20 % duty cycle (14 min every hour), while the other was set to 45 % duty cycle (9 min every 20 min). All recorders were suspended 5 m above the seafloor to minimize the risk of disturbance or damage from overhead ice keels. Archived digital acoustic data were downloaded from each recorder. For both years, full 9 or 14 min spectrograms (e.g., Fig. 2, fast Fourier transform (FFT) 2048, 50 % overlap, Hann window) of each acoustic data file from all recorders were visually examined for the presence of bearded seal vocalizations using the program Ishmael 1.0 (Mellinger 2001). A total of 43,296 h of acoustic data were examined for bearded seal calls. Files with calls were manually identified for presence or absence of bearded seal calls. Bearded seal calling was quantified as a total number of hours per day (h/d) with at least one bearded seal call observed, which will also be referred to as calling activity.

Each recorder was equipped with an internal temperature sensor that recorded water temperature at the

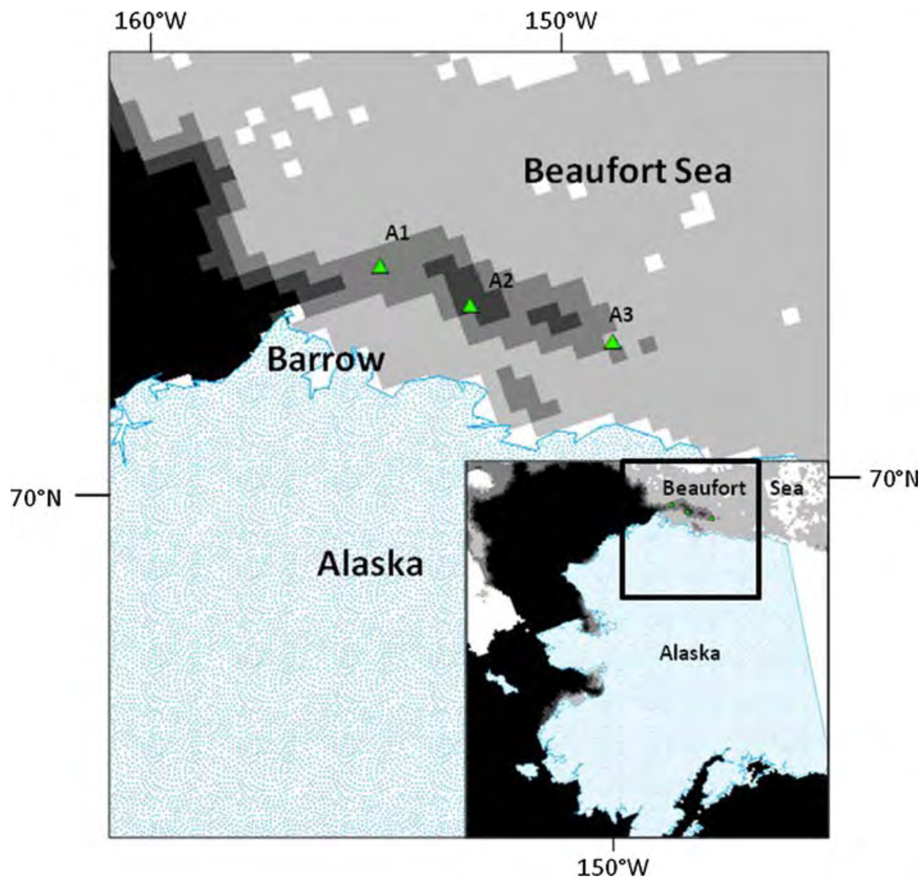

Fig. 1 Hydrophone locations in the flaw lead polynya in the Alaskan Beaufort Sea from 2008 to 2010. Sea ice depicted (12.5 km^2 resolution) is from October 31, 2008 and demonstrates a closing lead. Open water is represented as *black* and 100 % sea ice concentration as *white*, with a *grayscale* gradient representing ice concentrations at 20 % intervals between the minimum and maximum values. Sea ice data were obtained from the National Snow and Ice Data Center (NSIDC, http://n4eil01u.ecs.nasa.gov)

Table 1 Deployment details for 2008–2010

Instrument ID	Location	Recording dates	Instrument depth (m)	Sample rate (Hz)	Duty cycle (min)
A1 2008	71.56N 155.59W	8/15/08–7/27/09	94	8,192	9/30
A2 2008	71.46N 152.25W	8/15/08–8/2/09	131	8,192	9/30
A3 2008	71.13N 149.46W	8/15/08–8/1/09	46	8,192	9/30
A1 2009	71.76N 154.48W	8/1/09–8/14/10	102	16,384	14/60
A2 2009	71.45N 152.50W	8/4/09–8/11/10	95	8,192	9/20

beginning of each data file (duty cycle). The temperature sensor had a sensitivity between −10 and +40 °C and a resolution of 0.0625 °C. Average daily temperature values were computed from these measurements. Water temperature does not vary substantially from the surface to the bottom in these locations (S. Okkonen pers. comm.). Therefore, temperature sampled at depth (5 m above seafloor) was assumed to represent the water temperature experienced by bearded seals. Sea ice concentration data (AMSR-E Aqua 12.5 km resolution) used in this study were obtained from the National Snow and Ice Data Center (http://nsidc.org/data/collections.html, Cavalieri et al. 2004). Daily sea ice concentrations were extracted from a buffer with a 20-km radius that was centered on each mooring location. Mean daily sea ice concentrations were averaged at each location using the zonal statistics toolbox in ArcMap 10.0 (ESRI 2011. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute). While most bearded seal calls were likely within 5 km of the instruments, approximately 15 % of calls can be heard at distances up to 20 km (Cleator et al. 1989), therefore, a 20-km radius was chosen to obtain mean daily sea ice concentration values to be sure that the majority of all vocalizing bearded seals within the detectable range were accounted for. Daily water temperature and sea ice concentration at each mooring location were compared with the total number of hours per day with bearded seal calls.

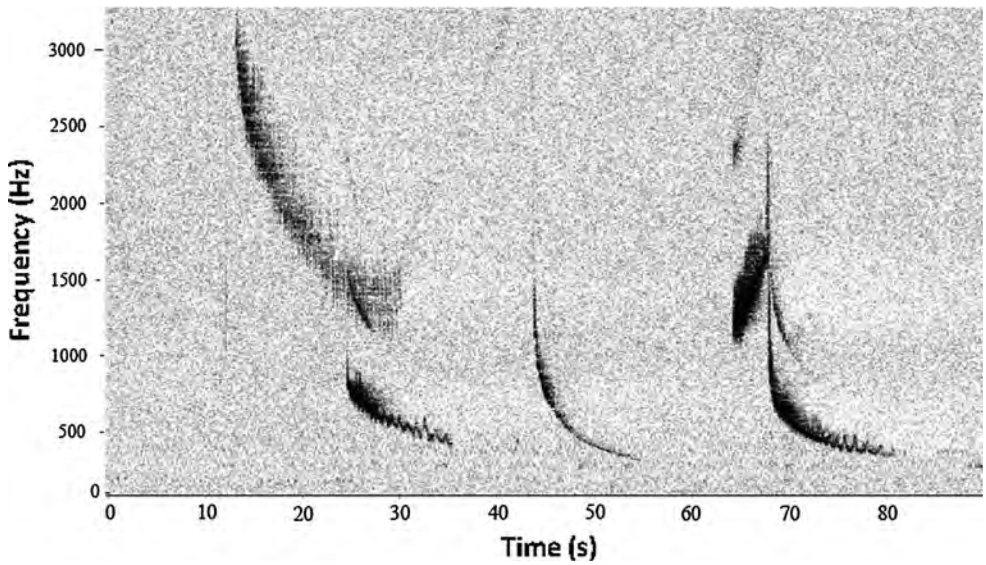

Fig. 2 Spectrogram displaying example bearded seal calls recorded at location A1 on March 3, 2010. FFT 2048, 50 % overlap, Hann window

Results

Bearded seal vocalizations were detected in the Beaufort Sea in all 12 months at sites A1 and A2 from 2008 to 2010 and 11 months at site A3 from 2008 to 2009. Of the 43,296 h of acoustic data recorded from all sites in both years, vocalizations were identified in 16,030 h (Table 2). There was, however, strong seasonal variation in the number of hours per day with calls. At all sites, the peak period of hours per day with calls occurred during the spring months and ended in late June, with the exception of site A1, where the peak period began in January rather than March (Figs. 3a, 4a, 5a). The fewest hours per day with calls at each site occurred from July to December although in both years at each location there was an increase (up to 15 h/d) in the hours per day with calls in late September or early October. At all recorder locations for both years of the study, the minimum number of hours with bearded seal calls occurred in the months of August and November.

Site A1

Bearded seal calls were recorded at site A1 (westernmost site, Fig. 1) from August 19, 2008, through July 17, 2009, and from August 1, 2009, to August 12, 2010. Few calls were present from July to mid-September 2008. In mid-September, call activity increased to over 15 h/d and then dropped back down in October. Call activity increased again in mid-December with calls present nearly every hour of the day beginning in February. This trend held until early July. A similar pattern was seen in the second year of recording, but the late summer increase (9 h/d) occurred in early October 2009 and calls were present nearly 24 h/d from March to early July 2010 (Fig. 3a). The percentage of the total hours with bearded seal calls at A1 was similar between years (Table 2): 53.7 % in 2008–2009 and 46.4 % in 2009–2010.

Table 2 Recording details for each location 2008–2010

Instrument ID	Total recorded hours	Number of hours with calls	Percent hours with calls (%)
A1 2008	8,328	4,474	53.7
A2 2008	8,472	2,367	27.9
A3 2008	8,448	2,865	33.9
A1 2009	9,096	4,217	46.4
A2 2009	8,952	2,107	23.5

Sea ice began to form at A1 on October 21, 2008, and increased to greater than 90 % mean concentration by November 7, 2008 (Fig. 3b). Maximum sea ice concentration (95–100 %) lasted from early November 2008 until June 30, 2009, when it dropped to approximately 75 % and then continued to decline rapidly; the mooring was in open water by 18 July 18, 2009. Sea ice around A1 began to form again on about November 14, 2009, and increased rapidly to greater than 80 % mean concentration by November 21, 2009. Maximum sea ice concentration persisted until July 15, 2010, when it dropped below 80 % and continued to decrease. By August 5, 2010, the area around the mooring was in open water.

During the first year of deployment (2008–2009), in situ water temperature at A1 ranged from −1.8° to 0.5 °C with a mean temperature of −1.4 °C (Fig. 3c). During the second year (2009–2010), the overall mean temperature was almost 1 °C higher (−0.7 °C, range −1.8° to 3.9 °C). From 15 August to 15 September for each year, the greatest difference can be attributed to a late summer pulse of warm

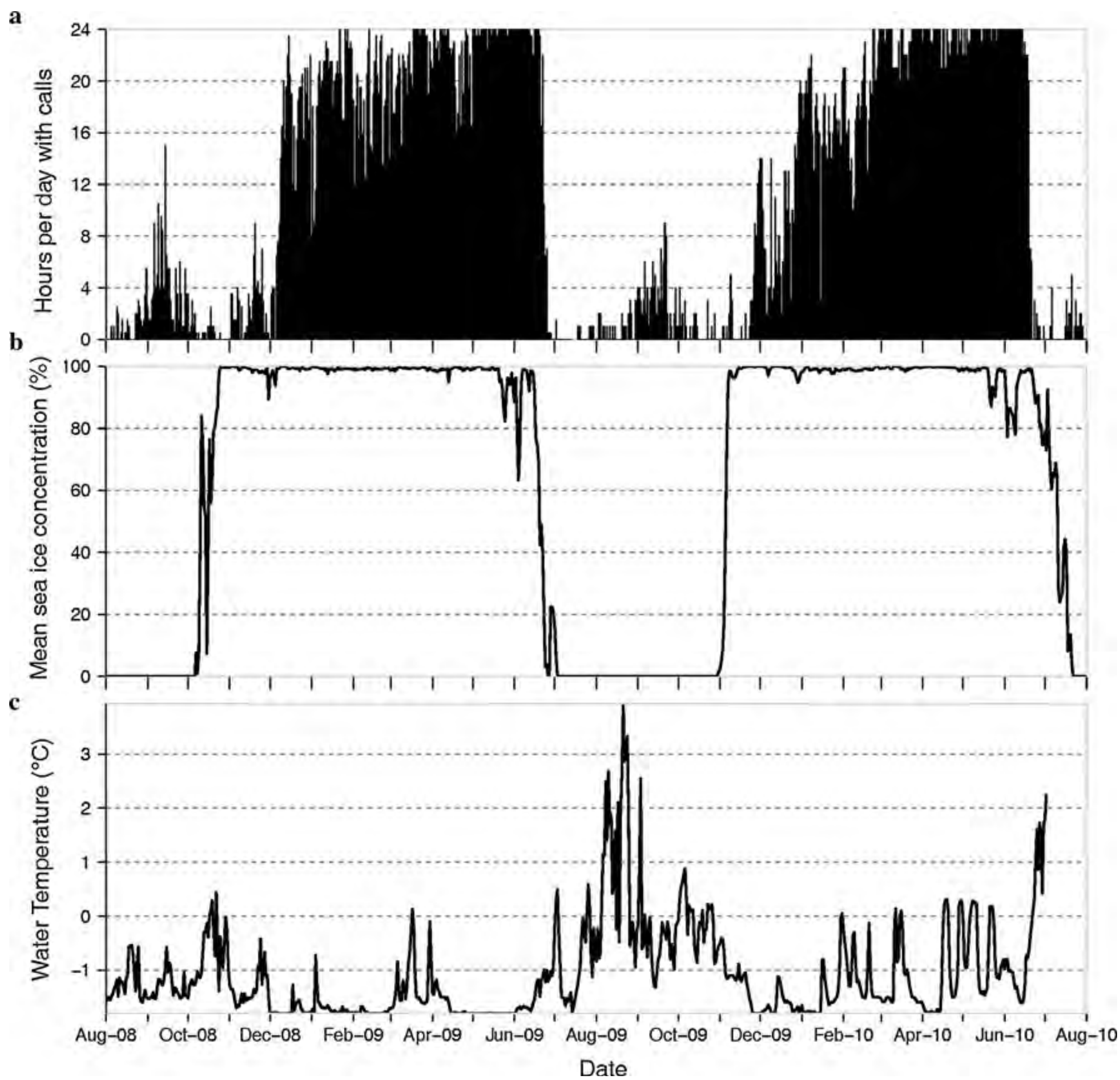

Fig. 3 Acoustic detections of bearded seal vocalizations from August 2008 to August 2010 from site A1 plotted with sea ice concentration and in situ water temperature: **a** The number of hours per day with bearded seal calls, **b** AMSR-E daily percent satellite-derived mean sea concentration (12.5 km resolution, NSIDC, http://n4eil01u.ecs.nasa.gov), **c** in situ water temperature. In general, the number of hours per day with calls was lower with 0 % sea ice concentration and higher as the sea ice increases to maximum concentration (95–100 %). Site A1 had many more hours over a long time period with calls in both 2008–2009 and 2009–2010 than site A2 or A3

water. In 2008, the mean temperature was −1.2 °C, whereas for the same period in 2009, it was +1.0 °C.

Site A2

Calls at A2 (central site, Fig. 1) were recorded year-round with the lowest number of hours with calls occurring in July, August, and November (Fig. 4a). There was a slight peak in call activity, similar to that seen at A1 but with fewer hours per day with calls (4.5 h/d), around late September. Bearded seal calls were primarily present at A2 from mid-February 2009 to early July 2009 and again from mid-March 2010 to early July 2010. Calls occurred nearly 24 h/d from mid-April through early July 2009, except for a slight drop in calling activity recorded during the last 3 weeks of May, where call activity ranged from 6 to 23.5 h/d, but with an average less than 15 h/d over a 3-week period. Call activity ceased in early July until mid-August 2009. From late April through late June 2010, calls were present nearly every hour. After this time, the number of hours/day with calls remained low (less than 6 h/d). Similar percentages were observed in 2008–2009 and 2009–2010 when comparing the number of hours with bearded seal calls to the total number of hours recorded (Table 2): 27.9 and 23.5 %, respectively.

Sea ice began to form at A2 on October 14, 2008, and by November 6, 2008, the area was completely ice-covered (Fig. 4b). Greater than 90 % sea ice concentration lasted

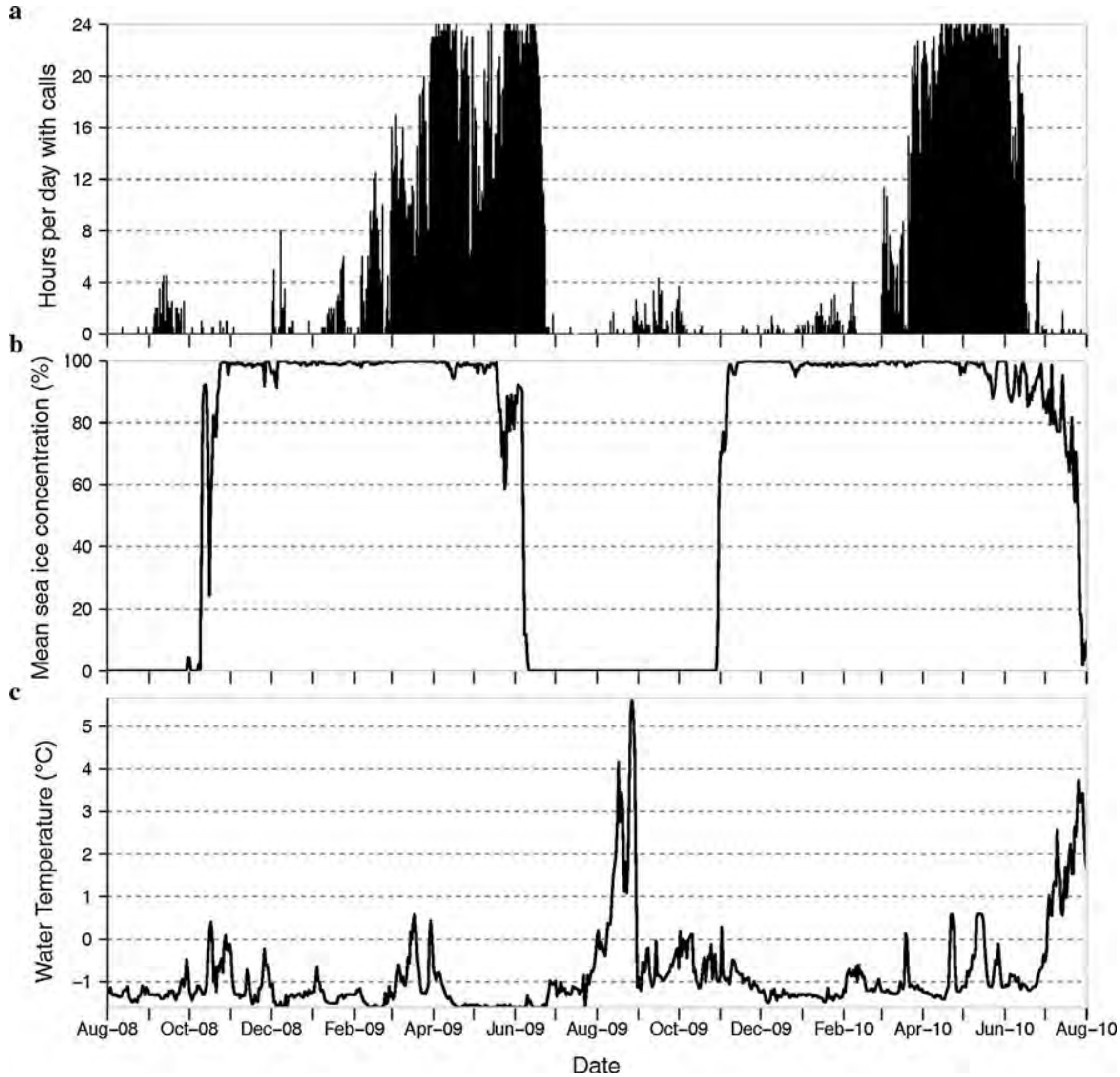

Fig. 4 Acoustic detections of bearded seal vocalizations from August 2008 to August 2010 from site A2 plotted with sea ice concentration and in situ water temperature: **a** the number of hours per day with bearded seal calls, **b** AMSR-E daily percent satellite-derived mean sea concentration (12.5 km resolution, NSIDC, http://n4eil01u.ecs.nasa.gov), **c** in situ water temperature

from November 6, 2008, until June 21, 2009, when it dropped to approximately 43 % and then decreased rapidly such that the mooring was in open water by June 25, 2009. Sea ice formed again on November 12, 2009, and increased rapidly to greater than 90 % mean concentration by November 21, 2009; 95–100 % sea ice concentration persisted 1 month longer in 2010, until 27 July, at which time it declined to below 90 % and continued to decline to completely open water by August 16, 2010.

During the first year of deployment (2008–2009), in situ water temperature at A2 ranged from −1.6° to 0.6 °C with a mean temperature of −1.2 °C (Fig. 4c). During the second year (2009–2010), the overall mean temperature was approximately 0.7 °C higher with an average temperature of −0.5 °C and in situ water temperature ranged from −1.5° to 5.7 °C. From 15 August to 15 September, the mean temperature for this time period in 2008 was −1.1 °C, whereas for the corresponding period in 2009, it was +1.7 °C.

Site A3

A recorder was deployed at the A3 location (easternmost site, Fig. 1) for only 1 year during 2008–2009 (Table 1). Bearded seal calls were present at site A3 from September 19, 2008, through July 16, 2009 (Fig. 5a). No calls were recorded prior to mid-September, when call activity increased to 6.5 h/d. These quickly decreased to zero again

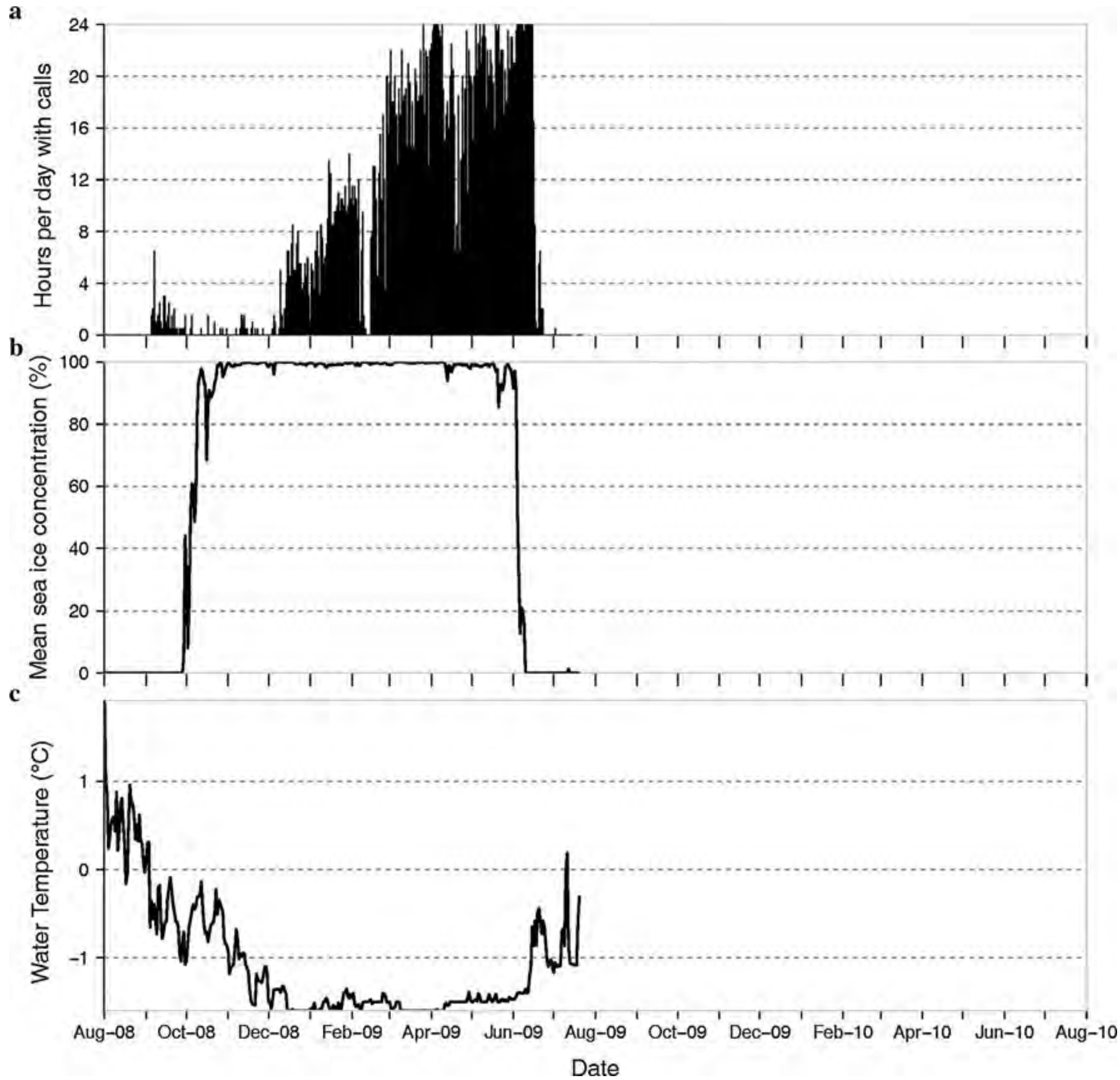

Fig. 5 Acoustic detections of bearded seal vocalizations from August 2008 to August 2009 from site A3 plotted with sea ice concentration and in situ water temperature: **a** the number of hours per day with bearded seal calls, **b** AMSR-E daily percent satellite-derived mean sea concentration (12.5 km resolution, NSIDC, http://n4eil01u.ecs.nasa.gov), **c** in situ water temperature. No data were available for 2009–2010 for this site

before increasing for the winter. The number of hours with calls increased gradually from mid-December 2008 to early March 2009, when they dropped off briefly. Calls were present nearly every hour from mid-March until late June 2009 at which time with call activity decreased to near zero. There was a slight drop in call activity in early May that was similar to the one observed at site A2 in 2009, where the number of hour/day with calls ranged from 6.5 to 23.5 and averaged only 16 h/d for a 2-week period. Bearded seal calls were detected in 33.9 % of the total recorded hours at A3 during 2008–2009 (Table 2).

Sea ice began to form at A3 on October 13, 2008, and remained above 90 % mean concentration from November 1, 2008, to June 16, 2009 (Fig. 5b). Ice concentration continued to rapidly decline, and the instrument was in open water 8 days later.

In situ water temperature at A3 during 2008–2009 ranged from −1.6° to 1.9 °C with a mean temperature of −1.1 °C (Fig. 5c).

Discussion

This is the first study to show year-round production of sound by bearded seals. Throughout this study, bearded seal calls were recorded nearly year-round (i.e., 11–12 months) at all locations in the Beaufort Sea. In a previous study, recordings were made throughout the year in Kongsfjorden, Svalbard, and bearded seal calls were detected only during the breeding season (early April to mid-July). The absence of calls during the fall and winter in that study may have been due to the movement of seals out of the fjord and into open water at the end of breeding season (Van Parijs et al. 2001). In the present study, bearded seal vocalizations in the Beaufort Sea were recorded throughout the entire year irrespective of the presence of sea ice or open water.

At all sites, daily call activity was greatest from January to early July with nearly continuous calling (i.e., calls detected in all 24 h of the day) from mid-March through late June, which coincides with the breeding season for this species (Burns 1970, 1981; Cleator et al. 1989). The fewest hours per day with calls occurred from July to December (minimum in August and November), although at all locations and in both years, there was a slight increase in the number of hours per day with calls in late September or early October.

The overall springtime increase in the number of hours with bearded seal calls at each site is similar to what is known about bearded seals and other pinnipeds. Increased calling during the breeding season and reduced calling outside of these months have been observed in many aquatic-mating pinnipeds (e.g., harbor seals, *Phoca vitulina*, Van Parijs et al. 1999; Weddell seals, *Leptonychotes weddellii*, Rouget et al. 2007; Weddell, Ross, *Ommatophoca rossii*, leopard, *Hydrurga leptonyx*, and crabeater seals, *Lobodon carcinophaga*, Van Opzeeland et al. 2010) as well as other species. Not only does vocal activity increase, new call types are also introduced during mating season (e.g., harp seals, *Pagophilus groenlandicus*, Serrano and Miller 2000). Furthermore, studies have shown correlations between increases in calling behavior and testosterone levels in both terrestrial and aquatic animals (e.g., Bartsh et al. 1992; Marler et al. 2004; Tripovich et al. 2009). Captive male bearded seals did not begin to vocalize until they reached sexual maturity (Davies et al. 2006). These results, in conjunction with studies on other species, support the notion that seasonality in call activity may in part be a reflection of changes in hormone levels.

Another, not mutually exclusive, explanation may account for the seasonal variability of bearded seal call activity. Male bearded seals have been shown to increase their call activity and occupy overlapping territories during breeding season (Van Parijs et al. 2002). In fact, increasing numbers of calls have been associated with an increased number of males rather than an increase in the call rates of individual males (Van Parijs et al. 2001, 2002). It is therefore likely that the increase in the number of hours with calls in this study is indicative of an increase in the number of vocalizing seals within acoustic range of each recorder.

The seasonal peak of call activity in this study was longer than that reported for bearded seals elsewhere (e.g., Van Parijs et al. 2001) although many studies only made recordings from March until June (Cleator et al. 1989; Cleator and Stirling 1990; Risch et al. 2007). Other studies have shown that some aquatic-mating pinnipeds produce calls year-round (Rouget et al. 2007; Van Opzeeland et al. 2010). The year-round occupancy of certain areas may give "territorial" males an advantage over the non-territorial or "roaming" males at the onset of mating season and simultaneous arrival of female seals to the area (Harcourt et al. 2007; Harcourt et al. 2008; Van Opzeeland et al. 2010). The elevated bearded seal call activity in the early winter in the Beaufort Sea suggests that males are engaging in acoustic displays in their breeding territory for a large portion of the year and are, therefore, establishing and defending aquatic territories prior to spring. A similar year-round acoustic presence was observed in Weddell seals (Van Opzeeland et al. 2010).

Wintertime calling of bearded seals was most prevalent at the A1 location, typically intensifying around mid-December and continuing into the spring calling season through mid-late July. Location A1 also had a longer period of increased winter and spring calling behavior (late December through July) in both 2008–2009 and 2009–2010 and almost twice the total number of hours with calls recorded (both years) than either of the other locations. Additionally, the number of hours per day with calls peaked much earlier at A1, beginning January, rather than March. This increased number of hours with calls detected at A1 may be due to its more westerly location in the flaw lead polynya that forms off Barrow (Stirling 1997), making it more accessible to bearded seals earlier in the spring months. The geographic differences in call activity between sites suggest that the area around A1 may be a more important habitat for bearded seals in winter and spring because it may be an area of higher or more enriched benthic productivity, or sea ice conditions at this location may be more suitable for overwintering due to enhanced primary production in the flaw lead polynya or along the sea ice edge (Bluhm and Gradinger 2008). The spatial variation in call activity may also be a result of fine-scale changes in sea ice that are not reflected in the 12.5 km resolution of our sea ice data. The distribution of vocalizing male bearded seals is dependent on available suitable haul out sites or ice conditions and by female distribution, which is determined by sea ice conditions and ecological requirements (Van Parijs et al. 2001, 2004). Therefore, spatial variation in calling activity of males in the Beaufort Sea may be the result of more females congregating in areas of higher concentrations of prey and thereby influencing the distribution of vocalizing males (Van Parijs et al. 2001; Van Opzeeland et al. 2010).

Although qualitative, the results of this study demonstrate an association between bearded seal call activity and sea ice formation and retreat. The clearest illustration of this is from late June to early July, at all sites and years, where the rapid decrease in number of hours with bearded seal calls responded to the rapid decrease in ice concentration. At site A1, there was less than 1 day, in 2009, and less than 1 week, in 2010, between the decrease in sea ice concentration and the decline in bearded seal vocalizations in the summer months. However, at the other two sites, a 2–3 week gap was typically observed between the drop in sea ice concentration and the subsequent decline in call activity.

The relationship between increasing number of hours with calls and increasing ice concentration in the early winter is less obvious, as sea ice concentrations were well above 90 % by the time bearded seals began calling during more than half of the hours available each day (12 h/d). However, the interannual differences in the timing of sea ice formation at sites A1 and A2 were reflected in changes in the timing of bearded seal call detections. At site A1, sea ice started forming more than 3 weeks later in 2009 than in 2008, and 90 % ice concentration occurred almost 3 weeks later in 2009. The occurrence of bearded seal vocalizations mirrored this interannual difference: 24 h/d calling started 1 month later in 2009 than in 2008. A similar pattern was seen at A2. The observed shift in the timing of sea ice formation and call detection between years suggests a change in timing of available sea ice habitat for bearded seals. Extreme variations in available sea ice habitat may have implications for the reproductive success of the bearded seal as well as other ice-obligate species (Moore and Huntington 2008; Kovacs et al. 2011).

This shift in the potential mating or territorial establishment season due to changes in seasonal sea ice formation could affect the mating success of bearded seals by disrupting the timing of key reproductive events. Female bearded seals enter estrous at the end of lactation and mating season typically occurs between March and May (Atkinson 1997). At both A1 and A2, there were fewer hours per day with bearded seal calls between December and June 2009–2010 than during the same time period in 2008–2009. The reduced call activity may indicate a decline in the number of seals that moved into or established territories in the Beaufort Sea during the spring of 2009–2010, or it might indicate a change in the distribution of bearded seals within the acoustic detection range of the hydrophones. Another possible explanation for the reduced call activity in 2009–2010 may be a result of less suitable habitat in the early winter due to fine-scale changes in local sea ice conditions. Van Parijs et al. (2004) found that between-year fluctuations in local sea ice habitat influenced bearded seal vocal activity by restricting the number of displaying males in the early part of mating season, while less overall ice cover in May resulted in an increase in the number of vocalizing males. Territorial males in Svalbard were present in all sea ice conditions, while roaming males tended to be more restricted by extensive fast ice cover (Van Parijs et al. 2004). Unlike in Svalbard, Van Parijs and Clark (2006) observed a greater percentage of roaming males than territorial males in the Beaufort Sea. If roaming males are also restricted by fast ice cover in the Beaufort Sea, then fluctuations in ice cover may be of greater importance to a larger percentage of bearded seals in the Beaufort Sea than off Svalbard.

The greatest concentration of bearded seal calls at all locations was recorded during 100 % sea ice cover. These results are somewhat contradictory to those discovered by Simpkins et al. (2003), which showed that bearded seals off of St. Lawrence Island preferred sea ice cover between 70 and 90 % and tended to avoid areas with greater than 90 % cover. However, a more recent study showed that bearded seals seem to be a more "interior" seal species and were typically found on sea ice cover between 25 and 100 % (Ver Hoef et al. 2013). Our results support the more recent findings; however, sea ice concentration in this study is measured at 12.5 km resolution and averaged over a 20 km radius. Therefore, the remotely sensed sea ice concentration data may not fully represent the more localized or fine-scale habitat variability, which may be most evident during the freeze-up/retreat seasons, when sea ice conditions are changing rapidly. While the remotely sensed sea ice data may not be on a fine-scale relative to individual bearded seals as it was in prior studies (Van Parijs et al. 2001, 2004; Van Parijs and Clark 2006), it is nevertheless useful in comparing broad-scale relationships. The acoustic data presented here were collected using single hydrophones. This does not allow for localization or abundance assessments, therefore, the exact locations of individual seals relative to the instruments were unknown. All detectable calls were within 20 km of the recorder, and the sea ice data were averaged over the same distance to account for all vocalizing seals. This comparison may not provide information on bearded seals at the individual level, and the effect of fine-scale sea ice changes, but it does offer a broad-scale view of the influence different sea ice conditions have on the distribution of vocalizing bearded seals in the Beaufort Sea. The association of increased hours/day with calls with increased sea ice concentration supports the idea that bearded seals tend to prefer high concentration sea ice. Furthermore, it demonstrates the exploitation of a stable sea ice platform during mating season.

Water temperature, although related to sea ice, may also be an important factor influencing bearded seal call activity. During the summer months, the ACC carries relatively warm water from the Bering and Chukchi Seas into the Beaufort Sea (Okkonen et al. 2009). Location A1 was positioned along the southern edge of Barrow Canyon and within the prevailing path of the ACC, while sites A2 and A3 were placed within the downstream extension of the ACC on the upper Beaufort slope. Hydrography data collected in the Beaufort Sea from 2005 to 2009 (S. Okkonen pers. comm.) showed a large amount of interannual variability in water temperatures recorded in the ACC. Weak or southerly winds that occur in the Chukchi Sea allow the intrusion of warm Bering/Chukchi waters onto the western Beaufort shelf leading to warmer summer water temperatures recorded in the ACC. Alternatively, summer water temperatures are relatively cool when winds in the Chukchi originate in the north/northeast (Okkonen et al. 2009).

Conductivity, temperature, depth (CTD) data showed that between 2008 and 2010, the warmest recorded water temperatures were found during the summers of 2009 and 2010 (up to 5–6 °C) and the coldest were recorded in 2008 (less than 1 °C) especially at depths between 70 and 100 m; a range that encompasses the depths at which our recorders (A1 and A2) were moored (S. Okkonen pers. comm). These results support water temperature data recorded on our recorders; warm summer water influxes occurred between 15 August and 15 September in both 2009 and 2010, but did not occur during the same time period in 2008. Water temperature data were not available before 15 August in 2008; therefore it is unknown whether or not the intrusion of warmer water occurred earlier that year. Increased summer water temperatures can delay the formation of sea ice (e.g., fall/winter of 2009) changing the timing of available habitat for bearded seals. The effect on timing of available habitat was reflected in the data presented here when comparing 2008–2009 to 2009–2010; sea ice formed approximately 3 weeks later at sites A1 and A2 in 2009, which resulted in a later detection of increased call activity on the recorders.

Outside of the breeding season, bearded seals were detected as early as late August in all years. There was a consistent presence of bearded seal calls in autumn at all locations from 2008 to 2010 with a slight peak occurring in late September/early October for both years. The autumn presence of bearded seals during the open water period suggests possible year-round residency of a small subpopulation of bearded seals in the Beaufort Sea or the early establishment of aquatic territories by “territorial” males (Van Parijs et al. 2002; Van Opzeeland et al. 2010).

Autumn and winter call activity has a number of possible explanations. Early singing might be related to the development of a vocal repertoire by juvenile or subadult animals or adults may be “warming up” in preparation for breeding season (Davies et al. 2006). Autumn vocalizations were typically lower in frequency and shorter in duration, which may support this latter observation (MacIntyre et al. unpublished data). Alternatively, the different structure of the autumn vocalizations may indicate a functional difference in calls produced by adult males outside of the breeding season (Serrano and Miller 2000). The early season onset might also be due to seasonal changes in testosterone as is well documented for song birds (cf. Smith et al. 1997; Brenowitz 2004) and has been shown for other pinnipeds (captive Australian fur seals, *Arctocephalus pusillus,* Tripovich et al. 2009; captive walrus, *Odobenus rosmarus*, Hughes et al. 2011). As noted previously, in many species of pinniped, both land- and aquatic-mating, where males defend a territory or resource attractive to females, males establish these territories well before females give birth and then come into estrous (i.e., Le Boeuf and Peterson 1969; Van Parijs et al. 1999; Kunc and Wolf 2008; Van Opzeeland et al. 2010). The production, duration, and frequency range of trills produced by bearded seals are used by males to advertise quality to other males, and potentially females, as the breeding season progresses (Van Parijs et al. 2001).

Marine mammal distributions in the Arctic are commonly documented using visual surveys (Simpkins et al. 2003; Bengtson et al. 2005). However, such surveys require adequate sighting conditions, including good visibility and low sea state, and are limited by both time of day and surface presence of animals (Mellinger et al. 2007). The relative inaccessibility of the Arctic (poor weather, heavy ice cover and little or no daylight) can make it difficult to assess the abundance, distribution, and behavior of bearded seals. Passive acoustic sampling is robust by comparison, as data can be collected continuously and in all weather conditions (Stirling et al. 1983). During much of the year, this species produces underwater vocalizations, thereby making the utilization of passive acoustics to study them an invaluable tool, particularly in winter months. The biggest drawback of passive acoustic studies of marine mammals is that only animals that vocalize are detectable. Additionally, in the case of bearded seals, only males have been shown to vocalize; therefore, in the current study, only vocalizing males were accounted for (Ray et al. 1969; Davies et al. 2006). However, as this study shows, bearded seals produce sounds all year and the seasonal decrease of sound production occurs in summer when they are more easily studied using traditional visual methods. A combination of these two methods, then, will provide a better understanding of bearded seal occurrence in the Beaufort Sea and elsewhere.

Based on the results of this study, acoustic monitoring can be an effective method to examine the broad spatial and temporal relationship between bearded seal presence and changing sea ice conditions. Differences in sea ice conditions have been shown to influence mating tactics used by males (territorial vs. roaming, Van Parijs et al. 2004) which needs to be taken into account when evaluating the relationship between bearded seals and changing sea ice conditions. With the increased loss of sea ice in the Arctic, there is greater interest in obtaining abundance estimations of bearded seals as well as other ice-obligate species. The recent development of methods that utilize passive acoustic detections to provide estimates of density or abundance could be applied to bearded seals (Marques et al. 2012). By combining call rates of these animals (e.g., Van Parijs et al. 2001) with density estimation techniques (Marques et al. 2012), it may be possible to obtain estimates of relative abundance and density of this typically solitary and widespread pan-Arctic species.

Beyond the seasonal and geographic occurrence of the species, acoustic monitoring can provide more information on the acoustic behavior of bearded seals than is presented here. For instance, the methods used in this study to determine bearded seal calling activity do not take into account the number of calls produced by one or multiple seals. The number of hours per day with calls does not reflect the number of calls produced in a given hour; the presence of at least one call per hour was used to document bearded seal presence. A next step is to determine the number of vocal seals (i.e., males) present and determine individual call rates (e.g., Van Parijs et al. 2001; Davies et al. 2006). Future analysis of these data will elucidate whether the increase in the number of hours per day with calls observed in the autumn, winter, and spring months represents an increase in the number of animals present, or an increase in the calling rate of a few individuals, or both. And because it is speculated only male bearded seals produce trills (Ray et al. 1969), any assessment of numbers of animals heard needs to take into account the females that are present, but silent.

Additional investigations into the calling activity of bearded seals will be needed to more accurately assess the relationship between bearded seal seasonal, interannual and geographic calling behavior. Examining call types to compare between seasons might provide insight into the function of autumn and winter bearded seal vocal activity. Expanding the study to the Bering and Chukchi Seas will cover much of the range of Alaskan bearded seals and provide a broader picture of their seasonal occurrence under the different ice conditions they experience over this range. Finally, detailed analysis of call types can be used to determine whether or not geographic variation exists among the three seas as has been shown in other regions and with other species (Van Parijs et al. 1999; Bjørgesæter et al. 2004; Risch et al. 2007; Van Opzeeland et al. 2009). There are potential subpopulations that reside in each region throughout the year that may be determined by comparing call types present throughout the year at each location.

The observed interannual shift in the timing of sea ice formation and retreat between 2008–2009 and 2009–2010 has implications for habitat availability and stability for ice-obligate species if this variability persists (cf. Laidre and Heide-Jørgensen 2005). The results of this study help to explain seasonal vocal activity of bearded seals as well as begin to establish a baseline of bearded seal year-round occurrence in the Beaufort Sea. The institution of such a baseline (although perhaps a decade too late) of bearded seal occurrence in the BCB will permit future detection of changes in bearded seal behavior as sea ice conditions vary with the changing Arctic climate. Additionally, demonstrating the strength of the relationship between bearded seal call activity and sea ice concentration reinforces the claim that extreme variation in their habitat (loss of sea ice) will likely negatively affect bearded seal survival.

Acknowledgments We thank the captain and crew of the USCGC *Healy*, John Kemp (WHOI), Dave Leech (UAF), and Sharon Nieukirk (OSU) for assistance with deployment and recovery of the moorings. Funding for this project was provided by the National Ocean Partnership Program grants WHOI A100587, and UAF 080047, the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement NA10OAR4320148 and the U.S. Department of the Interior, Bureau of Ocean Energy Management (BOEM) Inter-agency Agreement M07RG13317 with the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, as part of the BOEM Alaska Environmental Studies Program. We also thank Steve Okkonen for his assistance with the analysis of our water temperature data and for providing us with data to support our findings. Comments from Dr. Sofie Van Parijs and two anonymous reviewers greatly improved this manuscript. The findings and conclusions in the paper are those of the author(s) and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA. This is JISAO Contribution No. 2095.

References

Ashjian CJ, Braund SR, Campbell RG, George JC, Kruse J, Maslowski W, Moore SE, Nicolson CR, Okkonen SR, Sherr BF, Sherr EB, Spitz YH (2010) Climate variability, oceanography, bowhead whale distribution, and Iñupiat subsistence whaling near Barrow, Alaska. Arctic 63:179–194

Atkinson S (1997) Reproductive biology of seals. Rev Reprod 2:175–194

Bartsh SS, Johnston SD, Siniff DB (1992) Territorial behavior and breeding frequency of male Weddell seals (*Leptonychotes weddelli*) in relation to age, size, and concentrations of serum testosterone and cortisol. Can J Zool 70:680–692

Bengtson JL, Hiruki-Raring LM, Simpkins MA, Boveng PL (2005) Ringed and bearded seal densities in the eastern Chukchi Sea, 1999–2000. Polar Biol 28:833–845

Bjørgesæter A, Ugland KI, Bjørge A (2004) Geographic variation and acoustic structure of the underwater vocalization of harbor seal (*Phoca vitulina*) in Norway, Sweden and Scotland. J Acoust Soc Am 116:2459–2468

Bluhm BA, Gradinger R (2008) Regional variability in food availability for Arctic marine mammals. Ecol Appl 18:S77–S96

Brenowitz EA (2004) Plasticity of the adult avian song control system. Ann NY Acad Sci 1016:560–585. doi:10.1196/annals.1298.006

Burns JJ (1970) Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. J Mammal 51:445–454

Burns JJ (1981) Bearded seal *Erignathus barbatus* Erxleben, 1777. In: Ridgway SH, Harrison RJ (eds) Handbook of Marine Mammals, vol 2., SealsAcademic Press, London, pp 145–170

Cavalieri D, Markus T, Comiso J (2004) AMSR-E/Aqua daily L3 12.5 km brightness temperature, sea ice concentration, & snow depth polar grids V002, [l8-15-2008–8-15-2010]. Boulder, Colorado USA: National Snow and Ice Data Center. Digital media

Cleator HJ, Stirling I (1990) Winter distribution of bearded seals (*Erignathus barbatus*) in the Penny Strait area, Northwest Territories, as determined by underwater vocalizations. Can J Fish Aquat Sci 47:1071–1076

Cleator HJ, Stirling I, Smith TG (1989) Underwater vocalizations of the bearded seal (*Erignathus barbatus*). Can J Zool 67:1900–1910

Davies CE, Kovacs KM, Lydersen C, Van Parijs SM (2006) Development of display behavior in young captive bearded seals. Mar Mamm Sci 22:952–965

Delarue J, Todd SK, Van Parijs SM, Di lorio L (2009) Geographic variation in Northwest Atlantic fin whale (*Balenoptera physalus*) song: Implications for stock structure assessment. J Acoust Soc Am 125:1774–1782

Frost KJ, Whiting A, Cameron MF, Simpkins MA (2008) Habitat use, seasonal movements and stock structure of bearded seals in Kotzebue Sound, Alaska. Tribal Wildlife Grants Program, Fish and Wildlife Service, Tribal Wildlife Grants Study U-4-IT. Final report from the Native Village of Kotzebue, Kotzebue, AK, for U.S. Fish and Wildlife Service, Anchorage, AK, pp 1–16

Harcourt RG, Kingston JJ, Cameron MF, Waas JR, Hindell MA (2007) Paternity analysis shows experience, not age, enhances mating success in an aquatically mating pinniped the Weddell seal (*Leptonychotes weddellii*). Behav Ecol Sociobiol 61:643–652

Harcourt RG, Kingston JJ, Waas JR, Hindell MA (2008) Foraging while breeding: alternative mating strategies by male Weddell seals? Aquat Conserv Mar Freshw Ecosyst 17:68–78

Hughes WR, Reichmuth C, Mulsow JL, Larsen ON (2011) Source characteristics of the underwater knocking displays of a male Pacific walrus (*Odobenus rosmarus divergens*). J Acoust Soc Am 129:2506

Kovacs KM, Lydersen C, Overland JE, Moore SE (2011) Impacts of changing sea ice conditions on Arctic marine mammals. Mar Biodiv 41:181–194

Kunc HP, Wolf JBW (2008) Seasonal changes of vocal rates and their relation to territorial status in male Galapagos sea lions (*Zalophus wollebaeki*). Ethology 114:381–388

Laidre KL, Heide-Jørgensen MP (2005) Arctic sea ice trends and narwhal vulnerability. Biol Conserv 121:509–517

Le Boeuf BJ, Peterson RS (1969) Social status and mating activity in elephant seals. Science 163:91–93

Marler P, Peters S, Wingfield J (2004) Correlations between song acquisition, song production, and plasma levels of testosterone and estradiol in sparrows. Dev Neurobiol 18:531–548. doi:10.1002/neu.480180605

Marques TA, Thomas L, Martin SW, Mellinger DK, Ward JA, Moretti DJ, Harris D, Tyack PL (2012) Estimating animal population density using passive acoustics. Biol Rev Camb Philos Soc. doi:10.1111/brv.12001

Maslanik J, Stroeve J, Fowler C, Emery W (2011) Distribution and trends in Arctic sea ice age through spring 2011. Geophys Res Lett. doi:10.1029/2011GL047735

McLaren I (1958) Some aspects of growth and reproduction of the bearded seal, *Erignathus-barbatus* (Erxleben). J Fish Res Board Can 15:219–227

Mellinger DK (2001) *Ishmael 1.0 user's guide*. NOAA Tech. Memo. OAR–PMEL–120 (NOAA PMEL, Seattle), pp 1–30

Mellinger DK, Stafford KM, Moore SE, Dziak RP, Matsumoto H (2007) An overview of fixed passive acoustic observation methods for cetaceans. Oceanography 20:36–45

Moore SE, Huntington HP (2008) Arctic marine mammals and climate change impacts and resilience. Ecol Appl 18:S157–S174

Moore SE, Stafford KM, Melling H, Berchok C, Wiig Ø, Kovacs KM, Lydersen C, Richter-Menge J (2012) Comparing marine mammal acoustic habitats in Atlantic and Pacific sectors of the High Arctic: year-long records from Fram Strait and the Chukchi Plateau. Polar Bio 35:475–480

Nelson RR, Burns JJ, Frost KJ (1984) The bearded seal (*Erignathus barbatus*). In: Burns JJ (ed) Marine mammal species accounts, wildlife technical bulletin no. 7. Alaska Department of Fish and Game, Juneau, AK, pp 1–6

Okkonen SR, Ashjian CJ, Campbell RG, Maslowski W, Clement-Kinney JL, Potter R (2009) Intrusion of warm Bering/Chukchi waters onto the shelf in the western Beaufort Sea. J Geophys Res. doi:10.1029/2008JC004870

Potelov VA (1969) Distribution and migrations of bearded seals in the White, Barents and Kara seas. Third All-Union Conference on Marine Mammals Publishing House "Nauka". (Translated from Russian by Fish Res Board of Can, Transl Ser No. 1510)

Ray C, Watkins WA, Burns JJ (1969) The underwater song of *Erignathus* (bearded seal). Zoologica 54:79–83

Risch D, Clark CW, Corkeron PJ, Elepfandt A, Kovacs KM, Lydersen C, Stirling I, Van Parijs SM (2007) Vocalizations of male bearded seals, *Erignathus barbatus*: classification and geographical variation. Anim Behav 73:747–762

Roth EH, Hildebrand JA, Wiggins SM, Ross D (2012) Underwater ambient noise on the Chukchi Sea continental slope from 2006–2009. J Acoust Soc Am 131:104–110

Rouget PA, Terhune JM, Burton HR (2007) Weddell seal underwater calling rates during the winter and spring near Mawson station, Antarctica. Mar Mamm Sci 23:508–523

Serrano A, Miller EH (2000) How vocal are harp seals (*Pagophilus groenlandicus*)? A captive study of seasonal and diel patterns. Aquat Mamm 26:253–259

Simpkins MA, Hiruki-Raring LM, Sheffield G, Grebmeier JM, Bengston JL (2003) Habitat selection by ice-associated pinnipeds near St. Lawrence Island, Alaska in March 2001. Polar Biol 26:577–586

Smith G, Brenowitz E, Beecher M, Wingfield J (1997) Seasonal changes in testosterone, neural attributes of song control nuclei, and song structure in wild songbirds. J Neurosci 17:6001–6010

Stirling I (1997) The importance of polynyas, ice edges, and leads to marine mammals and birds. J Mar Syst 10:9–21

Stirling I, Calvert W, Cleator H (1983) Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the High Arctic. Arctic 36:262–274

Timmermans ML, Proshutinsky A, Krishfield RA Perovich DK, Richter-Menge JA, Stanton TP, Toole JM (2011) Surface freshening in the Arctic Ocean's Eurasian Basin: an apparent consequence of recent change in the wind-driven circulation. J Geophys Res 116, C00D03. doi:10.1029/2011JC006975

Tripovich JS, Rogers TL, Dutton G (2009) Faecal testosterone concentrations and the acoustic behaviour of two captive male Australian fur seals. Aust Mammal 31:117

Van Opzeeland IC, Corkeron PJ, Risch D, Stenson G, Van Parijs SM (2009) Geographic variation in vocalizations of pups and mother-pup behavior of harp seals *Pagophilus groenlandicus*. Aquat Biol 6:109–120

Van Opzeeland IC, Van Parijs S, Bornemann H, Frickenhaus S, Kindermann L, Klinck H, Plotz J, Boebel O (2010) Acoustic ecology of Antarctic pinnipeds. Mar Ecol Prog Ser 414:267–291

Van Parijs SM, Clark C (2006) Long-term mating tactics in an aquatic-mating pinniped, the bearded seal, *Erignathus barbatus*. Anim Behav 72:1269–1277

Van Parijs SM, Hastie GD, Thompson PM (1999) Geographic variation in temporal and spatial vocalization patterns of male harbor seals in the mating season. Anim Behav 58:1231–1239

Van Parijs SM, Kovacs KM, Lydersen C (2001) Spatial and temporal distribution of vocalizing male bearded seals: implications for male mating strategies. Behavior 138:905–922

Van Parijs SM, Lydersen C, Kovacs KM (2002) Vocalizations and movements suggest alternative mating tactics in male bearded seals. Anim Behav 65:273–283

Van Parijs SM, Lydersen C, Kovacs KM (2004) The effects of ice cover on the behaviour of aquatic-mating male bearded seals. Anim Behav 68:89–96

Ver Hoef JM, Cameron MF, Boveng PL, London JM, Moreland EM (2013) A spatial hierarchical model for abundance of three ice-associated seal species in the eastern Bering Sea. Stat Meth. doi: 10.1016/j.stamet.2013.03.001

Walsh JE (2008) Climate of the Arctic marine environment. Ecol Appl 18:S3–S22

Woodgate RA, Weingarter TJ, Lindsay R (2012) Observed increases in oceanic fluxes from the Pacific to the Arctic from 2001 to 2011 and their impacts on the Arctic. Geophys Res Lett. doi: 10.1029/2012GL054092