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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 to 2011

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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, 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 its range. To test the hypothesis that the vocal activity of bearded seals is related to variations in sea ice, passive acoustic data were collected from nine locations throughout the BCB from 2008 to 2011. Recording instruments sampled on varying duty cycles ranging from 20% to 100% of each hour, and recorded frequencies up to 8192 Hz. Spectrograms of acoustic data were analyzed manually to calculate the daily proportion of hours with bearded seal calls at each sampling location, and these call activity proportions were correlated with daily satellite-derived estimates of sea ice concentration. Bearded seals were vocally active nearly year-round in the Beaufort and Chukchi Seas with peak activity occurring from mid-March to late June during the mating season. The duration of call activity in the Bering Sea was shorter, lasting typically only five months, and peaked from mid-March to May at the northernmost recorders. In all areas, call activity was significantly correlated with higher sea ice concentrations ($p < 0.01$). These results suggest that losses in ice cover may negatively impact bearded seals, not just by loss of habitat but also by altering the behavioral ecology of the BCB population.

1. Introduction

Bearded seals (*Erignathus barbatus*) are a pan-Arctic pinniped species whose life history is closely coupled with the presence of sea ice. Bearded seals are often considered to be benthic foragers although they are capable of foraging on a wide variety of species throughout the water column (Stirling and Archibald, 1977; Stirling et al., 1983; Kovacs, 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 sources such as mollusks and crustaceans (Stirling, 1977; Stirling et al., 1983; Kovacs, 2002). Arctic-wide, there are two recognized subspecies of bearded seals of which the Pacific subspecies (*E. b. nauticus*), occurs in the Pacific Arctic and Sea of Okhotsk (Cameron et al., 2010). These regions are occupied by two geographically isolated discrete population segments (DPS). The Beringia DPS of bearded seals is found throughout the Bering, Chukchi and Beaufort Seas (BCB) in Alaskan and Russian waters. 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 again in the autumn/winter as sea ice forms (Potelov, 1969; Burns, 1981; Simpkins et al., 2003; Frost et al., 2008). Recent satellite telemetry data have confirmed this pattern, and showed male bearded seals in the Bering Sea appear to exhibit strong winter site fidelity, often establishing territories at preferred sites as sub-adults (Boveng and Cameron, 2013). Previous studies have shown that vocal bearded seals are present year-round in the Beaufort Sea (MacIntyre et al., 2013) and nearly year-round in the Chukchi Sea (Hannay et al., 2013). This suggests they may not migrate with the ice edge as it advances and retreats through the Bering Strait (Potelov, 1969; Burns, 1981; Simpkins et al., 2003; Frost et al., 2008). Bearded seals

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rely on sea ice as a platform for critical life history activities such as reproduction, molting, and rest between foraging trips (Burns, 1970, 1981; Nelson et al., 1984; Moore and Huntington, 2008).

The seasonal formation and retreat of sea ice in the BCB influences the ecosystem both regionally and locally; there are distinct oceanographic processes that occur within each region that influence the formation/retreat cycle (Hunt et al., 2011; Sigler et al., 2011; Grebmeier, 2012; Stabeno et al., 2012). Sea ice begins to form in mid-autumn in the Beaufort Sea and remains frozen until early summer creating a stable platform for bearded seals to haul out upon during key life history activities (Burns, 1970, 1981; Nelson et al., 1984). 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). Finally, the Bering Sea experiences more dynamic sea ice conditions than the either the Chukchi or Beaufort Seas due to the repeated growth and melt of sea ice during winter and spring.

Upper trophic level species, such as bearded seals, are especially vulnerable to changing sea ice conditions through the loss of habitat and a shift in prey distribution (Bluhm and Gradinger, 2008; Laidre et al., 2008; Kovacs et al., 2011; Stenson and Hammill, 2014). Access to benthic prey may become more limited with further sea ice decline by forcing bearded seals and other benthic feeders (i.e. walrus, *Odobenus rosmarus*) onto shore or into deeper waters (Udevitz et al., 2013). This may subject bearded seals to energetic stress as they attempt to forage in less desirable habitat. Additionally, previously benthic-dominated regions may become more pelagic-dominated, leading to increased competition for preferred prey species or a change in prey species (Moore and Huntington, 2008).

The calls of bearded seals are readily identifiable and therefore passive acoustic monitoring is a useful tool to assess their distribution. Male bearded seals produce distinctive trills that range in frequency from 200 Hz to 6 kHz, and can last from 10 s to as long as 3 min (Ray et al., 1969; Cleator et al., 1989). Male bearded seals begin vocalizing as juveniles and continue to develop their vocal repertoire throughout their lives (Davies et al., 2006). 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, in spring, acoustic detection can be considered representative of the presence of both male and female seals although the ratio of the sexes is unknown. 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), possibly due to males establishing territories and dominance hierarchies and/or induced by seasonal changes in hormone levels (Davies et al., 2006).

This study examines year-round distributions of vocally active bearded seals in the BCB and correlates the vocal pattern with sea ice throughout the year to provide insight on how local, regional, and interannual variability influence bearded seal occurrence. We test the hypothesis that sea ice concentration influences the presence of vocal bearded seals throughout the year and throughout their range.

2. Methods

2.1. Acoustic sampling

Passive acoustic recorders (Aural-M2, http://www.Multi-Electronique.com) were deployed on nine sub-surface oceanographic moorings (Fig. 1) in the BCB for one to three years. Three were moored in the Beaufort Sea (A1, A2, A3), two in the Chukchi Sea (CZA3, CZC2), and four in the Bering Sea (M2, M4, M5, M8). Data from the Beaufort Sea moorings from 2008 to 2010 were previously analyzed in MacIntyre et al. (2013); however, the results are included in the analysis here for comparison. A third year of data from site A2 (2010–2011) was added to this study. The nine instruments sampled in frequency ranges 10–4096 Hz, or 10–8192 Hz (Table 1). All recorders were suspended 5 m above the seafloor to minimize the risk of damage from overhead ice keels in water depths around 40 m in the Chukchi Sea, 70 m in the Bering Sea, and up to 180 m in the Beaufort Sea (Table 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 1). Instruments sampled on duty cycles ranging from 23% of each hour (e.g., recorded 14 min out of every hour) to continuous recordings (Table 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. The replacement instrument recorded continuously rather than on a duty cycle and stopped early on 6 March 2010 (Table 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 were 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 different 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 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, 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) using the program Ishmael 1.0 (Mellinger, 2001). A total of 113,462 h of acoustic data were examined for bearded seal calls in the BCB: 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 (Table 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 had fewer total hours per day available at both sites than the other regions, comparisons between all sites and regions were made based on daily proportions of hours with calls out of the total recorded hours per day.

2.2. Sea ice data

Sea ice concentration data (AMSR-E Aqua 12.5 km resolution) of the BCB from 2008 to 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

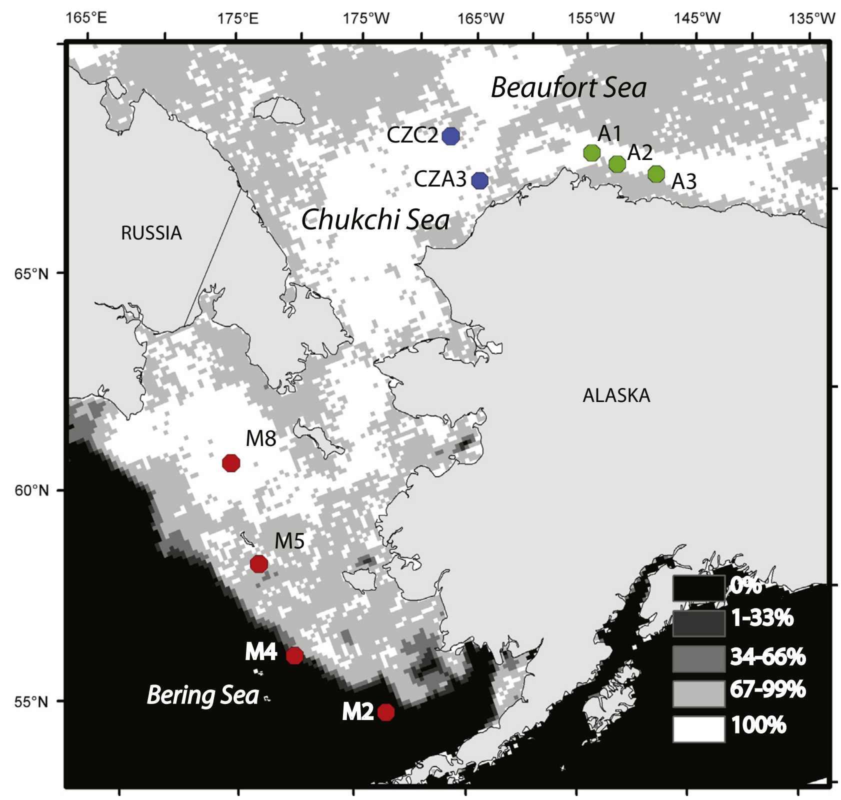

Fig. 1. Hydrophone locations in the BCB from 2008 to 2011. Sea ice depicted (12.5 km^2 resolution) is from 25 April 2011. Open water is represented as black and 100% sea ice concentration as white, with a gray-scale gradient represents ice concentrations of 5 graded levels from the minimum to the maximum values. Sea ice data were obtained from the National Snow and Ice Data Center (NSIDC, http://n4eil01u.ecs.nasa.gov).

Table 1
BCB deployment details for 2008–2011.

Region	Instrument ID	Location	Recording dates	Instrument depth (m)	Sample rate (Hz)	Duty cycle
Beaufort Sea	A1 2008	71.56N 155.59W	8/15/08–7/27/09	94	8192	9/30 min
	A1 2009	71.76N 154.48W	8/1/09–8/14/10	102	16,384	14/60 min
	A2 2008	71.46N 152.25W	8/15/08–8/2/09	131	8192	9/30 min
	A2 2009	71.45N 152.50W	8/4/09–8/11/10	95	8192	9/30 min
	A2 2010	71.42N 152.01W	9/25/10–9/12/11	180	16,384	15/60 min
	A3 2008	71.13N 149.46W	8/15/08–8/1/09	46	8192	9/30 min
Chukchi Sea	CZA3 2010	70.80N 163.08W	9/10/10–6/27/11	43	16,384	95/300 min
	CZC2 2010	71.83N 165.90W	9/10/10–6/8/11	42	16,384	95/300 min
Bering Sea	M8 2008	62.20N 174.66W	10/1/08–7/2/09	71	8192	9/30 min
	M8 2009	62.20N 174.66W	9/30/09–5/6/10	74	8192	9/20 min
	M8 2010	62.20N 174.66W	10/3/10–2/1/11	72	8192	12/20 min
	M5 2008	59.90N 171.70W	10/1/08–5/29/09	71	8192	9/30 min
	M5 2009	59.91N 171.71W	6/1/09–3/29/10	71	8192	9/20 min
	M5 2010	59.91N 171.71W	10/3/10–6/9/11	70	8192	8/20 min
	M4 2009	57.85N 168.87W	5/6/09–4/1/10	71.5	8192	9/20 min
	M4 2010	57.85N 168.87W	10/3/10–5/19/11	72	8192	8/20 min
	M2-1 2009	56.9N 164.0W	5/1/09–9/25/09	72	8192	Continuous
	M2-2 2009	56.9N 164.1W	10/15/09–3/7/10	73	8192	26/30 min

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 (Cleator et al., 1989, a small percentage of calls (~15%) may 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. This range may change based on water depths and ice concentration and thickness. Daily sea ice concentration data at each mooring location were compared with the proportion of hours per day with bearded seal calls.

2.3. Statistical analysis

To investigate whether seal vocal presence was related to percent sea ice concentration, general estimating equation (GEE) models were fit to the seal vocalization and sea ice concentration data. These models were chosen because several sources of error/bias may occur in time series data, including the temporal autocorrelation of data collected at each site and/or error associated with different duty cycles of acoustic recording time periods among sites. The first consideration is important because ignoring

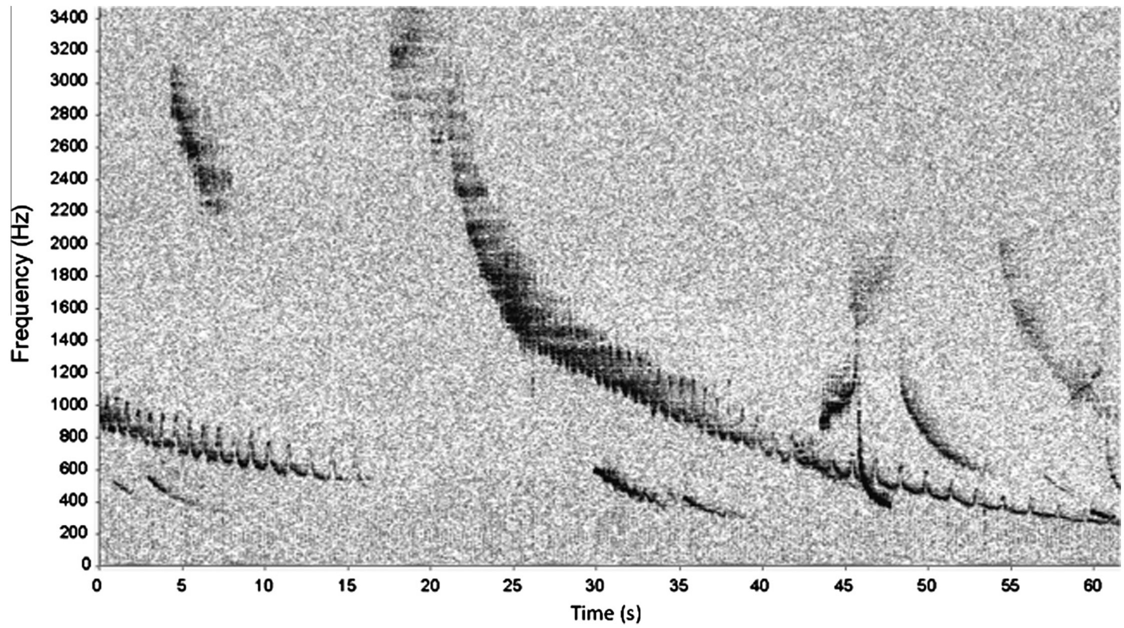

Fig. 2. Spectrogram displaying example bearded seal calls recorded at location A1 in the Beaufort Sea on 05 April 2009. Fast Fourier transformation (FFT) 2048, 50% overlap, Hann window.

Table 2
Recording details for each location in the BCB 2008–2011.

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

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 record in any one hour. The variation in duty cycle length among hydrophones needed to be controlled for as the number of seal vocalizations detected can be influenced by the recording length. The key is to write statistical models in terms of one or more hazard rate parameters, and to describe the probability of an event E as a function of both the rate parameter(s) and the time interval modeled. 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. Therefore, the approach in this paper was to use GEEs with an autoregressive formulation for the second moments of the data (Zeger and Liang, 1986; Halekoh et al., 2006).

We let $N_{i,t}$ 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. Then the model

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

probabilistically described the number of successes (the number of duty cycles for which seal vocalizations are recorded). Further structure is provided on $p_{i,t}$ to permit the probability of recording a seal vocalization to depend both on the underlying hazard rate at which vocalizations are present ($\lambda_{i,t}$), and on the duty cycle length ($T_{i,t}$)

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

This formulation is a standard formulation based on the survivor function for an exponential distribution (i.e. a constant hazard rate within a duty cycle; Cox and Oakes, 1984).

The assumption that errors are independent and identically distributed was not met with seal vocalization records, as initial analysis with GAMs indicated considerable temporal autocorrelation in residuals (e.g., a lag-30 autocorrelation of 0.5). This autocorrelation is interpretable on biological grounds: individuals or groups of seals may move into the range of an acoustic detector and be in the vicinity for multiple days, weeks, or months before departing again.

We thus conducted the analysis using a generalized estimating equations (GEE; Liang and Zeger, 1986; Halekoh et al., 2006) framework, which can accommodate both variation in duty cycle length and temporal autocorrelation in responses. We used an AR1 covariance structure (a common specification for temporally autocorrelated time series) to account for autocorrelated residuals and better represent uncertainty in estimated parameters. To relate the rate of seal vocalizations to background sea ice concentration levels, we imposed the following linear model:

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

Here, $\mathbf{X}_{i,t}$ is a 3-element vector $[1\ \text{ice}_{it}\ \text{ice}_{it}^2]$ (where ice_{it} specifies sea ice concentration at site i at time t),and $\boldsymbol{\beta}$ is a vector of regression coefficients.

The R package geepack (Halekoh et al., 2006) was used to implement the proposed model and 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 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. Population mean predictions with 95% confidence intervals at different covariate values were generated from this fitted model as

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

where $\widetilde{\mathbf{X}}$ denotes a design matrix for prediction points, and $\hat{\boldsymbol{\beta}}$ denotes estimated regression coefficients. Here, predictions were standardized to a 20-min time interval (the average duty cycle length over the course of the study was 20.4 min) and the vector of standard errors, SE, was computed over the design points as the square root of the diagonal elements of $\widetilde{\boldsymbol{X}}\hat{\Sigma}\widetilde{\boldsymbol{X}}'$. Here, $\hat{\Sigma}$ denotes the estimated variance–covariance matrix of model parameters output by geepack.

3. Results

Bearded seal vocalizations were detected at all sites in the BCB from 2008 to 2011. Statistically significant 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 (Fig. 3). Of the total 113,462 h of acoustic data recorded from all sites from 2008 to 2011, bearded seal vocalizations were detected in 35,440 h (Table 2). In all three regions, the highest proportion of call activity occurred during the spring months, coinciding with mating season and periods of higher sea ice concentration. Overall vocal activity was similar in the Beaufort and Chukchi Seas, but less vocal activity was detected in the Bering Sea.

3.1. Beaufort Sea

Bearded seal vocalizations were detected in nearly all months from 2008 to 2011 at all locations in the Beaufort Sea (Fig. 4). Of the 51,672 h of acoustic data recorded from all sites the Beaufort Sea, vocalizations were identified in 18,751 h (Table 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.

The overall trend was similar at each site within the Beaufort Sea, but some site variability was observed (Fig. 4a–c). 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).

Sea ice conditions showed some seasonal and interannual variability. Sea ice began forming during autumn at all locations in the Beaufort Sea (Fig. 4), and maximum sea ice concentration (~100%) remained at each site into late June/early July at all sites. By mid-July the moorings were typically in open water and devoid of sea ice through mid-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 (linear effect, $p = 0.006$; quadratic effect, $p = 0.348$, Fig. 3).

3.2. Chukchi Sea

Bearded seal vocalizations were detected in all 10 months of recording at both sites in the Chukchi Sea (Fig. 4d and e). Of the 5630 h of acoustic data recorded from both sites, vocalizations were identified in 2027 h (Table 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.

Site variability in call activity was observed in the Chukchi Sea. The number of hours per day with calls was greater at CZA3, the inshore location, (1227 h) than CZC2, the offshore location (800 h). Site CZA3 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. However, since fine-scale changes in sea ice may not have been detected in the 12.5 km resolution of the sea ice data used, small amounts of sea ice may still have been present. The percentage of hours with call activity at site CZA3 was 42.2%. The offshore location (CZC2) in the Chukchi Sea had lower overall call activity than the inshore site (CZA3), where bearded seals were detected in 28.4% of recorded hours at site CZC2 (Table 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. 4). 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, indicating a slightly less stable sea ice platform than observed in the Beaufort Sea. The logarithm of the combined rate of bearded seal vocalizations from both sites in the Chukchi Sea increased with the proportion of sea ice concentration, and the rate of seal vocal presence increased as a function

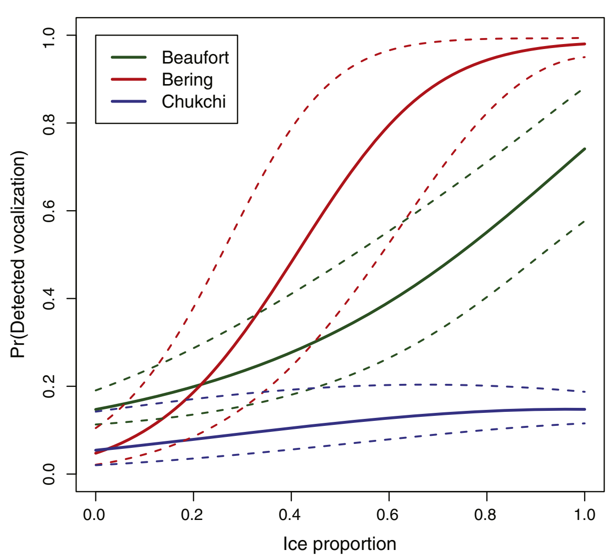

Fig. 3. Population-level mean predictions of the probability of detecting a seal vocalization as a function of sea ice concentration (solid lines), together with approximate 95% confidence intervals (dashed lines) from a generalized estimating equations analysis. Probabilities were standardized to a 20-min interval (for reference, the mean duty cycle length in this study was 20.4 min).

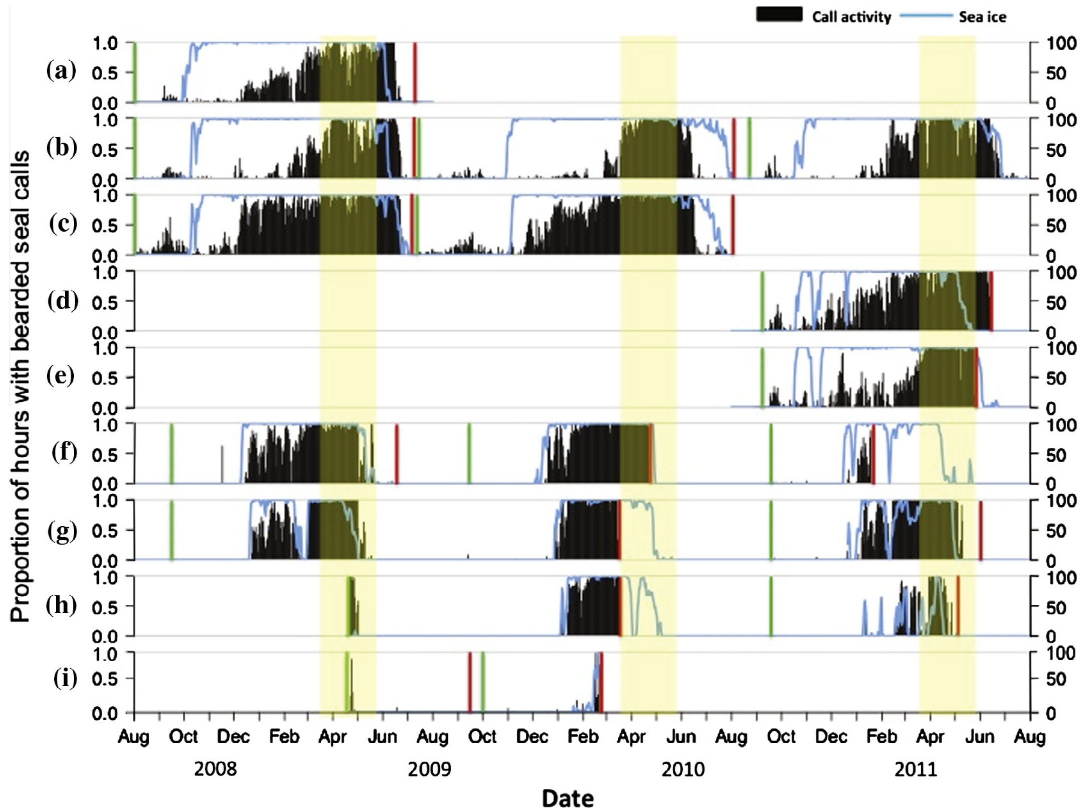

Fig. 4. Acoustic detections of bearded seal vocalizations from August 2008 to August 2011 in the BCB plotted with sea ice concentration. The histogram shows the proportion of hours with bearded seal calls (black) recorded, on hydrophones moored in the BCB. The secondary y-axis shows mean daily satellite-derived 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) A3; (b) A2; (c) A1; Chukchi Sea = (d) CZA3; (e) CZC2; Bering Sea = (f) M8; (g) M5; (h) M4; (i) 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. The breeding period for bearded seals (March–June) is highlighted in yellow for all years on each plot.

of sea ice concentration and linear and quadratic effects were significant (linear effect, $p < 0.001$; quadratic effect, $p < 0.001$; Fig. 3).

3.3. Bering Sea

In the Bering Sea, call activity was more variable among sites than the other two regions, and a lack of sea ice typically corresponded with a lack of bearded seal calls. Call activity decreased from north to south (Fig. 4f–i). The peak period of vocal activity occurred during the spring, with little vocal activity detected outside mating season at most of the locations (Fig. 4). Little to no call activity was observed at any site in the Bering Sea prior to January. Sea ice concentration increased with latitude and was correlated with vocal activity (Fig. 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), but with notable inter-annual variability by both site and year (Table 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. 4). At site M4, call activity varied between the two years of data collection; activity began in January in 2010 but not until March in 2011; bearded seal call occurrence reflected this two-month delay. Overall call occurrence 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. 4), while at the lower latitude sites, sea ice did not form until late January/early February. From 2008 to 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 (linear effect, $p < 0.001$; quadratic effect, $p = 0.004$; Fig. 3).

4. Discussion

The statistical relationship between call activity and sea ice concentration found in this study indicates that sea ice is the primary physical driver influencing the distribution of vocalizing bearded seals. Broad-scale regional variability was observed in bearded seal call activity and overall presence that aligns with previously defined biogeographical distinctions (Sigler et al., 2011). The Beaufort Sea and the Chirikov-Chukchi Provinces (the eastern Bering Sea shelf north of Saint Lawrence Island and the Chukchi Sea; Sigler et al., 2011) should be optimal habitat for bearded seals, providing shallow water access to benthic prey and more persistent seasonal sea ice (Grebmeier et al., 2010; Grebmeier, 2012).

Our results align with previous studies where bearded seal calls were recorded year-round in the Beaufort Sea and nearly year-round in the Chukchi Sea, (MacIntyre et al., 2013; Hannay et al., 2013) and call activity occurred only from January through May at most Bering Sea sites (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 lowest annual sea ice cover. Overall, bearded seal vocal activity was much greater for hydrophones at the northernmost sites in the BCB.

Bearded seal presence was previously 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 Beaufort and Chukchi Seas year-round (Hannay et al., 2013; MacIntyre et al., 2013). In contrast to Hannay et al. (2013), this study found that sea ice conditions influenced the distribution of vocalizing bearded seals, both regionally and by site. At all sites call activity peaked during bearded seal-breeding season. In the Beaufort Sea, call activity was greatest at the recording site closest to Barrow Canyon, a benthic hotspot in the Beaufort Sea (Grebmeier, 2012). Although fewer calls occurred at A2 than A1, the three-year time series from site A2 underscore the link between interannual variability in sea ice and the onset of calling by bearded seals.

Fine-scale oceanographic variability may affect the distribution of prey in different areas (Logerwell et al., 2011; Eisner et al., 2013), creating more/less desirable locations for male bearded seals to defend as territories (Van Parijs et al., 2003, 2004). The Beaufort Sea shelf break is heterogeneous with respect to water column properties both in summer/fall and winter (Pickart, 2004; Logerwell et al., 2011). This may explain some of the site differences observed at the beginning of the breeding season and increased call activity in early winter in the Beaufort Sea. Similar fine-scale habitat preference has been observed for planktivorous birds and bowhead whales, where changes in physical oceanographic conditions altered the prey distribution regionally, creating areas of dense prey aggregations, spawning an influx of upper trophic level animals foraging in these prey-rich areas (Okkonen et al., 2008; Moore et al., 2010).

At both sites in the Chukchi Sea, bearded seal call activity declined rapidly in June, however noticeable differences were observed between the inshore and offshore sites. The inshore site (CZA3) had more overall call activity, a longer peak in activity during the late winter/spring, and call activity continued after sea ice retreat (Fig. 4d). The hydrophone at the offshore site (CZC2) stopped recording early; therefore whether call activity continued post-sea ice retreat at that site is unknown. 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 (CZA3; Table 2). These findings are consistent with recent nearshore studies of seasonal movements and migration paths of tagged adult bearded seals that found most seals remained near the coast, usually within 50 km of shore (Boveng and Cameron, 2013). Additionally, similar regional distribution patterns were observed for walrus satellite tracked between 2009 and 2012, showing that walruses (also a benthic-feeding, sea ice obligate species) typically foraged in nearshore areas when there was a lack of sea ice offshore over benthic hotspots such as Hanna Shoal and the southwestern Chukchi Sea, foraging areas normally used by walrus (Jay et al., 2012).

In this study, differences in call activity between the Chukchi Sea inshore and offshore sites were likely a result of variability in physical oceanography and/or sea ice. The inshore mooring (CZA3) lies near the boundary between different water masses where temperature and salinity vary spatially (S. Okkonen pers. comm.) and close to where Bering Sea Water (BSW) passes through the Chukchi Sea. The BSW transports more nutrients and results in areas of higher productivity (Springer et al., 1989, 1996; Lee et al., 2007; Gradinger, 2009). The offshore mooring (CZC2) was deployed in a more oceanographically homogenous environment with less possibility of increased productivity. Although sea ice conditions appeared similar at both sites, the differences in call activity at each site may also be the result of conditions not detectable in the 12.5 km resolution of the sea ice concentration data used here. Another explanation for call variation may be the close proximity of the inshore mooring (CZA3) to the flaw lead polynya that forms in the Chukchi Sea in spring, allowing greater access for bearded seals to open water for foraging.

Sea ice in the Bering Sea observed during this study was much more variable than in the Chukchi and Beaufort Seas, there were rapid changes in concentration throughout the winter/spring seasons, creating less favorable conditions for bearded seals to haul out and establish and maintain aquatic territories (e.g. Van Parijs et al., 2003, 2004). Interestingly, however, call activity in the Bering Sea was much more closely coupled to the presence of sea ice here than in the Chukchi or Beaufort seas where sea ice concentrations were often >95%. Seasonal call activity in the Bering Sea decreased from north to south, and no calls were detected outside of the bearded seal breeding season. 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), compared to the southern sites (M4, M2), is their proximity to St. Lawrence Island and the rich foraging area to southwest of the island (Grebmeier and Cooper, 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, recordings ceased in early March at site M2.

4.1. Interannual variability

Interannual variability was only detected in the Beaufort and Bering Seas, where multiyear datasets were available at many of the sites. 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. 4c). Further south at M4, there was a 5 week time difference in the onset of call activity 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 both 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 in 2009 by Miksis-Olds et al. (2012).

Over the entire study area and duration, annual sea ice duration decreased over time at all but one site (A2) from 2008 to 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, with 124 days of sea ice in 2009–2010 but only 57 days of sea ice surrounding the mooring site in 2010–2011.

It is unclear whether seals were still present and stopped vocalizing during the periods of temporary sea ice retreat or if the lack of call activity indicates a distribution shift of vocalizing seals. A reduction in overall sea ice presence has the potential to negatively impact the temporal availability of habitat for the bearded seal during breeding season, which may impact the duration and onset of 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).

4.2. Behavioral ecology

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 data with results from aerial surveys and satellite telemetry. These auxiliary datasets may provide information on underlying seal densities, and thus might be used to help discriminate the relative contributions of density and seal behavior to the overall rate of seal vocal presence. This information could help answer whether a decrease in call activity is due to a reduction in the number of seals present or simply reduced calling rates. Additionally, examining the geographic variability of call types may uncover subpopulations that exist within the BCB, as has been observed for pinniped species, including bearded seals, in other regions (Pahl et al., 1997; Van Parijs et al., 1999; Risch et al., 2007; Charrier et al., 2013).

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 between call activity and sea ice concentration suggests that the increase in vocal activity during periods of higher sea ice concentration was not only due to the seasonal increase in bearded seal call production during the breeding season, but also a result of a distribution shift of vocalizing bearded seals associated with the sea ice. Call variability among regions of the BCB was largely determined by sea ice conditions; however, the physical drivers (depth, currents, freshwater input) that influence the formation and retreat of sea ice each year may have also had an indirect effect on bearded seal distributions. Spatial variability in call activity within each sea may have been more directly related to oceanographic or benthic variability (Grebmeier, 2012) rather than sea ice variability, since sea ice conditions within each region (especially the Beaufort and Chukchi Seas) were similar between sites.

Some bearded seals exhibit site fidelity during the winter months (January–April; Boveng and Cameron, 2013) and maintain aquatic territories during the spring months while others do not, and roam over much larger areas (Van Parijs et al., 2003, 2004). Territorial males may maintain similar aquatic territories each year during mating season. It is possible that regional variability in sea ice could be indirectly influencing the development of bearded seal subpopulations in the BCB by changing the habitat characteristics of these territories, and thereby altering the reproductive success of both territorial and roaming males. One could imagine a scenario in which less sea ice decreases the quality of territories and therefore decreases the reproductive success of territorial males. Under the same circumstances, roaming males might have increased success as they have larger home ranges. Alternately, territory holding might disappear altogether as a mating tactic. How this would alter the acoustic behavior of bearded seals is unknown but the positive correlation of bearded seal call activity with sea ice concentration strengthens the argument that reductions and variability in sea ice conditions are likely to negatively impact bearded seals (Learmonth et al., 2006; Moore and Huntington, 2008; Kovacs et al., 2011; MacIntyre et al., 2013), either directly through sea ice reduction or indirectly through access to prey (Laidre et al., 2008; Moore and Huntington, 2008).

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