

The distribution and timing of bearded seal (*Erignathus barbatus*) vocalizations reflect changing environmental conditions in the Bering, Chukchi, and Beaufort Seas

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**Abstract**

The distribution and timing of bearded seal (*Erignathus barbatus*) vocalizations reflect changing environmental conditions in the Bering, Chukchi, and Beaufort Seas

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The Arctic is experiencing dramatic shifts in climate that have led to changes in sea ice distribution, extent, and timing that pose adaptability challenges for Arctic species. Ice obligate species, such as the bearded seal, *Erignathus barbatus*, are inherently vulnerable to Arctic warming due to their reliance on seasonal sea ice as a platform for pupping and molting. Bearded seals are a highly vocal pan-Arctic species, in which males produce underwater vocal displays as part of courtship behavior during mating season. Bearded seal vocalizations were once believed to be a spring phenomenon, but results of this study have revealed year-round acoustic activity by bearded seals in the Bering, Chukchi, and Beaufort Seas (BCB). This new insight suggests that passive acoustic monitoring can be employed as an effective method to examine bearded seal distribution, migration patterns, and population structure year-round. This study provides a more complete understanding of bearded seal behavior and ecology through the analysis of year-round passive acoustic data collected in the BCB between 2008 and 2011. The BCB comprises three ecologically distinct bodies of water connected by the currents that flow northward from the Pacific Ocean through the Bering Strait and into the Arctic. The fine- and broad-scale oceanographic and physiographic variability that exists among the BCB may directly or indirectly (through sea ice conditions) affect bearded seal distributions. Analysis of seal vocal presence relative to sea ice distribution helped to clarify the relationships between bearded seal vocal behavior, habitat preferences and sea ice conditions. Regional and recording-site variability in call activity was largely related to sea ice conditions and geography, however oceanographic variability may contribute to the fine-scale variability in call activity that was present between closely located sites. This research provides a contemporary baseline of bearded seal distributions needed for detecting future population fluctuations as a result of sea ice variability in the disrupted polar climate. Results of this study revealed a positive correlation between bearded seal call activity and sea ice conditions. This tight coupling of sea ice and call activity provide evidence that variability in sea ice conditions may have major implications for the success of the bearded seal population in the BCB as the climate continues to change.

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## ***Introduction***

Recent warming trends of the earth's climate have been linked to dramatic environmental changes in marine polar environments (Stocker et al. 2013). This polar sensitivity is due in part to the ice-albedo feedback mechanism (Perovich et al. 2009), where melting snow and sea ice lowers reflectivity and thereby further increases surface warming by absorption of solar radiation (e.g., Weatherly et al. 1991; Francis et al. 2009). This warming climatic trend has been connected to changes in water temperature, sea level, ocean currents, and sea ice cover (Rothrock et al. 1999; Parkinson et al. 2002; Comiso et al. 2004; Walsh 2008; Woodgate et al. 2012; Timmermans et al. 2013). Sea ice plays an important role in climate and ocean circulation (Serreze et al. 2003) by driving changes in temperature, pressure, and precipitation. Sea ice conditions can vary regionally or locally based on oceanographic variability as well as other broad- and fine-scale climatic influences. Variations in sea ice conditions have implications for biological activity, ecosystems, and human use in the Arctic marine environment (Walsh 2008). Seasonal sea ice provides crucial habitat for many polar species, where extreme variations in its timing, extent, volume, and distribution throughout the year may negatively impact the survival of numerous marine fauna.

When exploring how changes in the climate will affect the ecosystems of Arctic and sub-Arctic waters, both fine- and broad- scale oceanographic variability must be considered. The Arctic waters surrounding Alaska comprise three ecologically distinct bodies of water: the Bering, Chukchi, and Beaufort Seas (Piatt and Springer 2007; Sigler et al. 2011). These seas are connected by ocean currents that flow from the Pacific Ocean through the Bering and Chukchi Seas northward into the Arctic Ocean (Coachman and Aagaard, 1966) yet, there is underlying oceanographic and physiographic variability among the areas. The middle shelf domain of the Bering Sea is a shallow, benthic-dominated system that is influenced by the stratification between the upper and lower layers; the upper layer is mixed by winds and the lower layer by tides (Stabeno et al. 2010). The Chukchi Sea is dominated by a broad, shallow shelf with depths less than 50 m. The Beaufort Sea shelf is 100 m deep and is much narrower, extending only 100 km offshore before dropping to 1000 m into the Canada Basin. The Chukchi Sea shelf oceanography is predominantly influenced by the northward flow of water through the Bering Strait from the North Pacific Ocean. In contrast, the Beaufort Sea is influenced by freshwater inflow from the rivers of Alaska and northern Canada (Carmack and Wassman 2006; Dunton et al. 2006; Weingartner et al. 2009). These factors, which drive the

major oceanographic processes, play a large role in defining the sea ice conditions in the three seas. The resulting water-mass differences among these areas can result in highly variable habitats between regions of a changing Arctic climate.

The current warming trend in the Arctic is causing a rapid shift in environmental stability (Walsh 2008) challenging the capacity of Arctic species to adapt to these changes (Moore and Huntington 2008). Ice-obligate species (species whose life histories are reliant on sea ice), 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). While some marine mammals may be directly impacted by sea ice loss as a loss of habitat, others may be affected more indirectly by oceanographic changes that occur regionally or locally, but the greatest impact would be on those marine mammals that are affected both directly and indirectly. Decline in seasonal sea ice extent and timing of sea ice freeze-up in the fall and break-up in the spring decrease the availability of habitat for resting, breeding, molting and hunting, posing the greatest threat to the survival of ice-obligate species (Moore and Huntington 2008).

Bearded seals represent a prime example of an ice-obligate species that is at risk of habitat loss as the climate continues its warming trend. These pan-Arctic pinnipeds are widely distributed throughout the northern Bering, Chukchi and Beaufort Seas (Cameron et al. 2010). 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 hauling out (Stirling et al. 1977; Stirling et al. 1982). Additionally, they typically prefer water depths between 25 and 75 meters (Stirling et al. 1977; Stirling et al. 1982) for easier access to benthic prey (Stirling 1997). Sea ice begins to break up during the late winter and spring, producing ice floes and exposing edges of fast ice (ice that is grounded to the seafloor or connected to the coastline) where females haul out and give birth to their pups (Burns 1981). Although there are some reports of parturition occurring in the water (Burns 1967), females are usually found on broken pack ice to whelp and nurse their young (Burns 1981). This inherent reliance on the timing of sea ice break-up in the spring and freeze-up in the fall may lead to significant impacts on their reproductive success if recent trends toward a growing ice-free summer period continue. In addition to using the sea ice for pupping, bearded seals haul out on sea ice in

May-June during their peak molting season. Typically, molting prompts bearded seals to haul out on sea ice more frequently to avoid increased susceptibility to cold temperatures and increase successful regrowth of hair (Burns 1981; Fedoseev 2000; Cameron et al. 2010). Declines in sea ice extent and presence may increase energetic costs for bearded seals to successfully molt and thereby decrease their survival rate.

Like walruses, bearded seals are primarily benthic feeders with the bulk of their diet made up of mollusks and crustaceans. Although they are considered foraging generalists due to their ability to incorporate a wide variety of prey in their diet, they generally prefer to forage on prey in water depths less than 100 m (Burns 1981; Burns 1981; Kingsley et al. 1991). If the spring and summer ice edge eventually retreats farther north into the deep waters of the Arctic Ocean basin, access to shallower waters to forage for benthic prey will decrease. This will lead to increased foraging efforts, resulting in increased energetic requirements and potentially, reduced vital rates.

Bearded seals are highly vocal and use elaborate underwater vocalizations to advertise breeding condition or establish aquatic territories (Cleator et al. 1989; Van Parijs et al. 2004; Risch et al. 2007). Males are the primary source of underwater vocalizations (Ray et al. 1969; Davies et al. 2006) producing reproductive displays during the breeding season (Van Parijs and Clark 2006). Typical call types consist of several variations of a long frequency modulated (FM) trill in addition to moans and groans that typically range in frequency from 130–4800 Hz (Ray et al. 1969; Stirling et al. 1983). Some trills can propagate more than 20 km and last as long as 3 min (Cleator et al. 1989). While most work on bearded seal acoustics has taken place during mating season (spring months) due to their increased vocal activity, relatively little work has been done during the rest of the year.

The introduction of passive acoustic monitoring has allowed for increased observations and a better understanding of marine mammal behavior in Arctic and sub-Arctic ecosystems (e.g. Moore et al. 2010). Most marine mammals spend a majority of their time underwater and produce underwater vocalizations to communicate, which has made passive acoustics an invaluable tool for examining marine mammal behavior. Acoustic observations provide a missing link in visual observational data collection, allowing for data to be collected in remote locations, in poor weather, at night (Mellinger et al. 2007), and during winter months when surface observations are simply impossible.

Autonomous passive acoustic monitoring employs hydrophones moored on the seafloor that collect

acoustic data for extended periods of time. This type of acoustic data collection allows underwater sounds to be recorded year-round and provides an index of occurrence for vocal species in proximity to recording locations (Mellinger et al. 2007). By identifying species acoustically, scientists have been able to track regional and seasonal interspecific and intraspecific movements and distributions (Mellinger et al. 2007).

Due to the recurrent vocal activity of bearded seals, acoustic monitoring can be an effective method to examine the relationship between bearded seal distribution and changing sea ice conditions.

The bearded seal is a widely distributed marine mammal, but they are a relatively solitary, which makes using typical investigative methods, such as visual observations, difficult. In circumstances such as this, passive acoustics can compensate for the lack of visually accessible information.

The present study examined the year-round vocal behavior of bearded seals in the Bering, Chukchi, and Beaufort Seas (BCB). The aims of this project were two-fold. The first objective was to investigate the year-round vocal behavior of male bearded seals in the Beaufort Sea from 2008 through 2010. Seasonal vocal activity was then compared to environmental conditions through the analysis of year-round vocal activity from three locations in the Beaufort Sea, *in situ* water temperature, and sea ice concentration around each location. Although bearded seal vocal activity has been studied in the Beaufort Sea, most research has only been performed during the spring months (Van Parijs et al. 2001; Van Parijs and Clark 2006). Furthermore, no research has examined the relationship between bearded seal presence and surrounding environmental conditions. Results from the present study are published in *Polar Biology* (Chapter 1; MacIntyre et al. 2013).

The second objective of this project was to examine the regional variability of bearded seal call activity in the BCB from 2008 through 2011. This study examined year-round distributions of vocally active bearded seals from 10 different locations in the BCB. Results of seasonal vocal activity were then compared with sea ice throughout the year to provide insight on how local, regional, seasonal, and interannual variability of sea ice conditions influence bearded seal distributions in Alaskan waters (Chapter 2). Previous acoustic research has examined bearded seal acoustic behavior in the BCB, but most work has focused on a single region (Risch et al. 2007; Van Parijs and Clark 2006; Hannay et al. 2013).

This study provides insight into the effect climate-induced sea ice loss will have on the bearded seal population in the BCB. Diminishing and variable sea ice conditions will lead to the loss of important

bearded seal habitat, thereby impacting bearded seal foraging and reproductive success. Results of this study indicate a significant correlation between the distribution of vocalizing bearded seals and sea ice presence and distribution; with this knowledge a reevaluation of this species' conservation status may be warranted. Additionally, determining the preferred habitat of bearded seals during key life history activities may impact critical habitat designation for this *threatened* Arctic species (US Endangered Species Act of 1973 (73 FR 16617)).

## Chapter One

### **Year-round acoustic detection of bearded seals (*Erignathus barbatus*) in the Beaufort Sea relative to changing environmental conditions, 2008-2010<sup>1</sup>**

#### **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 through August 2010 at two locations and a single year (2008-09) at a third location, in the western Beaufort Sea. Three recorders in 2008-09 and one in 2009-10, had a 30% duty cycle and a bandwidth of 10-4096 Hz, and one in 2009-10 had a 20% duty cycle and bandwidth of 10-8192 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 break-up 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.

#### **Key words:**

**bearded seal, *Erignathus barbatus*, Beaufort Sea, acoustics, sea ice concentration**

## 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 break-up 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 U.S. 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; Burns 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 – 4800 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 (McClaren 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 sub-surface oceanographic moorings (Fig. 1.1) in the Beaufort Sea over a 2-year period. These instruments recorded in the frequency range 10-4096 Hz or 10-8192 Hz (Table 1.1). 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 2008-09 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 1.1). The instruments redeployed in August of 2009 were recovered 1 year later. One instrument deployed in 2009-10 was set to record on a 20% duty cycle (14 min every hour), while the other retained the original 30% duty cycle (9 min every 30 min) used in the previous year. 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. 1.2, 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 was 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 beginning of each data file (duty cycle). The temperature sensor had a sensitivity between -10 to +40°C and a resolution of 0.0625°C. Average daily temperature values were computed from these hourly- or bi-hourly 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.

## **Results**

Bearded seal vocalizations were detected in the Beaufort Sea in all 12 months at sites A1 and A3 and 11 months at site A2 from 2008-2010. Of the 43,296 h of acoustic data recorded from all sites in both years, vocalizations were identified in 16,030 h (Table 1.2). 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, and 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 from 19 August 2008 through 17 July 2009 and from 1 August 2009 through 12 August 2010 (westernmost site, Fig. 1.1). Few calls were present from July through 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 through early July 2010 (Fig. 1.3a). The percentage of the total hours with bearded seal calls at A1 was similar between years (Table 1.2): 53.7% in 2008-09 and 46.4% in 2009-2010.

Sea ice began to form at A1 on 21 October 2008 and increased to greater than 90% mean concentration by 7 November 2008 (Fig. 1.3b). Maximum sea ice concentration (95-100%) lasted from early November 2008 until 30 June 2009, when it dropped to approximately 75% and then continued to decline rapidly; the mooring was in open water by 18 July 2009. Sea ice around A1 began to form again on

about 14 November 2009 and increased rapidly to greater than 80% mean concentration by 21 November 2009. Maximum sea ice concentration persisted until 15 July 2010, when it dropped below 80% and continued to decrease. By 5 August 2010, the area around the mooring was in open water.

During the first year of deployment (2008-09), *in situ* water temperature at A1 ranged from  $-1.8^{\circ}$  to  $0.5^{\circ}\text{C}$  with a mean temperature of  $-1.4^{\circ}\text{C}$  (Fig. 1.3c). During the second year (2009-10), the overall mean temperature was almost  $1^{\circ}\text{C}$  higher ( $-0.7^{\circ}\text{C}$ , range  $-1.8^{\circ}$  to  $3.9^{\circ}\text{C}$ ). From 15 August to 15 September for each year, the greatest difference can be attributed to a late summer pulse of warm water. In 2008, the mean temperature was  $-1.2^{\circ}\text{C}$ , whereas for the same period in 2009 it was  $+1.0^{\circ}\text{C}$ .

### Site A2

Calls at A2 (central site, Fig. 1.1) were recorded year-round with the lowest number of hours with calls occurring in July, August and November (Fig. 1.4a). 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 2008-09 and 2009-10 when comparing the number of hours with bearded seal calls to the total number of hours recorded (Table 1.2): 27.9% and 23.5%, respectively.

Sea ice began to form at A2 on 14 October 2008 and by 6 November 2008 the area was completely ice-covered (Fig. 1.4b). Greater than 90% sea ice concentration lasted from 6 November 2008 until 21 June 2009, when it dropped to approximately 43% and then decreased rapidly such that the mooring was in open water by 25 June 2009. Sea ice formed again on 12 November 2009 and increased rapidly to greater than 90% mean concentration by 21 November 2009; 95-100% sea ice concentration persisted one month longer in 2010, until 27 July, at which time it declined to below 90% and continued to decline to completely open water by 16 August 2010.

During the first year of deployment (2008-09), *in situ* water temperature at A2 ranged from -1.6° to 0.6°C with a mean temperature of -1.2°C (Fig. 1.4c). During the second year (2009-10), 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 in 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 one year during 2008-09 (Table 1.1). Bearded seal calls were present at site A3 from 19 September 2008 through 16 July 2009 (Fig. 1.5a). No calls were recorded prior to mid-September, when call activity increased to 6.5 h/d. These quickly decreased to zero again 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 A 2 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 2008-09 (Table 1.2).

Sea ice began to form at A3 on 13 October 2008 and remained above 90% mean concentration from 1 November 2008 to 16 June 2009 (Fig. 1.5b). Ice concentration continued to rapidly decline and the instrument was in open water 8 days later.

*In situ* water temperature at A3 during 2008-09 ranged from -1.6° to 1.9°C with a mean temperature of -1.1°C (Fig. 1.5c).

### **Discussion**

This is the first study to show year-round production of sound by bearded seals. In the Beaufort Sea from 2008-2010, bearded seal calls were recorded year-round (i.e., in all 12 mo) in both years and at all locations. 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; Burns 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, Van Parijs et al. 1999; Weddell seals, Rouget et al. 2007; Weddell, Ross, leopard, and crabeater seals, 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, 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. 2003). 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; Van Parijs et al. 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 season (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; 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 2008-09 and 2009-10 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; Van Parijs et al. 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 one day, in 2009, and less than one 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 to 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 one 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 2009-10 than in 2008-09. 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 2009-10 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 2009-10 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%-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. *In press*). 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; Van Parijs et al. 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 - 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 – 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 2008-09 to 2009-10; 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 2008-2010 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 sub-adult 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 romarus*, 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., LeBoeuf 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; Bengston 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 v. 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 2008-09 and 2009-10 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.

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## Figure Captions

**Fig. 1.1** Hydrophone locations in the flaw lead polynya in the Alaskan Beaufort Sea from 2008-2010. Sea ice depicted (12.5 km<sup>2</sup> 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>)

**Fig. 1.2** Spectrogram displaying example bearded seal calls recorded at location A1 on 03 March 2010. Fast Fourier transformation (FFT) 2048, 50% overlap, Hann window

**Fig. 1.3** 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 2008-09 and 2009-10 than site A2 or A3

**Fig. 1.4** 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

**Fig. 1.5** 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

**Table 1.1** Deployment details for the Beaufort Sea 2008–2010

Instrument ID	Location	Recording dates	Instrument Depth (m)	Sample rate (Hz)	Duty cycle
A1 2008	71.56N 155.59W	8/15/08-7/27/09	94	8192	9/30 min
A2 2008	71.46N 152.25W	8/15/08-8/2/09	131	8192	9/30 min
A3 2008	71.13N 149.46W	8/15/08-8/1/09	46	8192	9/30 min
A1 2009	71.76N 154.48W	8/1/09-8/14/10	102	16384	14/60 min
A2 2009	71.45N 152.50W	8/4/09-8/11/10	95	8192	9/30 min

**Table 1.2.** Recording details for each location 2008–2010

Instrument ID	Total recorded hours	Number of hours with calls	Percent hours with calls
A1 2008	8328	4474	53.7%
A2 2008	8472	2367	27.9%
A3 2008	8448	2865	33.9%
A1 2009	9096	4217	46.4%
A2 2009	8952	2107	23.5%

Fig. 1.1

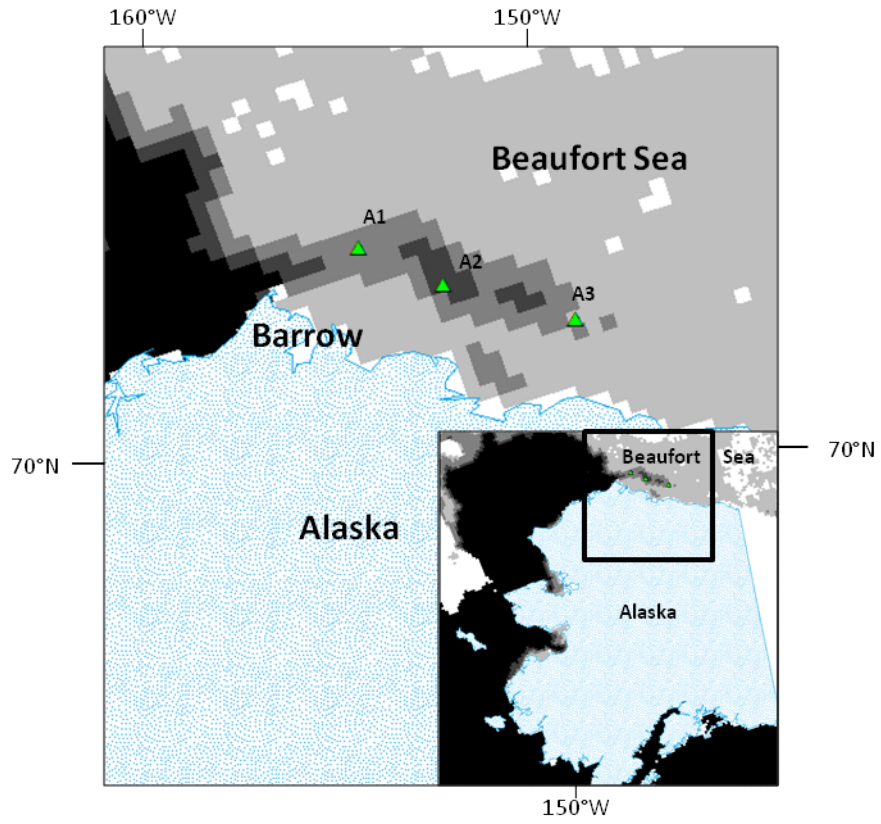


Fig. 1.2

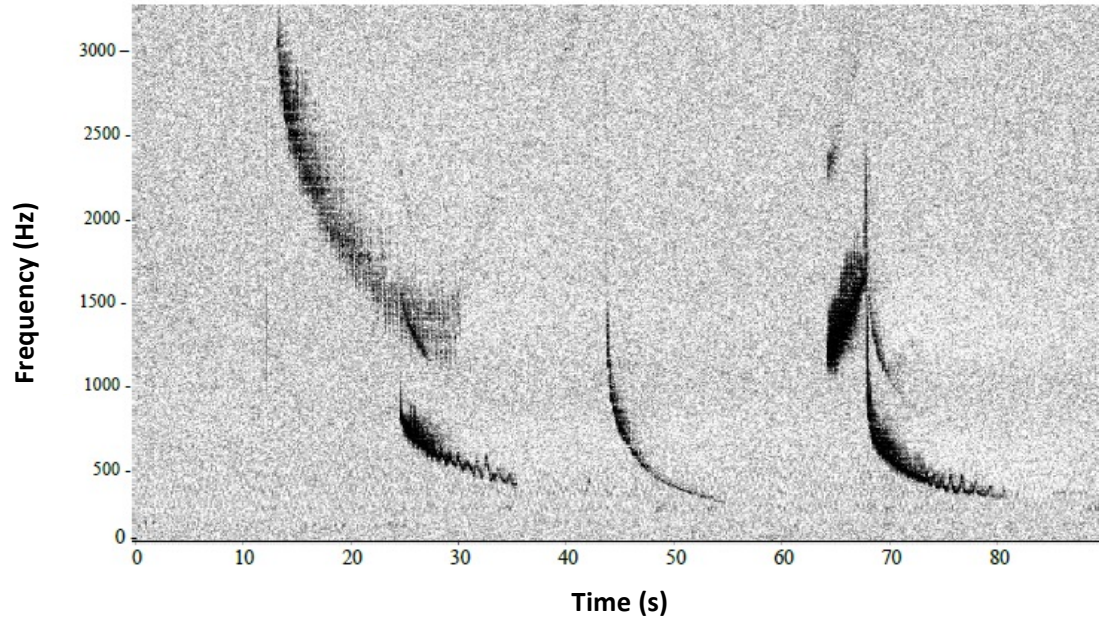


Fig. 1.3

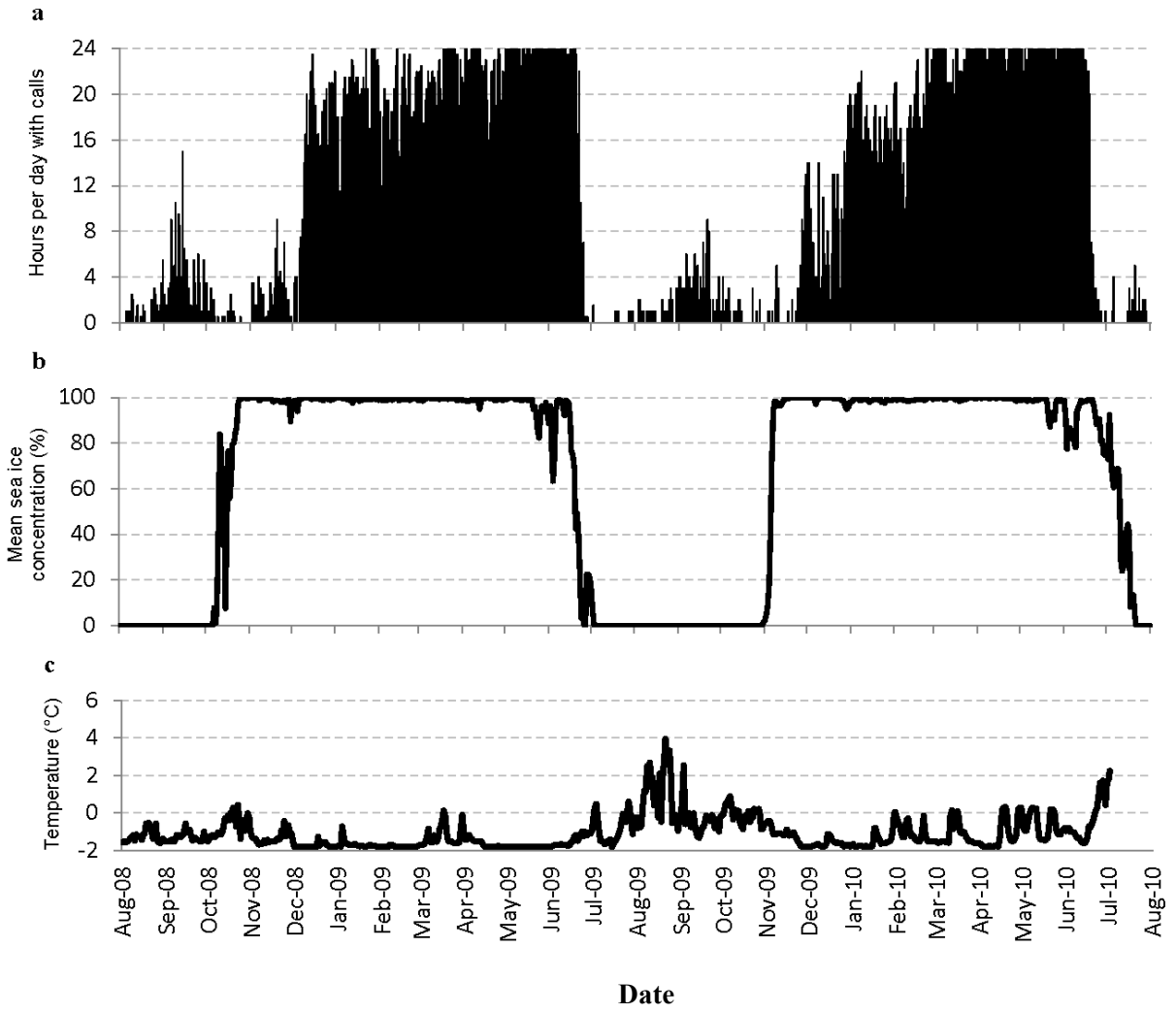


Fig. 1.4

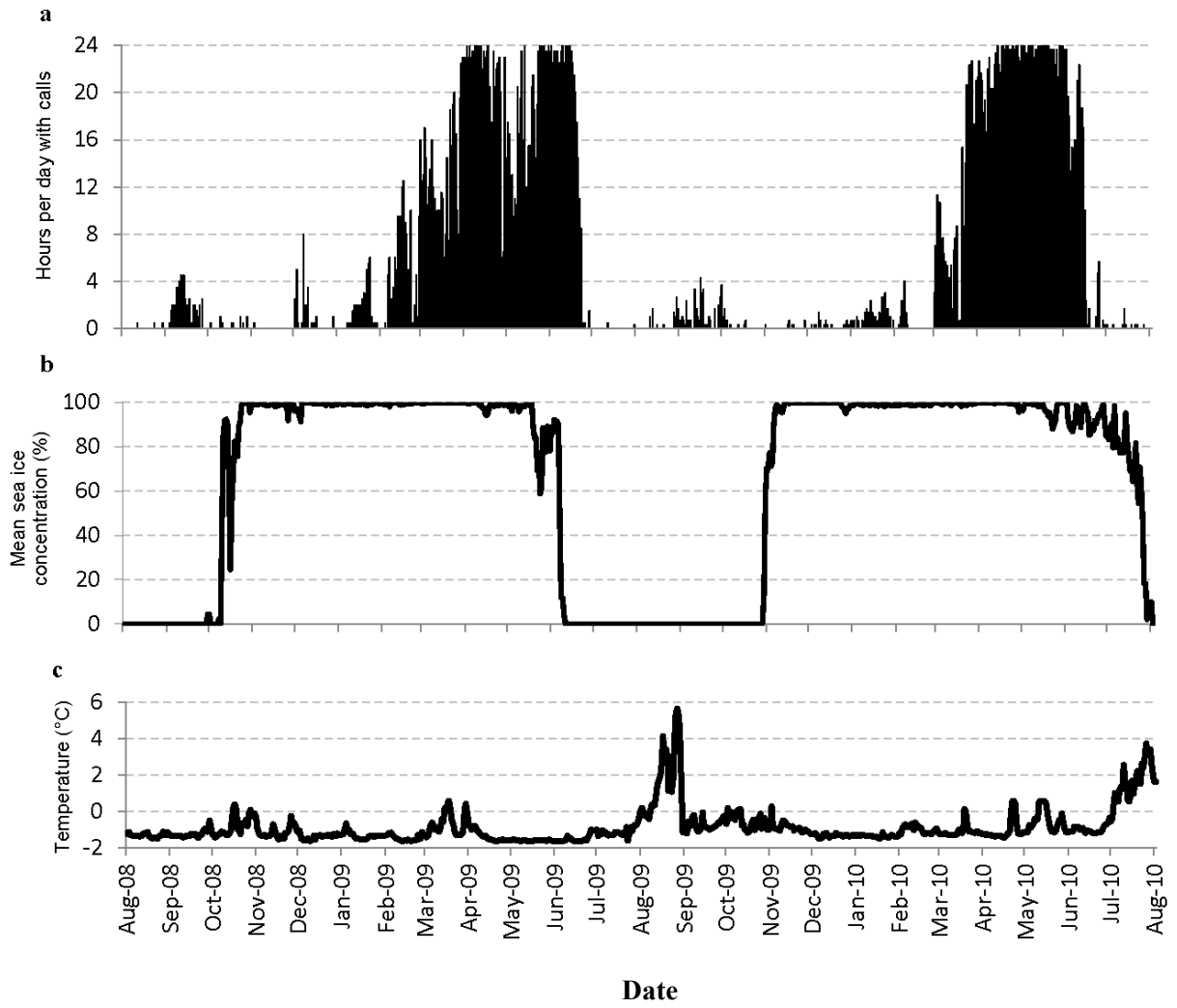
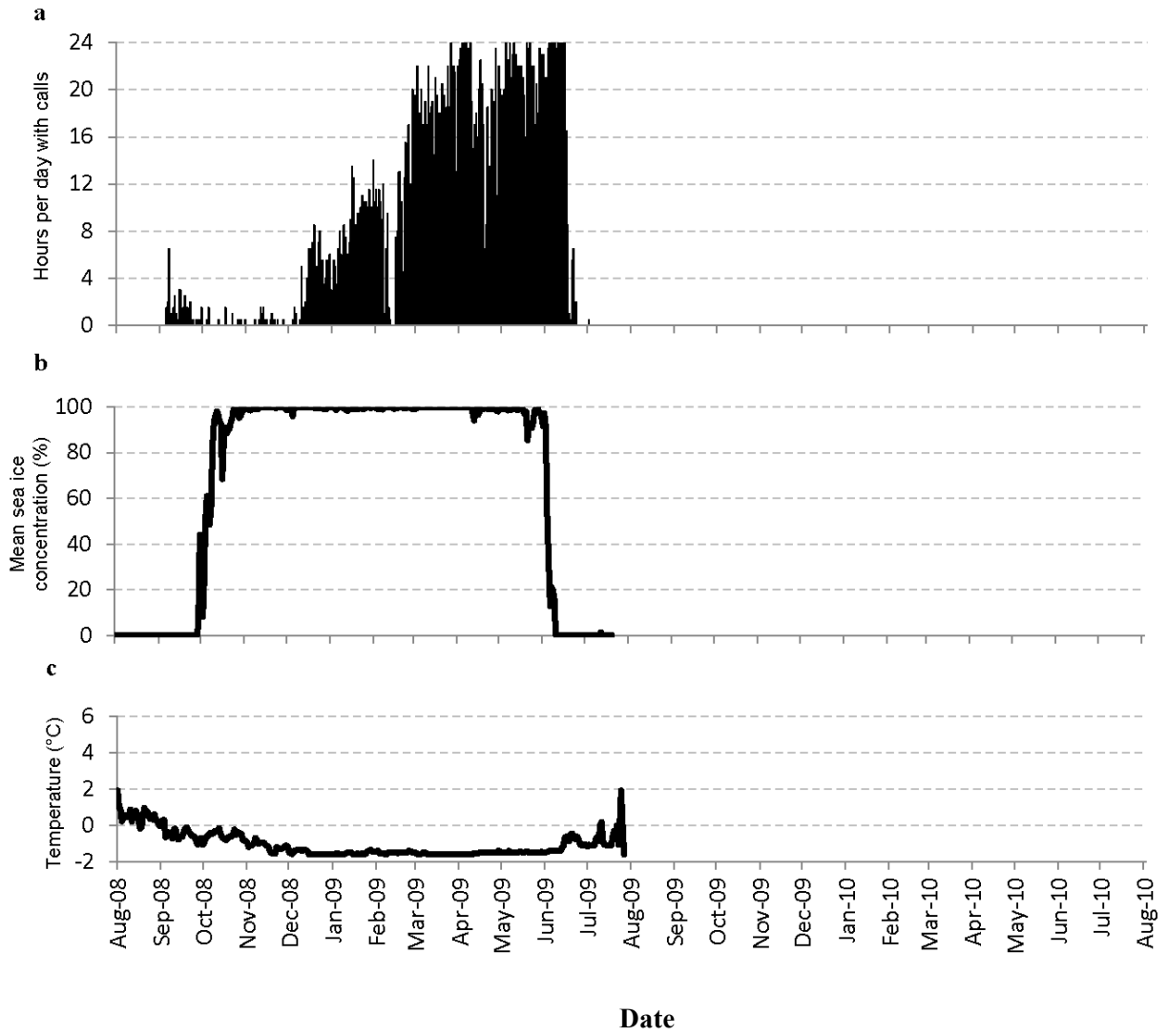


Fig. 1.5



**The relationship between sea ice concentration and the spatio-temporal distribution of vocalizing bearded seals (*Erignathus barbatus*) in the Bering, Chukchi, and Beaufort Seas from 2008-2011**

**Abstract**

Bearded seals (*Erignathus barbatus*) are widely distributed in the Arctic and sub-Arctic; the Beringia population is found throughout the Bering, Chukchi and Beaufort Seas (BCB). Bearded seals are highly vocal seals, using underwater calls to advertise their breeding condition and maintain aquatic territories. They are also closely associated with pack ice for reproductive activities, molting, and resting. Sea ice habitat for this species varies spatially and temporally throughout the year due to differences in underlying physical and oceanographic features across their range. To test the hypothesis that variations in sea ice will influence vocal activity of bearded seals and their distributions, passive acoustic data were collected from ten locations throughout the BCB from 2008–2011. Instruments sampled on varying duty cycles ranging from 20% to 100% of each hour, and at frequencies up to 8192 Hz. Spectrograms of acoustic data were analyzed to calculate the daily proportion of hours with bearded seal calls at each sampling location, and these call activity proportions were compared to satellite-derived daily sea ice concentration. Bearded seals were vocally active nearly year-round in the Beaufort and Chukchi Seas with peak activity occurring in the spring during the mating season. The duration of call activity in the Bering Sea was shorter, lasting typically only five months, and peaked in the spring. Call activity was found to increase with higher sea ice concentration ( $p < 0.01$ ), possibly due to the bearded seal's necessity of a stable platform during key life history activities (breeding, pupping and molting). These results suggest that recent Arctic warming and dramatic losses in ice cover, will negatively impact populations of bearded seals.

**Introduction**

Bearded seals are a pan-Arctic species that is closely associated with sea ice using the ice as a platform for reproduction, molting, and rest between foraging trips (Burns, 1970; Burns, 1981; Nelson et al. 1984; Moore and Huntington, 2008). Currently, very little is known about the bearded seal distribution and population size in Alaskan waters, or even across the circumpolar Arctic. Even less is known about the potential distribution shift of the bearded seal as the sea ice varies between years.

In recent years, the Arctic has experienced an increasingly variable climate and dramatic sea ice loss (Walsh 2008; Maslanik et al. 2011). Sea ice extent has declined over the past 30 years with a more noticeable decline in recent years (<http://nsidc.org/data/collections.html>, Cavalieri et al. 2004). In September 2013, the summer minimum sea ice extent reached a new record low (<http://nsidc.org/data/collections.html>). The reduction in sea ice cover has coincided with an increase in open water periods and a reduction in sea ice thickness (Maslanik et al. 2007; Tschudi et al. 2010; Maslanik et al. 2011; Richter-Menge et al. 2013). Continued seasonal sea ice loss will potentially impact marine mammal distributions in Arctic and sub-Arctic waters (Learmonth et al. 2006; Moore and Huntington 2008; Laidre et al. 2008; Kovacs et al. 2011; Van Opzeeland et al. 2012).

The seasonal formation and retreat of sea ice in the BCB influences the ecosystem regionally (by sea) as well as locally (fine-scale) and there are distinct oceanographic processes that occur within each region that influence the formation/retreat cycle (Hunt et al. 2011; Sigler 2011; Grebmeier 2012; Stabenot et al. 2012). Sea ice begins to form in mid-autumn in the Beaufort Sea and remains frozen until early summer. The clockwise motion of the Beaufort Gyre dominates the circulation in the Beaufort Sea and helps maintain the perennial and seasonal sea ice cover (Maslanik et al. 2011), creating a stable platform for bearded seals to haul out upon during key life history activities (Burns 1970; Burns 1981; Nelson et al. 1984; Moore and Huntington 2008). The Beaufort Sea is generally less productive than either the Chukchi or Bering Seas, though an important benthic hotspot exists within the Beaufort Sea at the head of Barrow Canyon (Grebmeier 2012).

Sea ice in the Alaskan Chukchi Sea is dominated by a flaw lead, which when combined with variable surface winds leads to more open water and highly mobile sea ice along the coast in the northern Chukchi Sea (George et al. 2004). Unlike in the Beaufort Sea, ice cover is primarily seasonal and more mobile in the Chukchi Sea (George et al. 2004). The Chukchi Sea is highly productive, containing many benthic hotspots (Springer et al. 1996; Lee et al. 2007; Gradinger 2009), but some areas, particularly the near shore waters that lie along the Alaska Coastal Current (ACC), are lower in nutrients and benthic biomass is more variable than the rest of the region (Feder et al. 2007).

Even more so than the Chukchi Sea, the Bering Sea experiences continual shifts in sea ice conditions. The Bering Sea lies furthest south leading to a delayed formation of sea ice in the winter and

earlier retreat of sea ice in the spring. Additionally, the sea ice in the Bering Sea is more dynamic in comparison to the Chukchi and Beaufort Seas, where the repeated growth and melt of sea ice strongly influences the ecosystem through its role in the timing and magnitude of the phytoplankton bloom. Changes in timing of sea ice formation and retreat will considerably impact the benthic-pelagic coupling in each region, having a cascading effect on upper trophic levels (Stabeno et al. 2001; Hunt et al. 2002).

During most of the year, bearded seals are typically found on pack ice in shallow shelf water areas (less than 100 m) and maintain proximity to their preferred benthic prey source (Stirling et al. 1977; Stirling et al. 1983; Kovacs 2002; Cameron and Boveng 2009). There is still little information available about their spatio-temporal distribution in the BCB throughout the year. Large numbers of bearded seals in Alaskan waters are thought to move north as the seasonal sea ice retreats in the spring, and subsequently move south in the autumn/winter as sea ice forms (Potelov 1969; Burns 1981; Simpkins et al. 2003; Frost et al. 2008). More recently, satellite telemetry data have confirmed this pattern, and male bearded seals in the Bering Sea subpopulation appear to exhibit strong winter site fidelity, establishing preferred sites as early as sub-adults (Boveng et al. 2013). At the same time, acoustic analyses of bearded seal calls have shown that some bearded seals are present year-round in the Beaufort (MacIntyre et al. 2013) and Chukchi Seas (Hannay et al. 2013) and therefore may not migrate with the ice edge as it advances and retreats through the Bering Strait. Bearded seals rely on sea ice for critical life history activities and the presence of vocalizing bearded seals is correlated with increased sea ice concentrations (MacIntyre et al. 2013); therefore, any extreme variation in their sea ice habitat may have a considerable effect on the persistence of the population.

Upper trophic level species, such as bearded seals, will be especially vulnerable to changing sea ice conditions through the loss of habitat and a shift in prey distribution (Tynan and DeMaster 1997). Bearded seals are shallow-diving benthic feeders that rely on sea ice to gain access to prey. This access may become more limited as the sea ice continues to decline by forcing bearded seals and other benthic feeders (especially walrus) onto shore or into areas past the continental shelf edge into deeper waters, making access to prey more difficult (Udevitz et al. 2013). Deeper dives and greater distances to travel for preferred prey may subject bearded seals to energetic stress as they attempt to gain access to, or forage in, areas outside of their typical shallow-water feeding habitat. Additionally, previously benthic-dominated

regions may become more pelagic-dominated, leading to increased competition for preferred prey species as more temperate species move north causing distributions of Arctic and temperate species to overlap (Moore and Huntington, 2008).

Bearded seals are readily identifiable as a species from their call types, and therefore passive acoustic monitoring can be used to assess their distribution. Because male bearded seals begin vocalizing as juveniles and continue to develop their vocal repertoire throughout their lives (Davies et al. 2006), analysis of acoustic activity can distinguish between a wide range of male ages within the population. Although males are the primary source of vocal activity, there is no conclusive evidence that gender-based habitat preferences exist, especially during mating season when the distribution of male bearded seals is influenced by female behavior (Van Parijs et al. 2004). Therefore, acoustic detection can be considered representative of the presence of male and female seals. Typically, bearded seal vocal activity increases during the spring months, which coincides with mating season but call activity begins much earlier (Hannay et al. 2013; MacIntyre et al. 2013).

This study examines year-round distributions of vocally active bearded seals in the BCB, and assesses their relationship with sea ice throughout the year to provide insight on how local, regional, and interannual variability influence bearded seal distributions. The key hypothesis we test is that sea ice concentration influences the presence of vocalizing bearded seals throughout the year and therefore more vocal activity should be detected during periods of higher sea ice concentration. Additionally, we explored the theory that geographic variability exists in bearded seal call activity among the BCB that may be directly or indirectly related to sea ice conditions.

## **Methods**

### ***Acoustic data collection and sampling procedures***

Passive acoustic recorders (Aural-M2, <http://www.MultiElectronique.com>) were deployed on ten sub-surface oceanographic moorings (Fig. 2.1) in the BCB for one to three years. Four were moored in the Beaufort Sea, two in the Chukchi Sea and four in the Bering Sea. Data from three of the Beaufort Sea moorings (A1, A2, and W1) from 2008–2011 were previously analyzed in MacIntyre et al. (2013), however, the results are included in the analysis implemented in this paper as a means of comparison with other regions. The ten instruments sampled in frequency ranges 10-2048 Hz, 10-4096 Hz, or 10-8192 Hz

(Table 2.1). All recorders were suspended 5 m above the seafloor to minimize the risk of disturbance or damage from overhead ice keels at depths around 40 m in the Chukchi Sea, 70 m in the Bering Sea, and up to 180 m in the Beaufort Sea (Table 2.1). Instrument packages were set to record for an entire year and sampling rates were sufficient for recording acoustic energy from bearded seals.

All instruments were deployed for a year, recovered in the following year and then redeployed for a nearly continuous dataset from many of the sites over the three-year study period (Table 2.1). Instruments sampled on varying duty cycles ranging from 23% of each hour (e.g., recorded 14 min out of every hour) to continuous recordings (Table 2.1). Site M2 had a unique deployment/recovery schedule. It was recovered in mid-October 2009 after it recorded for only 6 months, and a replacement instrument was deployed during the same cruise. This new instrument recorded continuously rather than on a duty cycle like the previous instrument at M2, and stopped early on 6 March 2010 (Table 2.1). Instruments deployed in 2009 at M5 and M4 in the Bering Sea were set to record until June 2010, but stopped prematurely in late March/early April 2010, while the instrument at site M8 recorded until early May 2010. A single year (2010–2011) of data was collected at two sites in the Chukchi Sea. Both instruments in the Chukchi Sea sampled in the frequency range 10–8192 Hz. The two Chukchi Sea instruments were set to unique duty cycles from the Beaufort and Bering Sea instruments. They recorded on a staggered loop 31% duty cycle, where 95 min out of every 300 min period for each day were recorded and each consecutive day the recording start time advanced by one hour, allowing for all hours in a day to be recorded every four days; this yielded an average of approximately 10 h/d sampled at both locations in the Chukchi Sea (Table 2.1).

Archived digital acoustic data were downloaded from each recorder. For all years, full file-length spectrograms, characterized by the duty cycle (e.g., Fig. 2.2, 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 (Fig. 2.2) using the program Ishmael 1.0 (Mellinger 2001). A total of 113,462 h of acoustic data, 51,572 h from the Beaufort Sea (including data from MacIntyre et al. 2013), 5630 h from the Chukchi Sea, and 56,160 h from the Bering Sea, were examined for bearded seal calls (Table 2.2). Files with calls were manually identified and the presence or absence of bearded seal calls was noted for each acoustic data file. Bearded seal presence was calculated as a ratio of hours per day with at least one bearded seal call observed. Because the data collected in the Chukchi Sea varied from the other

regions with fewer total hours per day available at both sites, comparisons between all sites and regions were made based on daily proportions of hours with calls out of the total recorded hours.

### ***Environmental data***

Sea ice concentration data (AMSR-E Aqua 12.5 km resolution) from the BCB from 2008–2011 were obtained from the National Snow and Ice Data Center (NSIDC, <http://nsidc.org/data/collections.html>). 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) to determine the mean daily sea ice concentration within a 20-km radius around each mooring site. While most bearded seal calls in the recordings were likely produced within 5 km of the instruments, a small percentage of calls (~15%) can be heard at distances up to 20 km (Cleator et al. 1989); therefore a 20-km radius was chosen to account for the maximum detectable range of all vocalizing bearded seals. Daily sea ice concentration data at each mooring location were compared with the proportion of hours per day with bearded seal calls.

### ***Statistical analysis***

We conducted statistical analysis of acoustic data recordings to investigate whether the rate of seal vocal presence was related to percent sea ice concentration. Several sources of error/bias may occur during data analysis, including (i) data collected at individual sites were subject to temporal autocorrelation and (ii) duty cycles of acoustic recording devices were different among sites and changed over time. The first consideration is important because ignoring temporal autocorrelation can result in overinflated measures of precision; the second is important because hydrophones are more likely to record seal vocalizations the longer they are left on.

To account for temporal autocorrelation and duty cycle variability, a time series model for acoustic records was specified that was parameterized in terms of continuous time hazard rates. Letting  $N_{i,t}$  denote the number of duty cycles on day  $t$  at site  $i$ ,  $Y_{i,t}$  denote the number of such duty cycles where seal vocalizations were detected, and  $p_{i,t}$  denote the probability that at least one seal vocalizes during a duty cycle, within the range of detectability at the site,

$$Y_{i,t} \sim \text{Binomial}(N_{i,t}, p_{i,t}).$$

Temporal autocorrelation was modeled and allowed unequal duty cycle lengths by providing further structure on  $p_{i,t}$ . Unequal duty cycle length was accommodated by writing the model in terms of the rate at which seal vocalizations are present. Assuming that the rate of vocalizations is constant within a given day at a given site (i.e., a constant hazard rate), the probability of detecting a seal call in a duty cycle of length  $T_{i,t}$  can be given by

$$p_{i,t} = 1 - \exp(-T_{i,t}\lambda_{i,t}),$$

where  $\lambda_{i,t}$  is the instantaneous rate at which seal vocalizations are present (see, e.g., Cox and Oakes 1984).

Environmental covariates were incorporated by imposing a linear model for this rate:

$$\log(\lambda_{i,t}) = \mathbf{X}_{i,t}\boldsymbol{\beta}.$$

Here,  $\mathbf{X}_{i,t}$  is a vector of environmental covariates for site  $i$  at time  $t$  (including a value of 1 for an intercept), and  $\boldsymbol{\beta}$  is a vector of regression coefficients.

Temporal autocorrelation within sites was accounted for by conducting estimation under a generalized estimating equations framework with an AR1 working correlation structure (Liang and Zeger 1986; Halekoh et al. 2006). This framework bases inference on the first two moments of the binomial response vector, namely the mean (which is possibly related to environmental covariates), and the variance-covariance matrix of the responses. It is in the latter component that a time-series structure with temporal autocorrelation can be specified.

The R package `geepack` (Halekoh et al. 2006) was used to fit generalized estimating equations models with AR1 autocorrelation structure to the bearded seal data. This analysis provides inference about the effect of covariates across the population of sites (i.e., not controlling for individual variation in sites). To implement the proposed model (i.e., to model the effects of covariates on the rate of seal vocalizations, as opposed to absolute probabilities), a binomial error structure was specified with a complementary log-log link function and an offset for duty cycle length. Separate analyses were conducted for hydrophones located in each of three regions (Beaufort, Bering, or Chukchi seas), using the proportion of sea ice as an explanatory variable (including both linear and quadratic effects). Wald-type test statistics were used to examine significance of sea ice and the choice of an AR1 error structure (note that formal model selection procedures are not possible using GEEs). Population mean predictions at different covariate values were generated from this fitted model as

$$\hat{p} = 1 - \exp(-20 \exp(\tilde{\mathbf{X}}\hat{\boldsymbol{\beta}})),$$

where  $\tilde{\mathbf{X}}$  denotes a design matrix for prediction points, and  $\hat{\boldsymbol{\beta}}$  denotes estimated regression coefficients. Here, predictions were standardized to a 20-minute time interval (the average duty cycle length over the course of the study was 20.4 minutes). A 95% confidence interval on population mean predictions were computed as

$$(LI, UI) = 1 - \exp(-20 \exp(\tilde{\mathbf{X}}\hat{\boldsymbol{\beta}} \pm 1.96\mathbf{SE})),$$

where the vector of standard errors,  $\mathbf{SE}$ , was computed over the design points as the square root of the diagonal elements of  $\tilde{\mathbf{X}}\hat{\boldsymbol{\Sigma}}\tilde{\mathbf{X}}'$ . Here,  $\hat{\boldsymbol{\Sigma}}$  denotes the estimated variance-covariance matrix of model parameters output by geepack (note that confidence intervals and prediction standard errors are not standard outputs of geepack) and  $LI$  and  $UI$  denote the lower and upper intervals of the 95% confidence interval.

Using a method that accounted for temporal autocorrelation in seal vocalizations was important in this application. Initial model fitting using generalized additive models (e.g., Wood 2006), produced residuals that were extremely autocorrelated (e.g., a lag-30 autocorrelation of 0.5) and covariate effects appeared multimodal. Temporal autocorrelation serves to decrease the number of data points that are truly independent; ignoring this feature in the data will overinflate precision and encourage overfitting. The approach in this paper was to use generalized estimating equations with an autoregressive formulation for the second moments of the data. This approach is common in longitudinal studies (i.e., where data are gathered at multiple points in time on the same subject), and is an accepted way to account for temporal autocorrelation in studies where population level effects are of interest. There are some disadvantages, however, as one cannot account for individual heterogeneity (e.g., through individual random effects) or use likelihood-based criteria for selecting amongst or averaging over alternative models.

## Results

Bearded seal vocalizations were detected at all sites in the BCB from 2008–2011. Seasonal variability in call activity was observed at each site and the overall trend in variability for all sites was correlated with the presence of sea ice. Of the total 113,462 h of acoustic data recorded from all sites from 2008–2011, bearded seal vocalizations were detected in 35,440 h (Table 2.2). In all three regions, the highest proportion of call activity occurred during the spring months, coinciding with mating season. Overall vocal activity was similar in the Beaufort and Chukchi Seas, but less vocal activity was detected in

the Bering Sea. Statistically significant curvilinear relationships were found between call activity and sea ice concentration where the rate of bearded seal vocal presence increased with the proportion of sea ice concentration ( $p < 0.01$ ) within all regions in the BCB, where both linear and quadratic effects were apparent for both the Bering and Chukchi Seas. Since the probability of vocal presence was modeled on the complementary log-log scale these effects appear curvilinear on the probability scale (Fig. 2.4).

### ***Beaufort Sea***

Bearded seal vocalizations were detected in nearly all months from 2008–2011 at all locations in the Beaufort Sea (Fig. 2.3). Of the 51,672 h of acoustic data recorded from all sites the Beaufort Sea, vocalizations were identified in 18,751 h (Table 2.2). Strong seasonal variability in call activity was observed at all sites and during all years in the Beaufort Sea. At all sites, call activity began increasing in January and continued through early July with nearly continuous calling (i.e. calls detected in all 24 h of the day) from mid-March through late June. During all three years of the study, there was a slight increase in call activity in the autumn (late September/early October) and the lowest call activity occurred during August and November. Call activity in the Beaufort Sea was highly correlated with sea ice concentration; the logarithm of the rate of bearded seal vocal presence in the Beaufort Sea was linearly related to the proportion of sea ice concentration (linear effect,  $p = 0.006$ ; quadratic effect,  $p = 0.348$ ). This relationship appears curvilinear because the probability of vocal presence was modeled on the complementary log-log scale (Fig. 2.4).

The overall trend was similar at each site, but some site variability was observed. As reported in MacIntyre et al. (2013), call activity was greatest at site A1, and the least amount of bearded seal call activity was recorded at site A2 during both years of data collection at that site. The percentage of total hours with bearded seal calls was similar at all sites in the Beaufort Sea (Table 2.2). Similar to results found at sites A1 and A2 from 2008–2010, reported in MacIntyre et al. (2013), there was strong seasonal variation in the call activity at the AON site (Fig. 2.3). The peak in call activity was also similar to other Beaufort locations occurring during the spring months.

Sea ice conditions were similar at all sites with some seasonal and interannual variability observed. Sea ice began forming during autumn at all locations in the Beaufort Sea (Fig. 2.3), and maximum sea ice concentration remained at each site into late June/early July. By mid-July the moorings

were typically in open water and void of sea ice through the beginning of October. These observed changes in seasonal sea ice conditions were linked with call activity, where the logarithm of the rate of bearded seal vocalizations in the Beaufort Sea increased linearly with the proportion of sea ice concentration. A plot of predicted ice effects by region indicated that the rate of seal vocal presence increases as a function of sea ice concentration (Fig. 2.4). The correlation parameter for the AR1 correlation structure indicated significant positive autocorrelation among consecutive duty cycles for the Beaufort Sea ( $\hat{\alpha} = 0.137$ ;  $SE = 0.006$ ;  $p < 0.001$ ).

### ***Chukchi Sea***

Bearded seal vocalizations were detected in all 10 months of recording at both sites in the Chukchi Sea (Fig. 2.3). Of the 5630 h of acoustic data recorded from both sites, vocalizations were identified in 2027 h (Table 2.2). There was, however, strong seasonal variation in the number of hours per day with calls. Calls began increasing during the early winter months (December/January) and continued through June. Nearly continuous calling (i.e. calls detected in all 24 h of the day) was observed at both sites from mid-March through late June. The lowest call activity at each site occurred in September, however a slight increase in call activity was observed in the autumn, which was similar to the increased activity observed at each site in the Beaufort Sea. Sea ice concentration was correlated with vocal activity. Both linear ( $p < 0.001$ ) and quadratic ( $p < 0.001$ ) effects of sea ice were significant, where call activity increased with increased sea ice concentration. Similar to the relationship observed in the Beaufort Sea, this relationship has a curvilinear appearance because the probability of vocal presence was modeled on the complementary log-log scale (Fig. 2.4).

Site variability in call activity was observed in the Chukchi Sea. The number of hours per day with calls was greater at A3, the inshore location, (1227 h) than C2, the offshore location (800 h). Site A3 is the only site where bearded seals remained highly active for several weeks after sea ice had melted in the area surrounding the mooring site. Other sites in the study had some activity in open water, but the activity was much less and duration shorter. However, small amounts of sea ice may still be present because fine-scale changes in sea ice are not reflected in the 12.5 km resolution of our sea ice data. The percentage of hours with call activity out of the total recorded hours at site A3 was 42.2. The offshore location (C2) in the

Chukchi Sea had much less overall call activity than the inshore site. Bearded seals were detected in 28.4 % of the total hours per recorded day at site C2 (Table 2.2).

Sea ice was less stable and the duration was slightly shorter in the Chukchi Sea than in the Beaufort Sea. Sea ice began forming in the autumn at both sites in the Chukchi Sea (Fig. 2.3). Maximum sea ice concentration (> 95%) lasted until early June at both sites. During the period of complete ice cover there were periods of lower sea ice concentration, which demonstrates a slightly less stable sea ice platform than observed in the Beaufort Sea. Declines in sea ice concentration coincided with decreased call activity. The logarithm of the rate of bearded seal vocalizations in the Chukchi Sea increased with the proportion of sea ice concentration, where the rate of seal vocal presence increased as a function of sea ice concentration and linear and quadratic effects were significant (Fig. 2.4). The correlation parameter for the AR1 correlation structure indicated significant positive autocorrelation among consecutive duty cycles for the Chukchi Sea ( $\hat{\alpha} = 0.011$ ;  $SE = 0.001$ ;  $p < 0.001$ ).

### ***Bering Sea***

In the Bering Sea, call activity was more variable between sites than the other two regions, and a lack of sea ice typically led to a lack of bearded seal calls. Call activity decreased from north to south (Fig. 2.3). The peak period of vocal activity occurred during the spring, with little vocal activity detected outside mating season at most of the locations (Fig. 2.3). Little to no call activity was observed at any site in the Bering Sea prior to January (except for a few anomalies, which could be a single seal vocalizing). Sea ice concentration increased with latitude and was correlated with vocal activity (Fig. 2.3). The logarithm of the rate of bearded seal vocalizations in the Bering Sea increased with the proportion of sea ice concentration, where both linear ( $p < 0.001$ ) and quadratic ( $p = 0.004$ ) effects of sea ice were significant. The effects of this relationship appear curvilinear because the probability of vocal presence was modeled on the complementary log-log scale (Fig. 2.4).

Variability in call activity was detected at all sites in the Bering Sea. The percentage of the total hours with bearded seal calls increased with latitude (i.e. M8, the northernmost site, had more overall vocal activity than the southernmost site, M2; Table 2.2) varying by both site and year (Table 2.2). The seasonal trend of call activity at sites M8 and M5 (the two northernmost sites) was similar to the trend observed at sites in the Beaufort and Chukchi Seas, but an autumn peak was absent at all of the Bering Sea sites. Calls

began increasing in January at M8 and M5 with nearly continuous calling (i.e. calls detected in all 24 h of the day) observed at both sites from mid-March through May (Fig. 2.3). Meanwhile at site M4 call activity was highly variable between the two years of data collection; activity began in January in 2010 and in March in 2011. Meanwhile, overall call activity was less at site M2 than all other sites with call activity detected during a single month. Vocal activity escalated and declined more rapidly in the Bering Sea than in the other two regions, with more abrupt increases in call activity in the early winter rather than gradual increases observed in the Beaufort and Chukchi Seas. Variation in call activity by site and year in the Bering Sea were typically correlated with increases and drops in sea ice concentration.

Temporal sea ice coverage was lower in the Bering Sea than the other two regions. The timing of sea ice formation and retreat was directly related to latitude—sea ice formed at the northernmost sites (M8 and M5) in late December/early January (Fig. 2.3). Meanwhile at the lower latitude sites, sea ice did not form until late January/early February. Additionally, seasonal sea ice melt was also correlated with latitude where seasonal sea ice would retreat at the southern sites first and continue retreating northward. The southernmost site (M2) never reached maximum concentration levels (>95%) during the study period. From 2008–2011, sea ice had melted at all Bering Sea sites by late May.

Sea ice was more dynamic and less stable in the Bering Sea than the Chukchi and Beaufort Seas. Sea ice dropped to near zero during peak calling periods at all sites during the study period. During the spring of 2011 all three instruments that were recording in the Bering Sea experienced multiple temporary retreats in sea ice. Many of the periods of lower call activity typically coincided with an abrupt reduction in sea ice concentration in the area surrounding the hydrophones. The logarithm of the rate of bearded seal vocalizations in the Bering Sea increased with the proportion of sea ice concentration with both significant linear and quadratic effects. The rate of seal vocalizations increased as a function of sea ice concentration (Fig. 2.4), where the correlation parameter for the AR1 correlation structure indicated significant positive autocorrelation among consecutive duty cycles for the Bering  $\hat{\alpha} = 0.091$ ;  $SE = 0.019$ ;  $p < 0.001$ ).

## **Discussion**

Bearded seals are considered ice-obligate species, meaning they rely on the sea ice for important life history activities (Laidre et al. 2008; Moore and Huntington 2008). They prefer pack ice in shallow depths with easy access to open water and benthic prey for mating and foraging (Burns and Frost 1979;

Burns 1981; Nelson et al. 1984; Stirling 1997; Simpkins et al. 2003). Results of this study confirm that bearded seal vocalizations throughout their range are tightly coupled with sea ice conditions. The curvilinear relationship between call activity and sea ice concentration found in this study indicates that sea ice (not regional oceanographic variability) is the primary physical driver influencing bearded seal call activity.

Bearded seal calls were recorded year-round in the Beaufort Sea and nearly year-round in the Chukchi Sea, consistent with previous findings (MacIntyre et al. 2013; Hannay et al. 2013). At most sites in the Bering Sea, call activity occurred only from January through May, similar to previous studies (Miksis-Olds et al. 2012). Not surprisingly, the lowest call activity was recorded at the Bering Sea M2 site, which is located in the southernmost extent of the bearded seal range with the least amount of annual sea ice cover. Overall, bearded seal vocal activity was much greater for hydrophones at the northernmost sites in the BCB. However, given that there were only a few hydrophones in each region and only one year of data available in the Chukchi Sea, it is unclear whether these results are indicative of larger regional trends or are simply an artifact of unequal sample sizes.

Visual surveys of bearded seals in Alaskan waters (Simpkins et al. 2003; Bengtson et al. 2005) have shown that bearded seals are widely distributed throughout the BCB with the Bering and Chukchi Seas constituting their largest continuous habitat (Burns 1981). This is likely due to the broad, shallow intercontinental shelf that encompasses nearly all of the Chukchi Sea and the northern half of the Bering Sea. This study offers new information beyond visual snapshots about how these animals are distributed throughout the year at regional and local scales.

Biological, chemical and physical oceanographic processes influence broad- and fine-scale variability in the BCB. The BCB can be divided based on differences in oceanographic and bathymetric features (Piatt and Springer 2007) and further refined by taking into consideration sea ice dynamics and density distributions of marine organisms (e.g. zooplankton, fish, seabirds; Sigler 2011). The three seas are all linked by water masses, currents, and sea ice, but they are also separated by unique regional differences that influence sea ice habitat and prey availability. In this study, broad-scale regional variability was observed in bearded seal call activity and overall presence that aligns with previously defined biogeographical distinctions (Sigler 2011). The Beaufort Sea and the Chirikov-Chukchi Provinces are

optimal habitat for bearded seals providing shallow water access to benthic prey and more northerly latitude where seasonal sea ice persists longer (Grebmeier et al. 2010; Grebmeier 2012).

### ***Beaufort Sea***

Bearded seal call activity was greatest in the Beaufort Sea coinciding with longer periods of sea ice cover and greater stability of sea ice in this region that provides suitable habitat conditions for pupping and molting (Burns 1970; Burns 1981; Nelson et al. 1984; Van Parijs et al. 2003; 2004; Laidre et al. 2008; Moore and Huntington 2008). Seasonal sea ice conditions were similar between years, but varied regionally. Some within-site variability was also observed, but typically trends within each region were consistent with previous studies (Stabeno et al. 2007; Stabeno et al. 2010; Hannay et al. 2013; MacIntyre et al. 2013). Until recently, bearded seal presence was thought to be closely tied with the formation and retreat of seasonal sea ice (Burns and Frost 1979; Burns 1981). However, more recent passive acoustic studies have shown that some bearded seals remain in the Alaskan Beaufort and Chukchi Seas year-round and may not follow the sea ice edge (Hannay et al. 2013; MacIntyre et al. 2013). Sea ice was present from October through July and was more stable in the Beaufort Sea due to the presence of perennial sea ice formed by the arrival of old, thick sea ice transported by the clockwise motion of the Beaufort Gyre (Maslanik et al. 2011).

This study found that sea ice conditions influenced the distribution of vocalizing bearded seals, both regionally and by site. At all sites in the Beaufort Sea (including those from MacIntyre et al. 2013), call activity peaked during bearded seal-breeding season. The seasonal trend was similar at each site, but some site variability was observed. Call activity was greatest at site A1, which was closest to Barrow Canyon, a benthic hotspot in the Beaufort Sea (Grebmeier 2012). The lowest bearded seal call activity was recorded at site A2 during both years of data collection at that site. The discernable contrast between A1 and A2, despite their relatively close proximity, may be due to a combination of prey availability as well as potential oceanographic variability between sites. Although in close proximity, the AON and A2 sites differed in timing of peak call activity by one month. This may be indicative of interannual variability, since A2 recorded from 2008–2010 and AON only recorded from 2010 - 2011, or the existence of fine-scale variability between these two closely located sites. The timing of sea ice formation in the autumn

does not seem to play a role in the difference in call activity between A2 and AON, however, depth differences may have affected the timing of peak call activity at these two sites.

Fine-scale oceanographic variability may affect the distribution of prey in different areas producing more/less desirable locations for males to defend as territories (Van Parijs et al. 2003; Van Parijs et al. 2004). This may explain some of the site variability observed at the beginning of the breeding season and increased call activity in early winter in the Beaufort Sea. Similar fine-scale habitat preference was observed for planktivorous birds and bowhead whales, where changes in physical oceanographic conditions altered the prey distribution regionally, creating areas of dense prey aggregations and therefore an influx of upper trophic level animals migrating and feeding in these prey-rich areas (Okkonen et al. 2008; Moore et al. 2010).

### ***Chukchi Sea***

Less call activity was observed in the Chukchi Sea compared to call activity observed in the Beaufort Sea due to slight differences in seasonal sea ice cover. Sea ice observed in the Chukchi Sea was more mobile and less stable than in the Beaufort Sea with several decreases in concentration during its early formation in the late autumn/early winter, similar to findings in George et al. (2004) and Hannay et al. (2013). The Chukchi Sea has a longer open water period (shorter sea ice period) than the Beaufort Sea due to the influence of the ACC as it transports warm, fresh water northwards through the Bering Strait, which causes a delay in the formation of sea ice (Ahl nas and Garrison 1984; George et al. 2004). During this study, sea ice formation occurred at nearly the same time in the Beaufort and Chukchi Seas in the fall, but retreated earlier in the Chukchi Sea, which may have resulted from a combination of depth differences, increased sunlight during the spring/summer months, and/or an insufficient dataset available from the Chukchi Sea to draw any clear conclusions.

Peak call activity in the Chukchi Sea coincided with mating season from March through early June, similar to call activity in the Beaufort Sea and consistent with findings in Hannay et al. (2013). However, at both sites in the Chukchi Sea, call activity declined rapidly in June rather than slowly as it did in the Beaufort Sea. Within the Chukchi Sea, there were noticeable differences between the offshore and inshore sites. The inshore site had more overall call activity, a longer peak in activity during the late winter/spring, and call activity continued beyond the presence of sea ice. The hydrophone at the offshore

site stopped recording early; therefore call activity was not detected beyond sea ice retreat in that region. Although call activity was detected during the same months at both locations, the percent hours with calls recorded was twice as high at the inshore site (Table 2.2). These findings are consistent with recent seasonal movements and migration paths of tagged adult bearded seals (Boveng et al. 2013). Similar regional distribution patterns were observed for walrus (*Odobenus rosmarus*) based on telemetry data from 2009-2012 that showed walruses (also a benthic-feeding, sea ice obligate species) foraging in nearshore areas that are typically deficient in benthic prey, rather than more productive offshore areas (Jay et al. 2012). This shoreward shift in walrus distribution was associated with a lack of sea ice offshore over benthic hotspots normally used by walrus such as Hanna Shoal and the southwestern Chukchi Sea (Jay et al. 2012).

In this study, differences between the inshore and offshore sites were likely a result of physical oceanographic differences between the two areas as well as differences in fine-scale sea ice conditions. The inshore mooring lies closer to the where Bering Sea Water passes through the Chukchi Sea, transporting more nutrient rich water and creating more productive areas and benthic hotspots (Springer et al. 1989; Springer et al. 1996; Lee et al. 2007; Gradinger 2009) rather than closer to the ACC, which creates areas lower in nutrients and benthic biomass (Ahlén and Garrison 1984; Aagaard and Carmack, 1989; Walsh et al. 1989; Feder et al. 2007). Based on current maps and conductivity, temperature and depth sensor (CTD) data, the inshore mooring lies near the boundary between different water masses where temperature and salinity vary spatially (S. Okkonen pers. comm.). The offshore mooring lies in an area where there is less spatial variability in temperature and salinity. Regions where temperature and salinity vary spatially are typically associated with an influx of organisms (S. Okkonen pers. comm.) creating the possibility that more benthic biomass was present near the inshore mooring.

The differences in call activity at each site may also be the result of sea ice conditions. Although sea ice appears similar at both locations, the inshore location lies closer to the flaw lead polynya that forms in the Chukchi Sea in spring, allowing greater access for bearded seals to open water for foraging. Fine-scale differences in sea ice conditions including small areas of open water are not detectable in the 12.5 km resolution of the sea ice concentration data. Therefore, fine-scale differences in the timing of sea ice formation and retreat may lead to small areas of increased productivity or benthic hotspots, thereby

influencing the distribution of upper trophic level species that feed on benthic prey (such as bearded seals or walrus).

### ***Bering Sea***

Sea ice in the Bering Sea observed during this study was much less stable, more dynamic, and present for a shorter time period than in the Chukchi and Beaufort Seas, creating less favorable conditions for bearded seals to haul out and establish and maintain aquatic territories (*cf* VanParijs et al. 2003; 2004). Call activity in the Bering Sea was shorter in duration and more variable compared to the Beaufort and Chukchi Seas. In the Bering Sea, sea ice formation in the winter was delayed and retreat was earlier due to its more southerly location. Further, the sea ice was more dynamic in the Bering Sea, with rapid changes in concentration throughout the winter/spring seasons when the Beaufort and Chukchi Seas had maximum sea ice concentrations (100%). The amount of time sea ice was present at each site decreased with latitude.

Call activity decreased from north to south and no calls were detected outside of the bearded seal-breeding season. Call activity also ended more abruptly with sea ice decline, similar to the trend observed in the Chukchi Sea versus the Beaufort Sea. Call activity at the northern Bering Sea sites (M8, M5) was similar to that in the Chukchi Sea, likely due to the oceanographic similarities that exist between the Chukchi and Bering Seas and the direct connection of the two by the Bering Strait. Another possible explanation for the greater call activity observed at the northern Bering Sea sites (M8, M5) is their proximity to St. Lawrence Island and the rich foraging area to southwest of the island, which contains some of the highest benthic biomass in the Bering Sea (Grebmeier et al. 1995; Grebmeier et al. 2010; Grebmeier 2012). Call activity was much lower at the southernmost sites: at site M4, calls were only detected for 3-4 months and at site M2 calls were only detected in February 2010, however, bearded seals may have been present and vocalizing, but recordings ceased in early March at site M2.

The tight coupling of sea ice conditions with bearded seal call activity throughout their range, shows that sea ice is the determining factor influencing the distribution of vocalizing bearded seals in the Bering Sea. Findings from this study were similar to Van Opzeeland et al. (2012), who showed that the detection of bearded seal calls in the Bering Sea coincided with the arrival of sea ice and ended when the sea ice retreated from the area.

### ***Interannual Variability***

Detecting interannual variability was only possible in the Beaufort and Bering Seas. Overall, regardless of year or location, a change in sea ice condition led to a change in call activity. Changes in the timing of sea ice formation between years was reflected in changes in the timing of when bearded seals first began calling 24 h/d at sites A1 and A2 in the Beaufort Sea in 2008 and 2009 (MacIntyre et al. 2013). In the Bering Sea, interannual differences were observed when comparing the onset of call activity from each winter between 2009 and 2011 at sites M5 and M4. At site M5, call activity began increasing one week later each winter from 2009 to 2011 (Fig. 2.3c). Further south at M4, the difference in the timing of call activity was 5 weeks from 2010 to 2011 and bearded seal calling activity decreased from roughly two months to two weeks. Additionally, any significant drop in sea ice concentration led to a comparable decline in bearded seal call activity within and between years which demonstrates the tight coupling between sea ice concentration and call activity as well as the interannual variability that occurred at a single site. The same relationship was observed at site M5 by Miksis-Olds et al. (2012) in 2009.

Over the entire study area and duration, sea ice duration decreased in successive years at all but one site (A2) from 2008–2011. Some sites only experienced a few days of sea ice loss each year (e.g. M5, A1), while others had a loss of a few weeks (M8). Site M4 had the most dramatic interannual loss of sea ice duration, dropping from 124 days of sea ice in 2009–2010 down to only 57 days of sea ice surrounding the mooring site in 2011.

It is unclear whether seals were still present when sea ice retreated or if vocalizations ceased and seals remained in the area. Regardless of whether the bearded seals were still present, a disruption in vocal activity during peak mating time was observed, either due to a change in their distribution following the sea ice, or the abrupt hiatus of their call activity.

A reduction in overall sea ice presence may negatively impact the availability of habitat and timing of the bearded seal-breeding season. The later formation and earlier retreat of sea ice may delay the arrival of female bearded seals to male territories leading to changes in timing of mating or a reduction in the mating season (Van Parijs et al. 2001; Van Opzeeland et al. 2010). Significant drops in sea ice concentration, or a temporary retreat in sea ice, may also disrupt mating activities and therefore may hinder reproductive success (Atkinson 1997).

Modeling the rate at which seal vocalizations occur allowed for proper control of differences in duty cycle length among sites. For instance, an unmodeled or untreated look at these data might suggest that seal vocalizations are more prevalent in the Chukchi sites than the other regions since seals were detected in a greater proportion of duty cycles in hydrophones in the Chukchi (0.45) when compared to the Beaufort (0.36) or the Bering (0.31). However, this figure does not account for duty cycles in the Chukchi (95 minutes) being much longer than for the Beaufort (mean 10.8 minutes) or Bering (mean 9.5 minutes). By contrast, analyzing data with respect to the rate of seal vocalization presence suggested that the rate of seal vocalizations was much lower for hydrophones in the Chukchi compared to the other two regions (Fig. 2.4).

The probability of seal vocal presence is a function of a number of different factors, including underlying seal density and seal behavior. A focus of future work should therefore be to integrate acoustic results with results of aerial survey and satellite tagging data. These auxiliary datasets can provide information on underlying seal densities and availability probability (probability of being in the water vs. hauled out on ice), and thus might be used to help discriminate the relative contributions of density and seal behavior on the overall rate of seal vocal presence. Additionally, vocalization techniques would be useful for determining source levels of bearded seal calls in the BCB and would help determine how many vocalizing individuals are near a mooring site (Marques et al. 2009; Marques et al. 2012). This information would be useful to discover whether or not a decrease in call activity is in fact a reduction in the number of seals present or simply reduced calling rates. Further, examining geographic variability of call types may uncover possible subpopulations that exist within the BCB that have been observed for bearded seals in other regions as well as other seal species (Pahl et al. 1997; Van Parijs et al. 1999; Risch et al. 2007). It would be useful to collect passive acoustic data and associated oceanographic data simultaneously during future studies to help clarify some of the fine-scale variability in call activity that exists within each region. A combination of visual survey efforts, satellite telemetry, passive acoustic studies will help paint a more complete picture of the seasonal distribution of bearded seals in the BCB. A combination of several multidisciplinary research techniques will create a better understanding of how sea ice influences bearded seal distribution and how variability in the climate may affect this ice-obligate species.

This study provides a contemporary baseline of year-round bearded seal distribution in the BCB based on acoustic activity and offers evidence of a positive correlation between bearded seal call activity and sea ice concentration. The tight coupling of variations in call activity and changes in sea ice concentration suggest that not only are seals vocalizing more during times of increased sea ice concentration, but that more seals are physically present in these areas as well. This study found regional and site variability in bearded seal call activity based on differences in sea ice condition and geography. Call variability among regions of the BCB was largely determined by sea ice conditions; however, many oceanographic features (depth, currents, freshwater input) influence the formation and retreat of sea ice each year, therefore they may have had an indirect effect on bearded seal distributions. Fine-scale variability in call activity within each region was likely related more directly to oceanographic variability rather than sea ice variability, since sea ice conditions within each region (especially the Beaufort and Chukchi Seas) were similar between sites.

***Possible effects of climate change on bearded seals***

Results of this study show that bearded seals are present in all three seas during the spring months, coinciding with mating season. Some bearded seals exhibit site fidelity during the winter months (January–April; Boveng et al. 2013) and maintain aquatic territories during the spring months (Van Parijs et al. 2003; Van Parijs et al. 2004), which suggests that bearded seals may maintain similar aquatic territories each year during mating season. If site fidelity exists during mating season, then it is possible that regional variability could be indirectly influencing the development of bearded seal subpopulations in the BCB. The positive correlation of bearded seal call activity with sea ice concentration strengthens the argument that reductions and variability in sea ice conditions may negatively impact bearded seals (Learmonth et al. 2006; Moore and Huntington 2008; Kovacs et al. 2011; MacIntyre et al. 2013). Bearded seals will experience both direct and indirect effects of sea ice reduction and variability through the loss of sea ice habitat, access to prey, and a reduction or disruption in their breeding season (Tynan and DeMaster 1997).

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## Figure Captions

**Fig. 2.1** Hydrophone locations BCB from 2008-2011. Sea ice depicted (12.5 km<sup>2</sup> 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 gray-scale gradient represents ice concentrations of 5 graded levels from the minimum to the maximum values. Sea ice data were obtained from the National Snow and Ice Data Center (NSIDC, <http://n4eil01u.ecs.nasa.gov>)

**Fig. 2.2** Spectrogram displaying example bearded seal calls recorded at location A3 in the Chukchi Sea on 08 April 2011. Fast Fourier transformation (FFT) 2048, 50% overlap, Hann window

**Fig. 2.3** Acoustic detections of bearded seal vocalizations from August 2008 to August 2011 in the BCB plotted with sea ice concentration. The histogram shows the proportion of hours with bearded seal calls (black) recorded, from 2008 – 2011 on hydrophones moored in the BCB. The secondary y-axis shows mean daily satellite-derived sea ice concentration (blue line) obtained from the National Snow and Ice Data Center (12.5 km resolution, NSIDC, <http://n4eil01u.ecs.nasa.gov>). Within each plot the vertical green and red lines correspond to the recording period at each site, where green is the beginning and red is the end of a recording period. Each plot compares the presence of bearded seal calls and changing sea ice conditions. Each subplot corresponds with the mooring location (north to south): Beaufort Sea = (a) W1; (b) AON; (c) A2; (d) A1; Chukchi Sea = (e) A3; (f) C2; Bering Sea = (g) M8; (h) M5; (i) M4; (j) M2. Call activity escalated with the formation of pack ice in winter and the peak occurred in spring, coinciding with mating season and preceding break-up of the sea ice.

**Fig. 2.4** Population-level mean predictions of the probability of detecting a seal vocalization as a function of sea ice concentration (solid lines), together with approximate 95% confidence intervals (dashed lines) from a generalized estimating equations analysis. Probabilities were standardized to a 20-minute interval (for reference, the mean duty cycle length in this study was 20.4 minutes).

**Table 2.1** BCB deployment details for 2008-2011. BF: Beaufort Sea; BS: Bering Sea; CZ: Chukchi Sea

Instrument ID	Location	Region	Recording dates	Instrument Depth (m)	Sample rate (Hz)	Duty cycle
A1 2008	71.56N 155.59W	BF	8/15/08-7/27/09	94	8192	9/30 min
A2 2008	71.46N 152.25W	BF	8/15/08-8/2/09	131	8192	9/30 min
A3 2008	71.13N 149.46W	BF	8/15/08-8/1/09	46	8192	9/30 min
M8 2008	62.20N 174.66W	BS	10/1/08 – 7/2/09	71	8192	9/30 min
M5 2008	59.90N 171.70W	BS	10/1/08 – 5/29/09	71	8192	9/30 min
A1 2009	71.76N 154.48W	BF	8/1/09-8/14/10	102	16384	14/60 min
A2 2009	71.45N 152.50W	BF	8/4/09-8/11/10	95	8192	9/30 min
M8 2009	62.20N 174.66W	BS	9/30/09 – 5/6/10	74	8192	9/20 min
M5 2009	59.91N 171.71W	BS	6/1/09 – 3/29/10	71	8192	9/20 min
M4 2009	57.85N 168.87W	BS	5/6/09 – 4/1/10	71.5	8192	9/20 min
M2-1 2009	56.9N 164.0W	BS	5/1/09 – 9/25/09	72	8192	Continuous
M2-2 2009	56.9N 164.1W	BS	10/15/09 – 3/7/10	73	8192	26/30 min
AON 2010	71.42N 152.01W	BF	9/25/10-9/12/11	180	16384	15/60 min
CZA3 2010	70.80N 163.08W	CZ	9/10/10 – 6/27/11	43	16384	95/300 min
CZC2 2010	71.83N 165.90W	CZ	9/10/10 – 6/8/11	42	16384	95/300 min
M8 2010	62.20N 174.66W	BS	10/3/10 – 2/1/11	72	8192	12/20 min
M5 2010	59.91N 171.71W	BS	10/3/10 – 6/9/11	70	8192	8/20 min
M4 2010	57.85N 168.87W	BS	10/3/10 – 5/19/11	72	8192	8/20 min

**Table 2.2** Recording details for each location in the BCB 2008 – 2011

Instrument ID	Region	Total recorded hours	Number of hours with calls	Percent hours with calls
AON 2010	Beaufort	8376	2721	32.5
CZA3 2010	Chukchi	2910	1227	42.2
CZC2 2010	Chukchi	2720	800	28.4
M8 2010	Bering	2976	205	6.9
M5 2010	Bering	6000	2503	41.7
M4 2010	Bering	5496	945	17.2
A2 2009	Beaufort	8952	2107	23.5
A1 2009	Beaufort	9096	4217	46.4
M8 2009	Bering	5256	2651	50.4
M5 2009	Bering	7248	1666	23.0
M4 2009	Bering	7944	1601	20.2
M2 2009	Bering	7344	116	1.6
A3 2008	Beaufort	8448	2865	33.9
A2 2008	Beaufort	8472	2367	27.9
A1 2009	Beaufort	8328	4474	53.7
M8 2008	Bering	6600	2733	41.4
M5 2008	Bering	7296	2242	30.7

Fig. 2.1

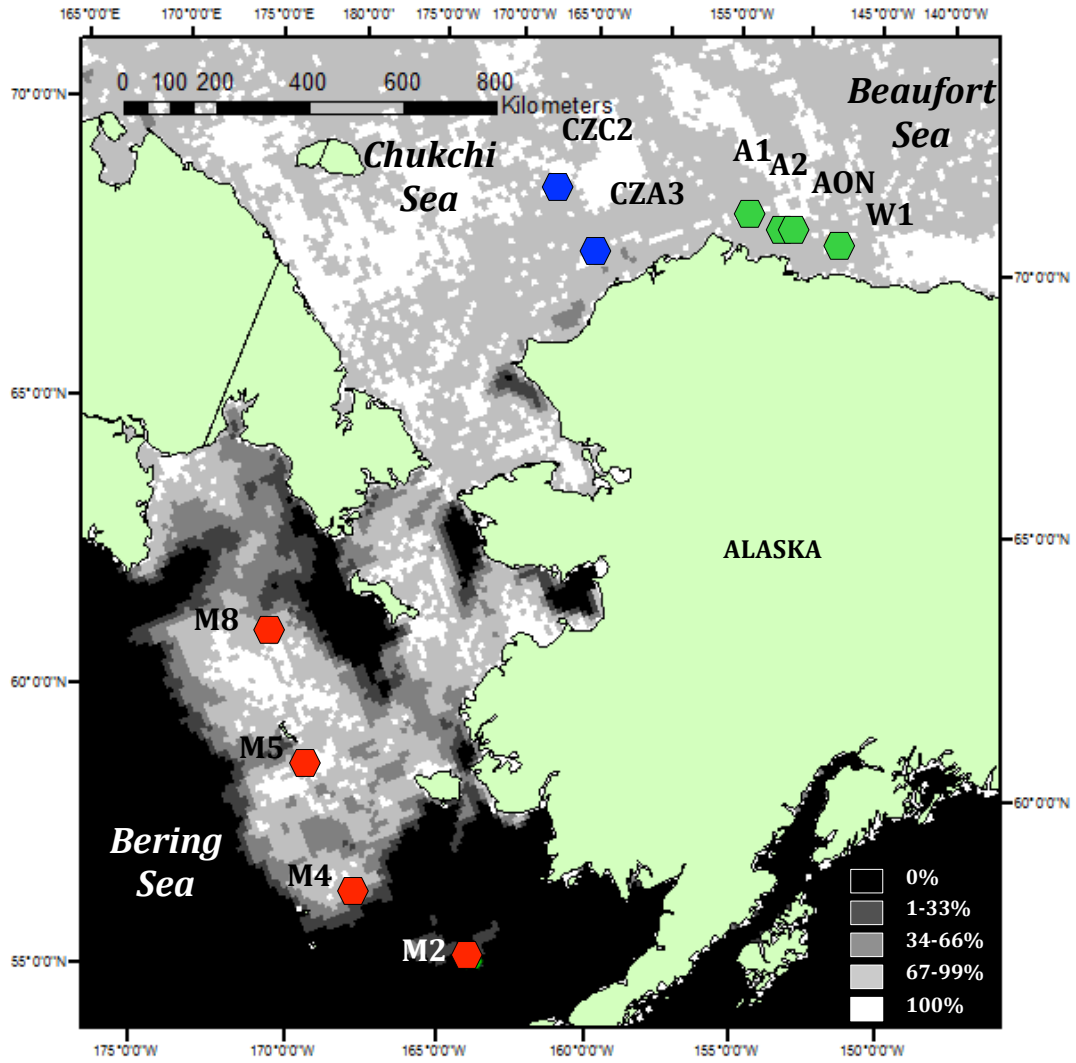


Fig. 2.2

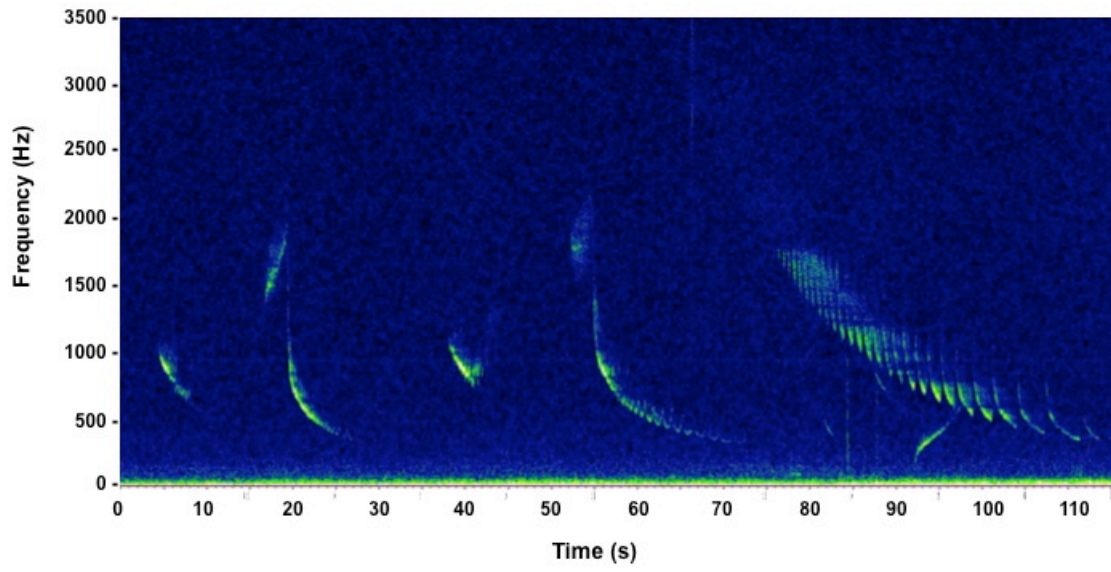


Fig. 2.3

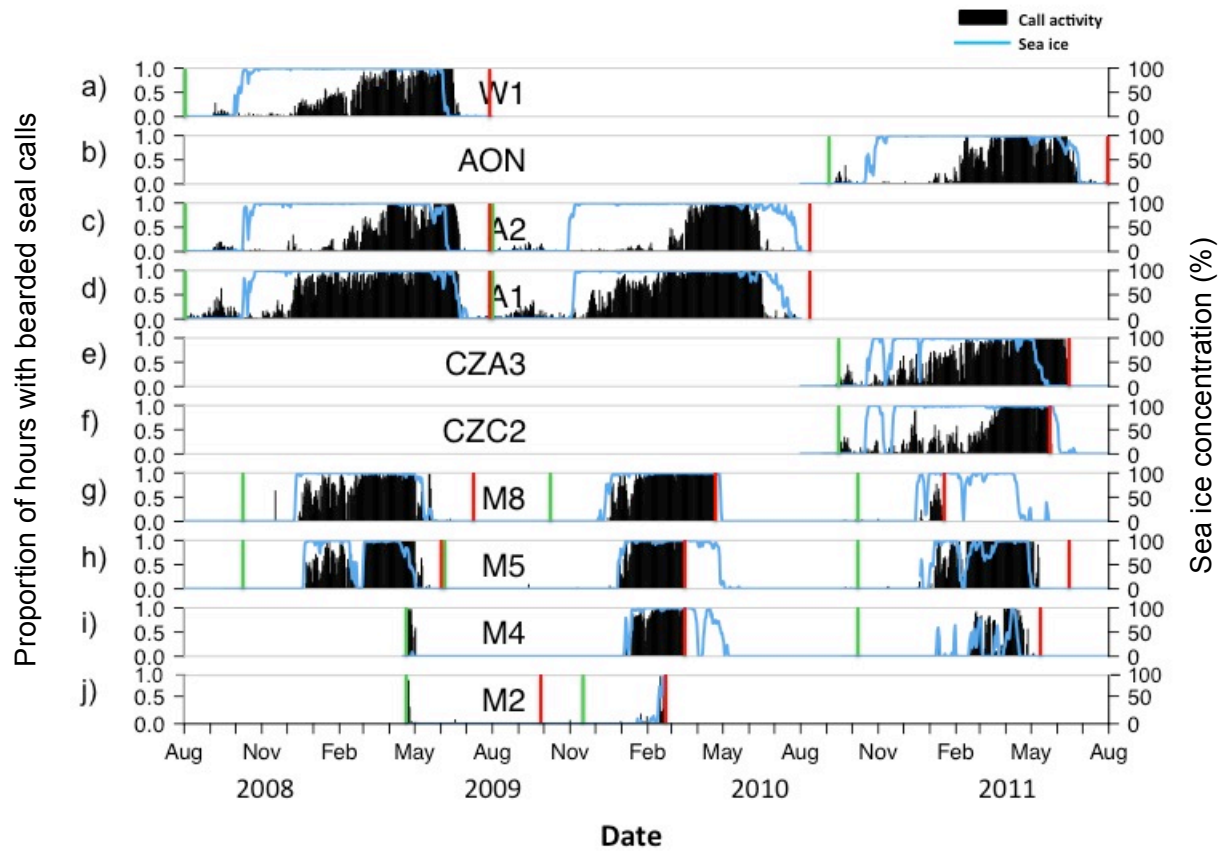
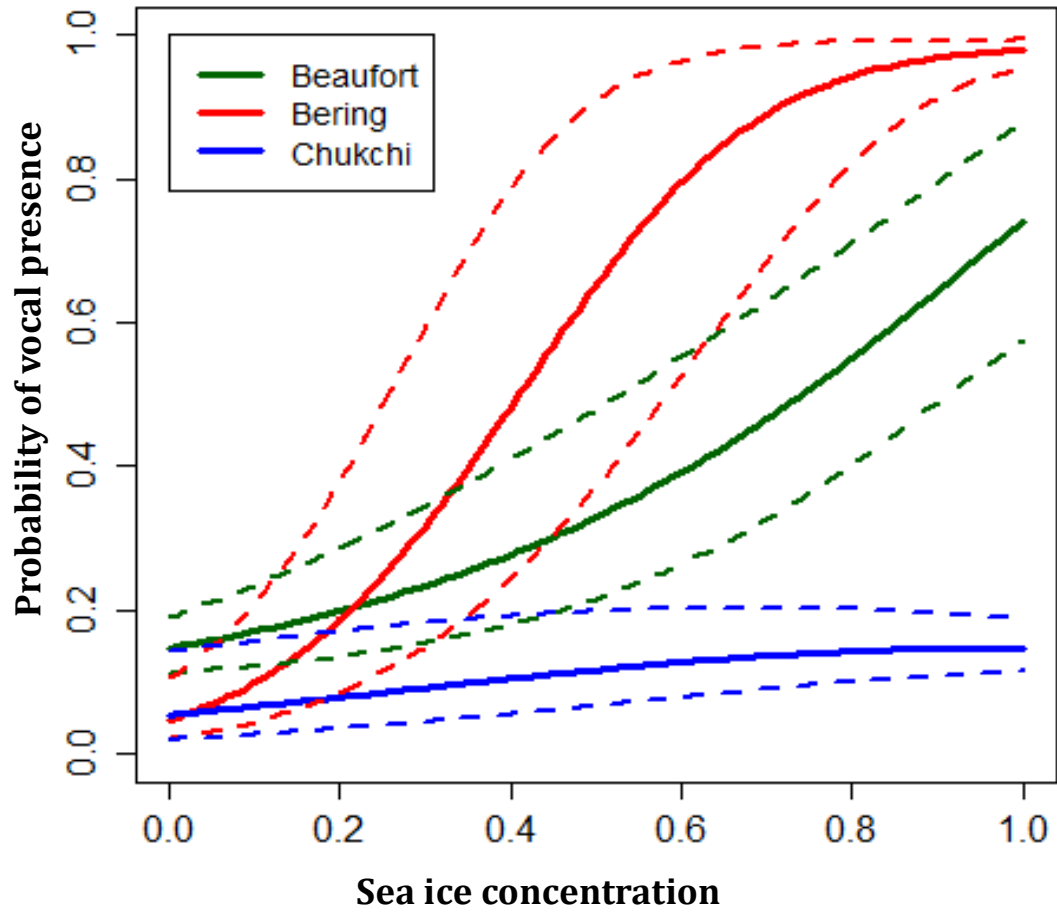


Fig. 2.4



### ***Summary***

The primary objectives of this study were to examine year-round bearded seal vocal activity in the Bering, Chukchi, and Beaufort Seas (BCB) and compare those results with regional, local, interannual and seasonal variability of sea ice conditions. Previous studies have focused on bearded seal acoustics during mating season (spring months) due to their increased vocal activity, while relatively little work has been done outside their breeding season. Additionally, most research has examined call activity from a single region, while this study expanded this research by comparing the regional variability of call activity among regions of the BCB. The aim of this study was to provide a baseline of bearded seal vocal activity in the BCB and compare variations in call activity with variations in sea ice conditions. Until now, the influences of variability in sea ice conditions and other oceanographic factors on bearded seal vocal activity were not considered. The present study provides an explanation for the regional, local, interannual, and seasonal variability of call activity in the BCB.

Chapter one examined year-round production of sound by bearded seals. In the Beaufort Sea from 2008-2010, bearded seal calls were recorded year-round at all sites during both years of data collection. Previous studies have made recordings year-round for the presence of bearded seals (Van Parijs et al. 2001), but this is the first study to detect year-round vocal activity. Additionally, this project revealed that not all bearded seals migrate with the formation of sea ice in the winter and leave the Beaufort Sea. Seasonal and interannual variability was detected in call activity and a tight coupling between call activity, sea ice concentration, and water temperature was observed.

Chapter two revealed bearded seal presence in the Beaufort, Chukchi and Bearing seas during the spring months, which coincided with mating season. Additionally, this study provides a contemporary baseline of bearded seal distributions in the BCB based on vocal activity. Regional and site variability in call activity was observed and was related to differences in sea ice conditions and geography. Call variability was largely determined by sea ice conditions; however, many oceanographic features influence formation and retreat of sea ice each year. These may also have indirect effects on bearded seal distribution. Site variability in call activity within each region was likely related to oceanographic variability rather than sea ice conditions since sea ice was similar between sites.

This study demonstrated that regional and site variability exists in bearded seal call activity in the

BCB and that call activity is positively correlated with sea ice concentration. Seasonal sea ice provides essential habitat for bearded seals to carry out important life history activities. The current warming trend in the Arctic is causing extreme variability and loss of annual sea ice. Due to threats posed by diminishing sea ice and changing water temperatures, bearded seals have been listed as *threatened* under the Endangered Species Act of 1973 (73 FR 16617). The present study helps to provide key information regarding bearded seal year-round distribution and behavior. Additionally, demonstrating a tight coupling between bearded seal vocal activity and sea ice presence strengthens the argument that reductions and variability in sea ice conditions may negatively impact bearded seal survival. Bearded seals will experience both direct and indirect affects of sea ice reduction and variability through the loss of sea ice habitat, access to prey, and a reduction or disruption in their breeding season (Tynan and DeMaster 1997).

Future work should integrate acoustic results with visual survey efforts and telemetry data to better understand the impact sea ice variability and a changing Arctic climate will have on bearded seals. Multiple datasets and data sources would provide a more complete assessment of bearded seal distribution, density and behavior. More extensive examination of current and future acoustic data will allow for a more complete seasonal and regional distribution based on underwater vocalizations. The examination of call types will help determine whether geographic variability exists in vocal repertoires within the BCB. Knowledge of mesoscale geographic variability within the BCB may also help reveal the existence of unique subpopulations within this area. The presence of subpopulations would in turn influence future management decisions of this species.

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