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Underwater acoustic behavior of bearded seals (*Erignathus barbatus*) in the northeastern Chukchi Sea, 2007–2010

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ABSTRACT

Bearded seal (*Erignathus barbatus*) calls were recorded using autonomous passive acoustic recorders deployed in the northeastern Chukchi Sea between October 2007 and October 2010. Continuous acoustic data were acquired during summer (August to mid-October), and overwinter data (mid-October through July) were acquired on a duty cycle of 40/48 min every 4 h. We investigated the spatio-temporal distribution and acoustic behavior of vocalizing bearded seals in this multiyear data set. Peaks in calling occurred in spring, coinciding with the mating period, and calls stopped abruptly in late June/early July. Fewer calls were detected in summer, and the vocal presence of seals increased with the formation of pack ice in winter. Vocal activity was higher at night than during the day, with a peak around 0400 (AKST). Monthly patterns in proportional use of each call type and call duration were examined for the first time. The proportion and duration of AL1(T) and AL2(T) call types increased during the mating period, suggesting that males advertise their breeding condition by producing those specific longer trills. The observed seasonal and diel trends were consistent between years. These results improve our understanding of occurrence and acoustic behavior of bearded seals across the northeastern Chukchi Sea.

Key words: *Erignathus barbatus*, bearded seal, acoustic behavior, Chukchi Sea, mating period, passive acoustic monitoring.

Bearded seals (*Erignathus barbatus*) have a circumpolar distribution throughout the Arctic and the Beringia population is found in the northern Bering, Chukchi, and Beaufort Seas (Mansfield 1967). Variation in seasonal movements has been seen in this species, with some individuals following the ice edge into and out of the Chukchi Sea and others overwintering in the Arctic in recurring polynyas or in drifting sea ice (Burns 1981).

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Reduced Arctic sea-ice cover, as observed over the last decade (*e.g.*, Comiso 2014, Frey *et al.* 2014), is likely to affect the distribution, reproduction, and ultimate survival and abundance of bearded seals. Effects could range from habitat loss to changes in the dynamics of primary productivity and benthic biomass (Bengston *et al.* 2005), reduced accessibility of prey (Hindell *et al.* 2012), and increased predation pressure (Higdon and Ferguson 2009); therefore, any large variation in their sea-ice habitat may considerably affect the persistence of the bearded seal population.

Bearded seals give birth, mate, and molt on the highly unstable and unpredictable substrate of drifting ice floes and the edge of fast ice, between March and late June (Burns 1981). In the Beringia population, the pupping period is long, extending from mid-March through the first week of May (Burns 1981). Pups are weaned when they are 12–24 d old (Burns 1967, Gjertz *et al.* 2000). Mating occurs toward the end of lactation, with males likely in breeding condition from April to early July (Burns 1981, Cleator and Stirling 1990, Cleator 1996). Male breeding condition, as indicated by sperm counts, testicular weight, and the presence of mature follicles (Burns 1967), peaks in May (McLaren 1958). One study of captive bearded seals suggested that males are the primary source of underwater calls, and that they begin to vocalize only after reaching sexual maturity (Davies *et al.* 2006). Wild male bearded seals reach sexual maturity at around 6 yr of age when they weigh approximately 240 kg (Andersen *et al.* 1999).

Studies of bearded seal calls have identified four main call categories: trills (T), moans (M), ascents (A), and sweeps (S) (Stirling *et al.* 1983, Cleator *et al.* 1989, Risch *et al.* 2007). Trills divide further into three subcategories: trills with ascent/plume, long trills, and short trills. In Alaska, sweeps are absent (Risch *et al.* 2007). Risch *et al.* (2007) found that each of the basic call categories has a variable number of call types in bearded seals from Alaska. Variants were characterized and designated with the prefix AL (*e.g.*, trills included several different types, AL1(T), AL1i(T), AL2(T), AL4(T), AL5(T) and AL6(T); moan and ascent categories included only one type, AL3(M) and AL7(A), respectively).

During the mating season mature males engage in reproductive displays consisting of long loud underwater trilling calls (*e.g.*, Cleator *et al.* 1989). In the Canadian Arctic and Svalbard, bearded seal calls show a diurnal pattern with a peak in vocal activity in early morning (Cleator *et al.* 1989, Cleator and Stirling 1990, Van Parijs *et al.* 2001). The predominant call types produced by bearded seals are variations of a distinct frequency-modulated trill ranging in frequency from 0.1 to 5 kHz (Ray *et al.* 1969, Burns 1981, Stirling *et al.* 1983). It has been hypothesized that males make these geographically distinct calls (Risch *et al.* 2007, Charrier *et al.* 2013) to advertise their breeding condition and display their fitness (Cleator *et al.* 1989) and/or establish aquatic territories (Van Parijs *et al.* 2004). In Svalbard (Van Parijs *et al.* 2003, 2004) and in northern Alaska (Van Parijs and Clark 2006), male bearded seals behave either as *territorial* males who defend small territories (<5 km^2) or as *roaming* males who roam over larger areas (>5 km^2). Although males can change mating strategies over time, this is rare in Alaska (Van Parijs and Clark 2006).

Passive acoustic monitoring (PAM) using multiple recorders has become a feasible method for investigating acoustic behavior, as well as measuring temporal and spatial distributions of marine mammals over large areas and when ship-based or on-ice studies are impossible (*e.g.*, Van Parijs *et al.* 2009, Hannay *et al.* 2013, Risch *et al.* 2013). Moored autonomous acoustic recorders allow PAM at all hours and during all seasons and can therefore provide information on the seasonal and diel occurrence of difficult-to-study aquatic species, such as bearded seals. Recently, MacIntyre *et al.*

(2013) demonstrated the year-round presence of bearded seals in the Beaufort Sea (2008–2010) using PAM.

The following work is part of a broad multidisciplinary study conducted in and near three proposed exploratory oil and gas prospects in the northeastern Chukchi Sea: Burger, Klondike, and Statoil (Day *et al.* 2013). In this multiyear data set, spatio-temporal distribution of vocalizing bearded seals was examined to improve our understanding of occurrence of bearded seals across the northeastern Chukchi Sea. This paper presents year-round recordings of male bearded seals at several locations in the Chukchi Sea over a 3 yr period (2007–2010) and compares these to sea-ice concentrations around each location. A comparison of the temporal occurrence of the various call types may lead to insights into the significance of each call type, as well as the ecology of bearded seals. Monthly patterns in proportional use of each call type and call duration were examined for the first time using 3 yr of overwinter data at 5–8 sites throughout the northeastern Chukchi Sea. Finally, to determine if bearded seals exhibit diel trends in vocal activity, 2 yr of overwinter data at 5–7 sites throughout the northeastern Chukchi Sea were examined for bearded seal calls.

Methods

Instruments and Data Collection

As part of a multidisciplinary study of the northeastern Chukchi Sea (Day *et al.* 2013), arrays of autonomous acoustic recorders were deployed to monitor marine mammals nearly continuously from October 2007 to October 2010 (Hannay *et al.* 2013). Two programs were conducted each year: an overwinter program consisting of 5–8 recorders deployed from early October to the following August (Fig. 1A, Table 1), and a summer program consisting of 10–44 recorders deployed from late July to early October (Fig. 1B, Table 1). The recording stations were aligned offshore of four Alaskan locations: Cape Lisburne (CL), Point Lay (PL), Wainwright (W), and Barrow (B).

Overwinter acoustic monitoring programs—Autonomous Underwater Recorders for Acoustic Listening (AURAL M2, Multi-Electronique Inc., Rimouski, Canada) were deployed for overwinter programs in 2007–2008, 2008–2009, and 2009–2010 (Fig. 1A). Data were recorded on a duty cycle of 48 min every 4 h during 2007–2008 and 40 min every 4 h during the following years. Each AURAL was fitted with an HTI-96-MIN hydrophone (High Tech Inc., Gulfport, MS) with nominal sensitivity of −164 dB re 1 V/μPa. The AURALs sampled at 16,384 Hz with 16-bit resolution and a recorder gain setting of +22 dB, which provided a spectral noise floor of 57 dB re 1 $\mu Pa^2/Hz$. The usable bandwidth was 10–7,700 Hz. For overwinter programs in 2007–2008 and 2008–2009, recorders started at different times (*cf*. Table 1).

Summer acoustic monitoring programs—Autonomous Multichannel Acoustic Recorders (AMAR, JASCO Applied Sciences, Halifax, Canada) were deployed between Cape Lisburne and Barrow (Fig. 1B) during summer 2009 and 2010. Data were recorded continuously in 30 min files. Each AMAR was equipped with a GTI-M15B hydrophone (GeoSpectrum Technologies Inc., Dartmouth, Canada) with nominal sensitivity −160 dB re 1 V/μPa. The acoustic data were recorded at 16,000 Hz with 24-bit resolution and a gain setting of 0 and 18 dB in 2009 and 2010, respectively. The usable bandwidth was 10–7,600 Hz, and the spectral noise floor was 45 and 42 dB re 1 $\mu Pa^2/Hz$ in 2009 and 2010, respectively.

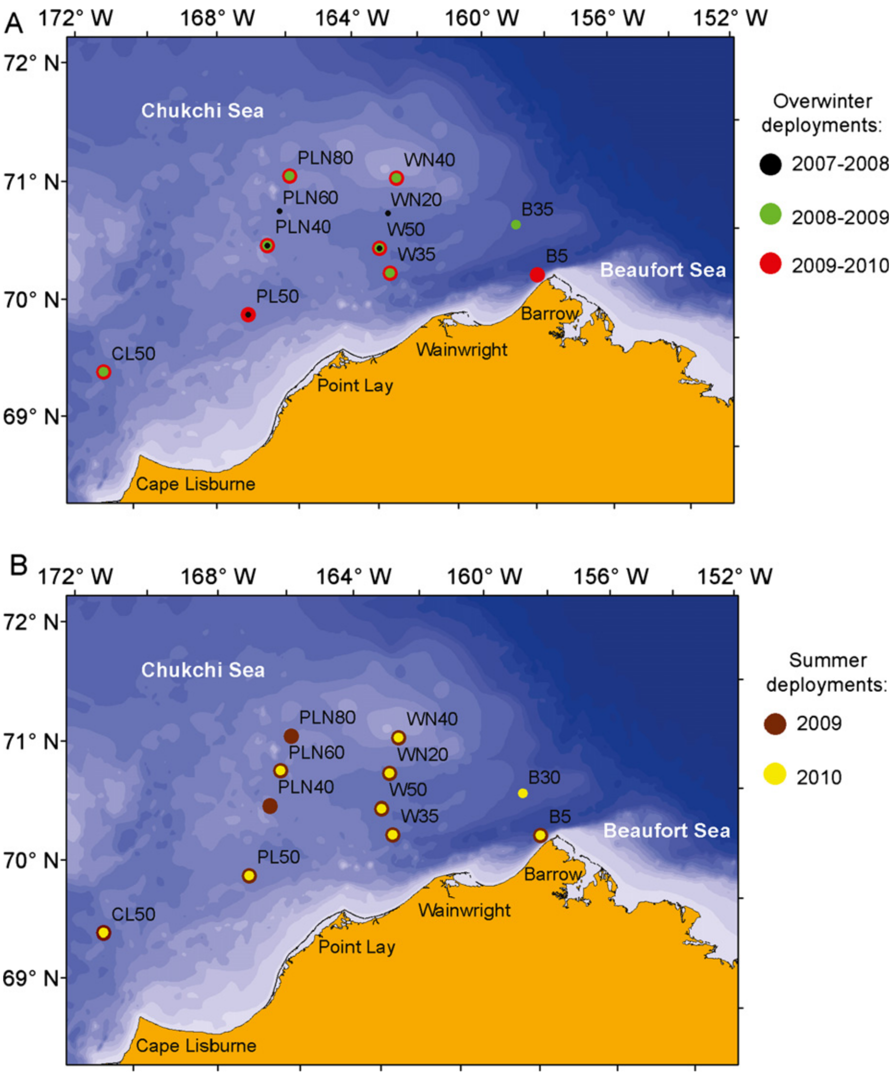

Figure 1. Recording station locations in the northeastern Chukchi Sea (Alaska, U.S.A.) for the 2007–2008, 2008–2009, and 2009–2010 overwinter programs (A) and for the summer 2009 and 2010 programs (B). Specifics on sampling effort are given in Table 1.

Analysis of Bearded Seal Call Detections

Three data analysis protocols, described in the sections below, were employed to investigate the annual variation in seal call behavior, the seasonal changes in call types and duration, and the diel call patterns. All protocols used the same manual analysis methods to identify the types and rates of bearded seal calls using a custom software program, SpectroPlotter (JASCO Applied Sciences).

Manual analysis of call types—Bearded seal characteristic calls were selected manually from spectrograms calculated by fast Fourier transform (FFT size: 1,024 points;

Table 1. Recorder deployment details for the overwinter and summer acoustic monitoring programs in the northeastern Chukchi Sea between 2007 and 2010.

Recording station	Location	Recording period (MM/DD/YY)	Recorder depth (m)	Sample rate (Hz)	Duty cycle (min)	Start time (AKST)
Overwinter 2007–2008 program						
WN20	71.64°N, 161.54°W	10/25/07–08/03/08	47.5	16,384	48/240	2000
PLN60	71.40°N, 164.59°W	10/22/07–07/30/08	43.9	16,384	48/240	0000
W50	71.31°N, 161.54°W	10/25/07–08/02/08	49.4	16,384	48/240	1700
PLN40	71.07°N, 164.57°W	10/21/07–07/20/08	38.4	16,384	48/240	2200
PL50	70.40°N, 164.57°W	10/21/07–07/20/08	42.1	16,384	48/240	1700
Overwinter 2008–2009 program						
WN40	71.97°N, 161.54°W	10/15/08–08/09/09	32.9	16,384	40/240	1430
PLN80	71.73°N, 164.59°W	10/16/08–06/04/09	38.4	16,384	40/240	0700
B35	71.78°N, 157.79°W	10/14/08–08/02/09	60.4	16,384	40/240	1130
W50	71.31°N, 161.54°W	10/15/08–08/08/09	49.4	16,384	40/240	0930
PLN40	71.06°N, 164.63°W	10/17/08–08/07/09	42.1	16,384	40/240	1700
W35	71.11°N, 161.08°W	10/14/08–04/14/09	45.7	16,384	40/240	1930
CL50	69.50°N, 167.78°W	10/12/08–05/31/09	49.4	16,384	40/240	0000
Summer 2009 program						
B05	71.36°N, 156.94°W	08/09/09–10/12/09	58.2	16,000	Continuous	1045
CL50	69.50°N, 167.78°W	08/05/09–10/06/09	45.7	16,000	Continuous	1600
PL50	70.40°N, 164.59°W	08/06/09–10/03/09	40.2	16,000	Continuous	1615
PLN60	71.40°N, 164.59°W	08/08/09–10/11/09	41.5	16,000	Continuous	1015
W35	71.10°N, 161.05°W	08/10/09–10/13/09	46.0	16,000	Continuous	1045
W50	71.31°N, 161.54°W	08/08/09–10/13/09	38.1	16,000	Continuous	1030
WN20	71.64°N, 161.55°W	08/08/09–10/13/09	43.9	16,000	Continuous	1030
WN40	71.97°N, 161.54°W	08/09/09–10/12/09	31.4	16,000	Continuous	1030
Overwinter 2009–2010 program						
WN40	71.97°N, 161.54°W	10/13/09–08/17/10	33.5	16,384	40/240	0300
PLN80	71.73°N, 164.24°W	10/13/09–03/21/10	38.4	16,384	40/240	0300
W50	71.31°N, 161.77°W	10/13/09–07/07/10	48.8	16,384	40/240	0300
PLN40	72.06°N, 164.63°W	10/12/09–07/27/10	40.1	16,384	40/240	0300
PL50	70.40°N, 164.59°W	10/15/09–05/21/10	43.0	16,384	40/240	0300
W35	71.10°N, 161.05°W	10/14/09–07/22/10	47.5	16,384	40/240	0300
CL50	69.50°N, 167.78°W	10/16/09–07/23/10	48.8	16,384	40/240	0300
B05	71.36°N, 156.93°W	10/12/09–07/31/10	60.0	16,384	40/240	0300
Summer 2010 program						
B5	71.36°N, 156.94°W	08/01/10–10/10/10	64.0	16,000	Continuous	1600
B30	71.71°N, 157.65°W	08/01/10–10/16/10	62.0	16,000	Continuous	1215
CL50	69.50°N, 167.78°W	07/26/10–10/15/10	45.7	16,000	Continuous	1045
PL50	70.40°N, 164.59°W	07/27/10–10/11/10	40.2	16,000	Continuous	1800
PLN40	71.07°N, 164.59°W	07/27/10–09/27/10	40.1	16,000	Continuous	1345
PLN60	71.40°N, 164.59°W	07/27/10–10/11/10	41.5	16,000	Continuous	0915
W35	71.11°N, 161.07°W	08/01/10–10/10/10	46.0	16,000	Continuous	1100
W50	71.31°N, 161.54°W	08/01/10–10/10/10	45.5	16,000	Continuous	0900
WN20	71.64°N, 161.54°W	07/30/10–10/10/10	43.9	16,000	Continuous	0400
WN40	71.97°N, 161.54°W	08/17/10–10/10/10	31.6	16,000	Continuous	0930

Hamming window; time resolution: 2.44 ms for all data; and frequency resolution: 16 Hz). The key parameters of start and end times and minimum and maximum frequencies were logged for each call. Calls corresponding to published call types were manually identified by types modified from Risch *et al.* (2007). The call types are described in Table S1 and illustrated in Figure 2, and divided into three basic call categories: trill (T), moan (M), and ascent (A). Moans, AL3(M), are distinguished from other bearded seal calls because they have little frequency modulation. However, when received levels of calls were low, distinguishing between AL3 moans, AL6 trills, and AL5 trills was often difficult. For this reason, a maximum frequency range of 120 Hz was used as the cut-off between AL3 moans and AL6 trills, and a maximum frequency range of 240 Hz as the cut-off between AL6 trills and AL5 trills. Descriptive statistics from this study, Risch *et al.* (2007) and Jones *et al.* (2014) are included in Table S2 to facilitate comparison with results of this analysis. All bearded seal calls were analyzed by a single acoustician throughout the 3 yr study period. Intraobserver variability as experience increased over time could influence results. To ensure consistent analysis, all data from the first and second year of recording were reanalyzed after the analysis of the third year of recording.

Spatio-temporal distribution in vocal presence and relationship with ice concentration—To remove the influence of diurnal patterns on vocal behavior from our analyses, a single

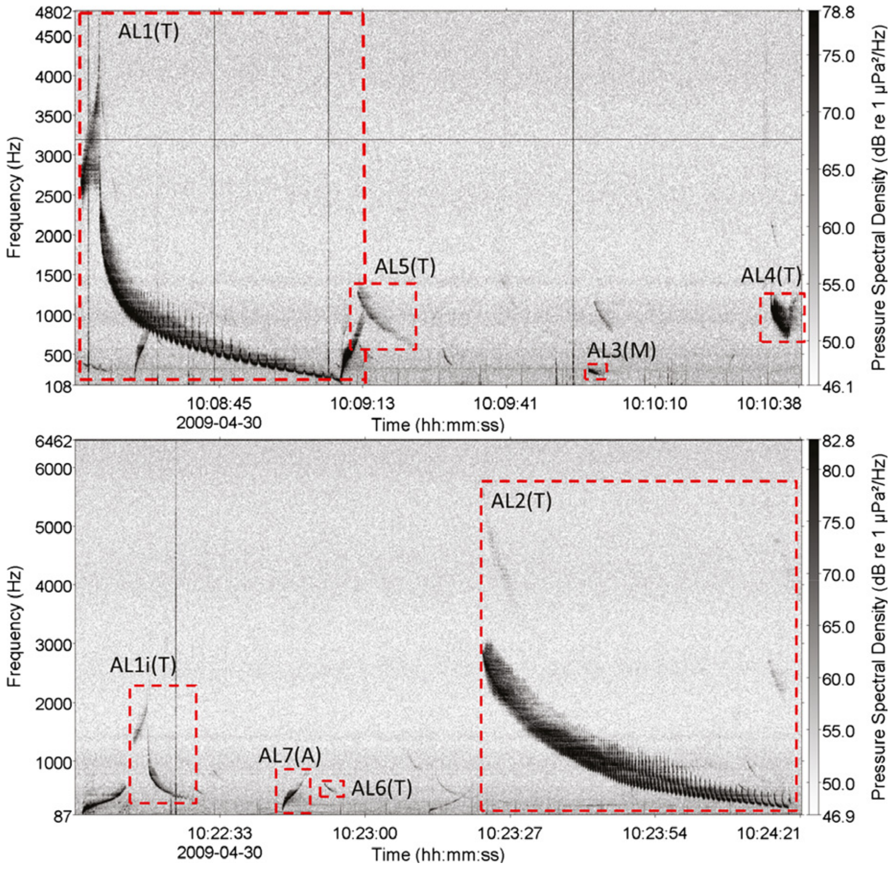

Figure 2. Bearded seal calls representing the major call types found in the Chukchi Sea dataset. Call types are modified from Risch *et al.* (2007). See Table 2 for call type definitions.

daily measurement of the number of calls was performed. Initial analyses of the bearded seal vocal presence in this study's data suggested that the daily peak in vocal activity occurred in early morning (around 0400 AKST), as previously reported for the Canadian Arctic and Svalbard (Cleator *et al.* 1989, Cleator and Stirling 1990, Van Parijs *et al.* 2001). Due to different start times among recorders, recording samples chosen in this analysis were between 0200 and 0600 AKST. The spatio-temporal distribution in male bearded seal calls was investigated for each recording station and each overwinter program by fully annotating one 20 min recording sample between 0200 and 0600 AKST every 3 d from mid-October to early August. This 20 min sample length was representative of longer recordings as determined by initial analyses. Due to the difference in the number of recorders and in recorder life span each year, the overall sample size of calls differed between years (overwinter 2007–2008: n = 39,225; overwinter 2008–2009: n = 24,749; overwinter 2009–2010: n = 51,765). The number of calls at each recording station and for each program was plotted against the percentage of sea-ice concentration obtained from 10 km resolution data from the Ocean and Sea Ice Satellite Application Facility (Eastwood 2011). Daily sea-ice concentrations were extracted from the single pixels in which mooring stations were located.

To investigate the effect of sea-ice coverage, month, station, latitude, longitude, ice edge distance, depth, and distance to shore on the call count, a Gaussian distribution generalized additive model (GAM) was fitted to the data from each overwinter deployment using the *gam* function from the *mgcv* package (Wood 2006) in R ver. 3.1.1 (R Development Core Team 2014). GAMs were chosen because of their ability to incorporate nonnormally distributed variables, flexibility with nonlinear relationships, and reduced restrictions with nonparametric generalizations (Wood 2006). Each variable or combination of variables was included in the models, and information on model performance (performance of explained variance, Akaike's Information Criterion, *etc*.) was determined. Only stations with full winter and spring data sets were included in the analysis. The distances between mooring locations and ice edge location were derived every third day from satellite imagery (NOAA National Ice Center, Washington, DC; http://www.natice.noaa.gov/products/).

Seasonal variation in call type occurrence and call duration—The seasonal variation in the bearded seal call repertoire and duration of each call type were analyzed on the overwinter 2007–2008, 2008–2009, and 2009–2010 data sets using the approach described in the section above. We did not analyze the seasonal variation in the bearded seal call repertoire and duration of each call type in the summer data due to lower call counts. To determine the monthly variation in the occurrence of the different call types (Fig. 2, Table S1), the number of each call type was counted in the 20 min recording samples. The monthly variation of bearded seal call types across all recording stations was calculated and compared across years. October, November, December, and July were not included, due to rare or null call detections during those months.

Because the number of samples per month and year varied, an ANOVA with 2-way and Type III sum of squares was used to account for the unbalanced data. Pairwise comparisons of adjusted means were used to determine which months or years were different. All statistical analyses were performed using the software R and the contributed packages (*car* and *lsmeans*).

The variation in the duration of each call type was also evaluated for each month (January, February, March, April, May, and June) among 3 yr (2008, 2009, and 2010).

Diel patterns in occurrence of bearded seal calls—For the 2009 and 2010 summer programs, the first 90 s of each 30 min file per station per day was analyzed manually using the protocol described in Hannay *et al.* (2013). To examine diel variation in hourly call occurrence, each hour (combination of two 30 min files) was scored for call presence (detection) or absence. Days for which no calls were detected were excluded from this analysis. Variability between days and stations was normalized by dividing the number of 1 h bins with calls present per period per day by the total number of 1 h bins per period per day, a method similar to Soldevilla *et al.* (2010). Call detections were rare before mid-September, so most days included in the analysis were from mid-September to early October.

For the overwinter programs, a 10 min recording every 4 h (due to the duty cycle of recordings) was fully annotated every 10th day. The overall sample size of calls varied between years (overwinter 2007–2008: n = 27,487 and overwinter 2008–2009: n = 19,602). Due to time and budget limited only two years (2007–2008 and 2008–2009) were included in this analysis. Days for which no calls were detected were excluded from the analysis. To correct for variability in call rates over time scales greater than 1 d, for each day of analysis, the number of calls in each 10 min sample (six in total per day) was divided by the total number of calls calculated for this 24 h period. For overwinter data sets, the relationship between the proportion of calls and the diel cycle was determined by a Kruskal-Wallis one-way analysis of variance by ranks (nonparametric method), followed by an all-pairwise multiple comparison procedure (Student-Newman-Keuls method) as appropriate, with $P < 0.05$ indicating statistical significance.

Results

Annual Spatio-temporal Distribution in Vocal Presence and Ice Concentration

A total of 1,732 recording days, including over 577 h of data, from all overwinter recording stations (5, 7, and 8 stations from the overwinter 2007–2008, 2008–2009, and 2009–2010 programs, respectively) in the northeastern Chukchi Sea were analyzed. Bearded seal calls were detected at all recording stations (Fig. 3). The number of calls (per 20 min sample) per day varied strongly over the year. In all three program years, bearded seal acoustic detections increased progressively from November to March, peaked between April and June, and were essentially absent in July. The lowest total call counts were measured in the overwinter 2008–2009 program.

The variable "station" explained <2% of the variation in calling count as the sole variable in the GAM (overwinter deployment 2007–2008 $P > 0.05$; Table S3) but explained 10% of the variance for overwinter deployment 2008–2009 and 5% of the variance for overwinter deployment 2009–2010 (both $P < 0.001$).

The variables "latitude," "longitude," "depth," and "distance to shore" provided similar or less explanation of the variance than the variable "station." The variable "ice edge" explained better the variance than the variable "station" for overwinter deployment 2007–2008 ("ice edge": 6.40%; "station": 5.53%) and overwinter deployment 2009–2010 ("ice edge": 5.47%; "station": 5.10%). The results for the variable "station" could actually be a combination of "latitude," "longitude," "depth," and "distance to shore" variables.

The GAM for each overwinter deployment indicated that sea-ice coverage could explain 11%–12% of the variation in calling count for all overwinter deployments ($P < 0.001$).

The GAM for each overwinter deployment indicated that month provided the highest explanatory power (40%–63% for the variance in calling count (all $P < 0.001$). The model with the lowest AIC value for each overwinter deployment indicated that ice, month, and station combined, significantly ($P < 0.001$) explained 67.9% and 49.3% of the variance in calling count for overwinter deployments 2007–2008 and 2009–2010, respectively. Furthermore, the model with the lowest AIC value for overwinter deployment 2008–2009 indicated that month and station combined, significantly ($P < 0.001$) explained 52% of the variance in calling count.

The models indicated that calling was better explained by the period of the year (month) and that the vocal presence of seals increased with the formation of pack ice in winter.

Seasonal Variation in Call Type Occurrence and Call Duration

In our data, the most common call was AL5(T) and the least common call was AL4(T) (Table S2). The proportion of each bearded seal call type by month and year is illustrated in Figure 4. The proportions were similar among years.

Results of ANOVA analyses indicated that month, year, and the interaction between month and year were significant sources of variability in proportion for bearded seal call types AL1(T), AL1i(T), AL3(M) and AL7(A). Pairwise comparisons demonstrated that the proportion of AL1(T) was significantly higher during April, May, and June and was significantly higher in 2010 than in 2008 or 2009. Pairwise comparisons demonstrated that the proportion of AL1i(T) was lower during January in 2008 and 2009 than in 2010. The proportion of AL3(M) was significantly lower in April, May, and June and was significantly lower in 2010 than in 2008 or 2009. Pairwise comparisons demonstrated that the proportion of AL7(A) was significantly lower in March and April and was significantly lower in 2010 than in 2008 or 2009.

For bearded seal call types AL2(T) and AL6(T), results of ANOVA analyses (Table S4) indicated that month and the interaction between month and year were significant sources of variability in proportion. Pairwise comparisons demonstrated that proportion of AL2(T) was significantly higher from April to June. The interaction effects of month and year indicated that the proportion of AL2(T) was statistically different in May and June over the 3 yr. Pairwise comparisons demonstrated that the proportion of AL6(T) was significantly lower in May and June. The interaction effects of month and year indicated that the proportion of AL6(T) in June was lower in 2009 than in 2010.

For bearded seal call type AL4(T), results of ANOVA analyses (Table S4) indicated that year and the interaction between month and year were significant sources of variability in proportion. The interaction effects of month and year indicated that the proportion of AL4(T) in January, February, and March was lower in 2009 than in 2010.

For bearded seal call type AL5(T), results of ANOVA analyses (Table S4) indicated that month and year were significant sources of variability in proportion. Pairwise comparisons demonstrated that the proportion of AL5(T) was significantly lower in January and increased up to April. Additionally, the proportion of AL5(T) was significantly higher in 2010 than in 2008 or 2009.

Notched box and whisker plots comparing monthly variation of the duration of each bearded seal call type illustrated the clear increase of duration for both AL1(T) and AL2(T) from January to June (Fig. 5) among three different years of recordings (2008, 2009, and 2010). The trends were constant among years. Duration for other call types appeared to be similar between months.

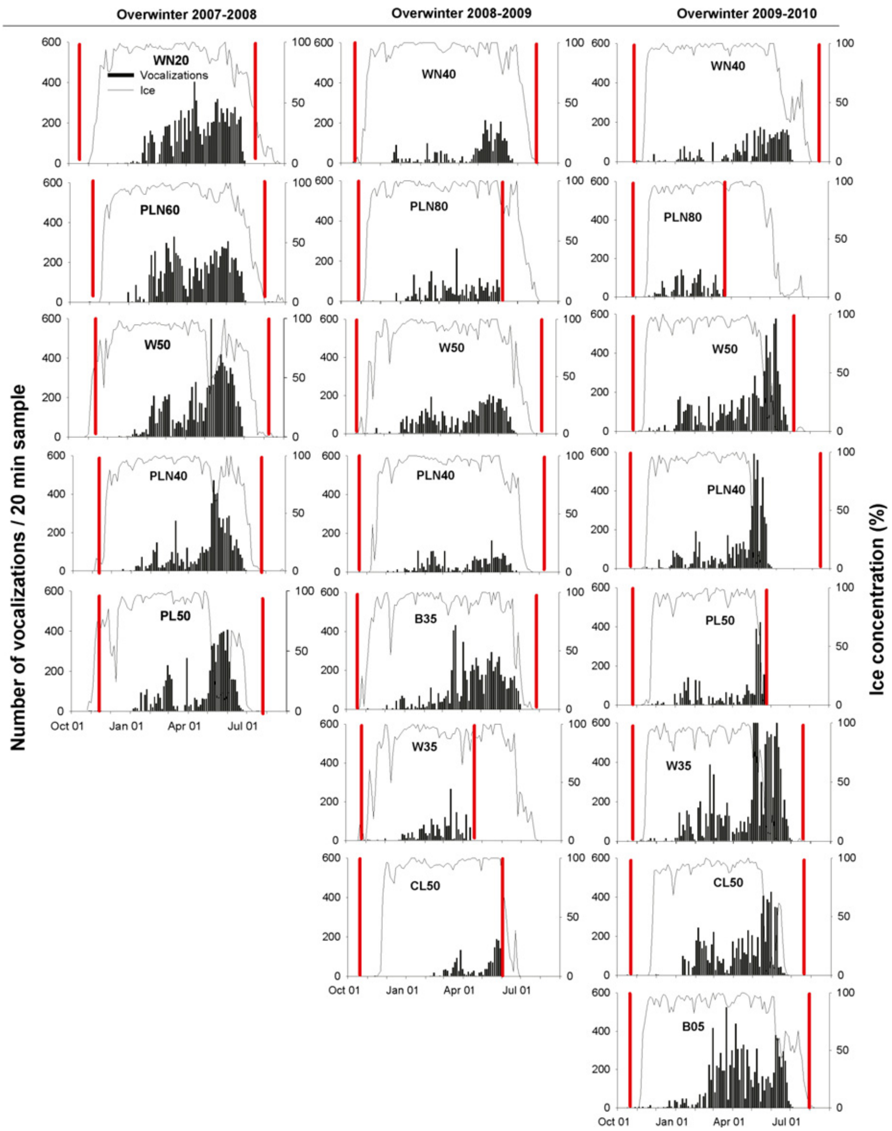

Figure 3. Number of male bearded seal calls per 20 min sample for each overwinter recording station. Red lines indicate recording start and end.

Diel Pattern in Occurrence of Bearded Seal Calls

During the summer programs, bearded seals were rarely detected, and detections increased only after mid-September. In the data from mid-September through mid-October, a diel pattern in the occurrence of bearded seal calls is evident. Across all recording stations night-time hours were more likely to contain calls than day-time hours, with a peak at 0400 AKST (Fig. 6). A diel pattern is also evident in the hourly occurrence of calls during the two overwinter years analyzed (2007–2008 and 2008–2009). During the overwinter 2007–2008 program, calling activity started to increase at 2000 AKST, and the number of calls peaked between 0200 and 0500 AKST (Fig. 7A). Similarly, during the overwinter 2008–2009 program, the number of calls increased from 19:30 onwards, peaking between 2330 and 0500 AKST (Fig. 7B). In a comparison of all six 4 h periods, the higher proportion of calls during late night/early morning was significant throughout all stations and overwinter program periods (Kruskal-Wallis, one-way ANOVA, $P < 0.05$; all *post hoc*, pairwise, multiple-comparison procedure, Student-Newman-Keuls method).

Discussion

Male bearded seals were detected frequently from January to June at all northeastern Chukchi Sea recording stations during the overwinter months. They were detected sporadically from October to December and during the summer (from July to September), as previously observed by Hannay *et al*. (2013) and MacIntyre *et al.* (in press). In Hannay *et al.* (2013), using the same data set as in our study, data were shown as presence or absence of bearded seal calls in each of six 4 h bins. On the contrary, in our analysis the sum of detections between 0200 and 0600 AKST was used. This allowed the detection of smaller fluctuations in abundance, which may remain

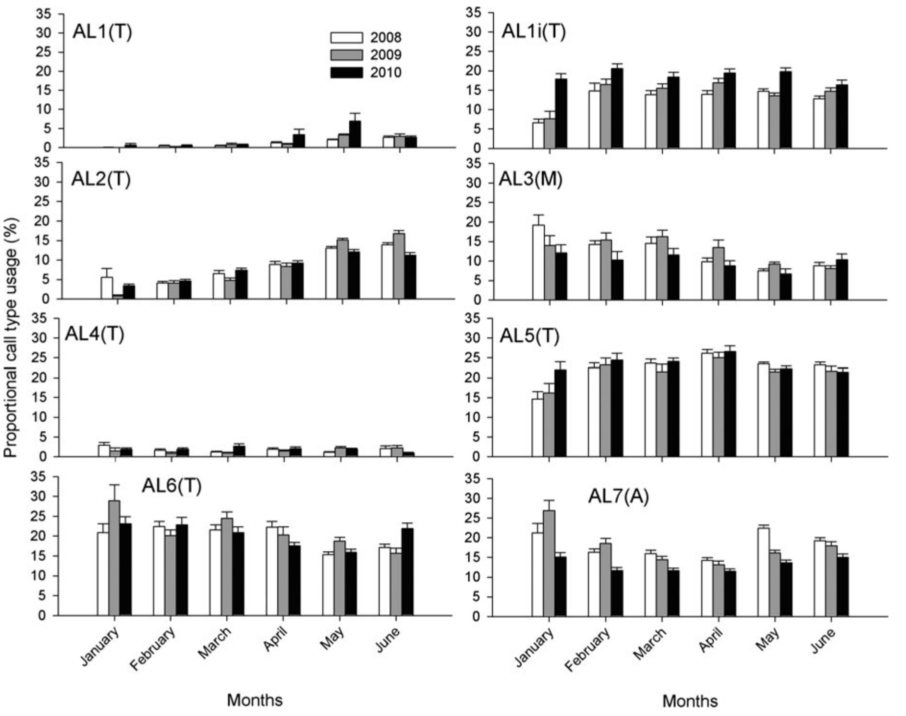

Figure 4. Monthly variation of bearded seal call types across all recording stations among three different years (2008, 2009, and 2010). Bar shading indicate year. Error bars are ± SE. See Table S2 for call type definitions.

unnoticed looking at daily presence/absence data. For example, Hannay *et al.* (2013) observed that period of high vocal activity ended abruptly, with call detection rates diminishing from maximum to near-zero over approximately one week. In our data, the number of calls decreased regularly at the end of the period of high vocal activity on a longer time frame.

The GAM analysis indicated that variance in number of acoustic detections was best explained by the variable month. This indicates that mating period was likely the main reason for the presence or absence of vocalizing male bearded seals. At all recording stations, bearded seal call activity was greatest from March to late June with a peak between mid-April and mid-June, which coincides with the mating season in this species (McLaren 1958, Burns 1981, Cleator *et al.* 1989). Similarly, MacIntyre *et al.* (2015) reported nearly continuous calling from mid-March through late June. This relationship between underwater calls and mating seasons has been observed in many phocid seals (reviewed by Stirling and Thomas 2003, Van Parijs 2003). In an earlier study, Ray *et al*. (1969) noted that while numerous seals of both sexes were observed in July near Gambell, Alaska, on St. Lawrence Island, "none were heard to sing." Bearded seals were sighted regularly during summer surveys (Day *et al.* 2013), thus the paucity of call detections in our data in July and August reflects a lack of calling rather than an absence of seals.

Male bearded seals show some breeding site fidelity, producing uniquely identifiable calls that have been tracked across studies spanning up to 16 yr (Van Parijs *et al.* 2003, Van Parijs and Clark 2006). Near Point Barrow, Van Parijs and Clark (2006) observed that roaming males made AL1i(T) trills longer than 11.9 s, while territorial males had trills less than 11.9 s. Over 16 yr (1985–2001), 66% of males were roamers (Van Parijs and Clark 2006). Interestingly, in our study using the classification of Van Parijs and Clark (2006), we observed 15% of males were roamers at B05 (close to Point Barrow) in overwinter 2009–2010 (Fig. S1), suggesting that male bearded seals might have switched tactic (from roaming to territorial) since 2001 (Van Parijs and Clark 2006). Moreover, in recent recordings (2006–2009) and in the same study area (continental slope break in the Chukchi Sea), Jones *et al.* (2014) reported that mean duration of AL1i(T) was substantially less than 11.9 s. In our study, only 4%–23% of male bearded seals were roamers (Fig. S1). Therefore, if the same relationship between trill duration and territorial holds in other locations in northeastern Chukchi Sea, the majority of bearded seals from our recording locations may have a territorial rather than a roaming strategy.

Ice conditions have a strong impact on the movements and distribution of bearded seals (Simpkins *et al.* 2003) and their mating tactics (Van Parijs *et al.* 2004). Recently, Ver Hoef *et al.* (2014) showed that bearded seals are typically found on sea-ice concentrations between 25% and 100%. Jensen (2005) demonstrated that the vocal patterns of male bearded seals differ significantly among populations and that these differences are related to local ice conditions. In Svalbard, where 71% of males were territorial and only 29% were roamers (Van Parijs *et al.* 2003), roaming males were not present when there was more than 60% of land-fast ice, whereas territorial males were present in all conditions (Van Parijs *et al.* 2004). The results of this study suggested that some vocalizing bearded seals remained in northeastern Chukchi Sea throughout most of the year and that during winter calling increased with increasing sea-ice coverage. Female bearded seals forage at sea during lactation (Lydersen and Kovacs 1999), and their distribution depends on the availability of suitable haul-out sites (Van Parijs *et al.* 2001). During the mating period, male distribution at sea reflects the areas where females are encountered regularly, suggesting that males are preferentially targeting areas frequented by estrous females (Van Parijs *et al.* 2001). Consequently, territorial males that are present earlier at a good spot for benthic foraging, where estrous females are more likely to pass during their foraging trips, may gain an advantage over roaming males.

In Risch *et al.* (2007) and Jones *et al.* (2014), AL3(M) and AL5(T) were the most commonly recorded call types. In our study, like these studies, AL5(T) was the most commonly recorded call type. However, AL3(M) was one of the less frequently used call types, which may be due to our modification of call type definitions from Risch *et al.* (2007). We may have included some of AL3(M), as classified by Risch *et al.* (2007) in our AL6(T) category, which could explain the higher proportion of AL6(T) in our study versus Risch *et al.* (2007).

Interestingly, some seasonal variation was observed in bearded seal call type usage. AL5(T) increased in proportional usage from January to April, the early onset of the breeding season. Moreover, AL3(M) and AL6(T) decreased in proportional usage in May and June. Most of the females are hauled out in March and April to give birth and nurse their pups (Burns 1981) and call types AL5(T), AL6(T), and AL3(M) might, therefore, serve a function in male-male competition. The proportional usage of these calls decreased towards the peak mating period in May to June, possibly reflecting that calls used for mate attraction become more prominent in this period. Alternatively, males might also use fewer male-male competition calls in this period because males are settled in their territories.

During the breeding period, male bearded seals advertise their breeding condition by producing long underwater trills (*e.g.*, Cleator *et al.* 1989, Van Parijs *et al.* 2001). Van Parijs *et al.* (2001) observed that, in Svalbard, individual bearded seals did not appear to significantly increase their rate of vocalizing (or reduce their inter vocal interval) throughout the mating season. However, they increased the duration of individual calls. The present study showed that during the mating period, male bearded seals in the northeastern Chukchi Sea increased the proportion and duration of AL2(T) and AL1(T) calls types to advertise their breeding condition. Van Parijs *et al*. (2003) suggested that trill duration may serve as a useful indicator of male quality in bearded seals. Our results suggest that, in northeastern Chukchi Sea, male bearded seal calls, notably AL1(T) and AL2(T) calls can be used as a crude indicator of the mating period.

Vocal repertoire size is largely determined by the function of vocal behavior and the distance between the vocalizing individual and their target audience (Rogers 2003). During the breeding season, the distribution of male bearded seals at sea increases in areas where females are found regularly, suggesting that males preferentially target areas frequented by estrous females (Van Parijs *et al.* 2001). However, females can be widely and unpredictably dispersed during the breeding season, and calls are thought to attract mating partners and to defend their territory against competitors over long distances. The intermediate-sized vocal repertoire of bearded seals as classified by Rogers (2003) with highly stereotyped narrowband calls may increase detectability of calls in spite of unfavorable propagation conditions and masking by background noise. In addition, the large frequency bandwidth of bearded seal calls and the long calling periods may also increase the chance that receivers (estrous females) detect calls under poor signal-to-noise ratios. A typical trill will propagate between 5 and 10 km; however, some can be heard up to 30 km away and have been reported to last as long as 3 min (Cleator *et al.* 1989). Stirling *et al*. (1983) suggested that under ideal conditions, some bearded seal calls may travel as far as 45 km in water.

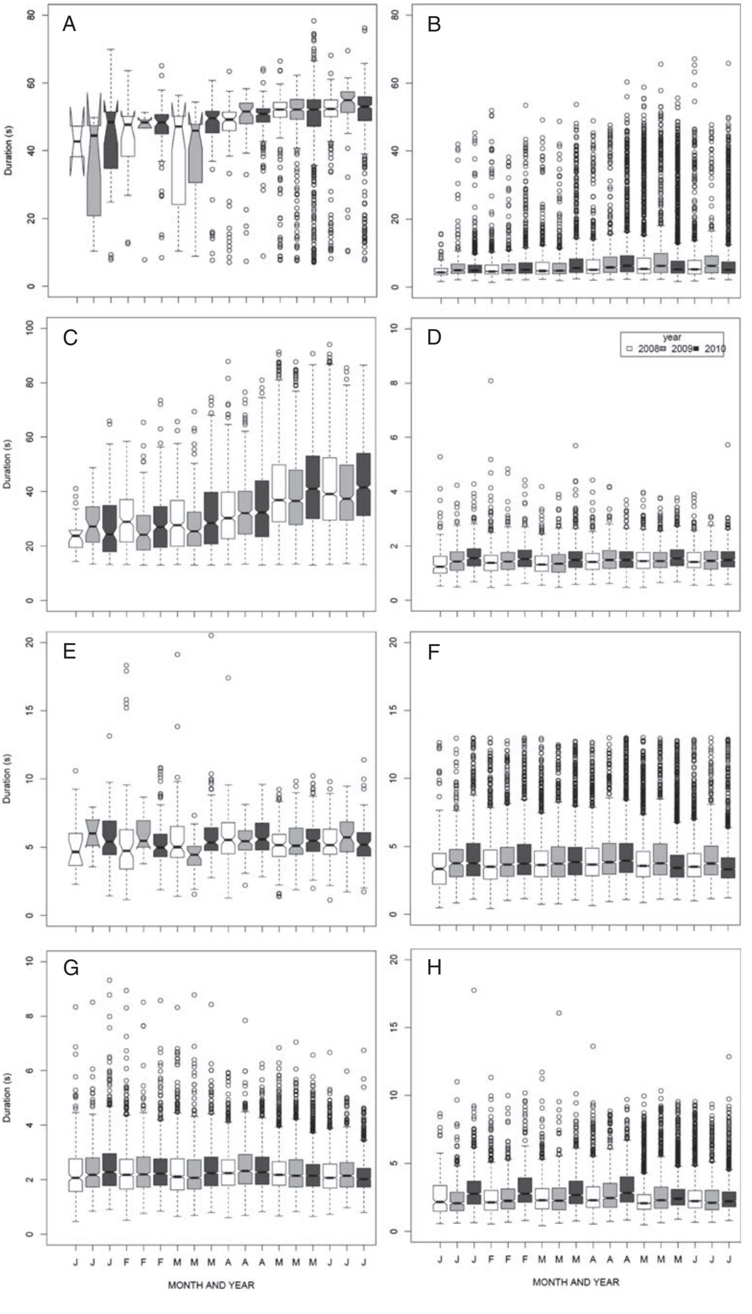

Figure 5. Notched box and whisker plots comparing monthly variation of the duration (s) of each bearded seal call type (A: AL1(T), B: AL1i(T), C: AL2(T), D: AL3(M), E: AL4(T), F: AL5(T), G: AL6(T) and H: AL7(A)) among three different years (2008: white, 2009: light gray, and 2010: dark gray). The notch represents the 95% simultaneous confidence interval on the means; dots indicate outliers. Nonoverlapping notches denote a significant difference.

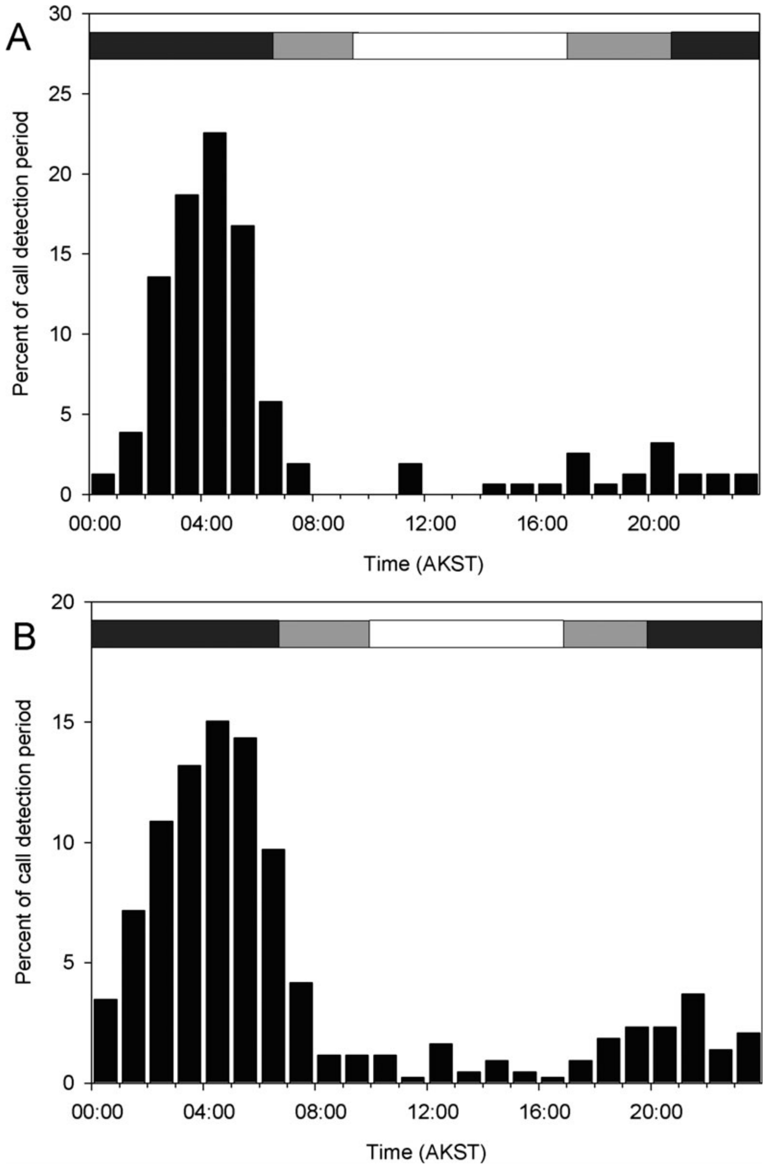

Figure 6. Diel pattern of bearded seal calls combined across all summer 2009 (A) and summer 2010 (B) recording stations. Vertical bars represent the percentage of time bins that have calls present in each 1 h time bin. Horizontal bars indicate periods of daylight (white), periods of darkness (dark gray), and periods of daylight or darkness depending on the time of recording (light gray).

Prominent temporal pattern in vocal activity in relation to diel cycle were evident in both the overwinter and summer program data, with an increase in calls by the end of the afternoon and a peak around 0400 AKST. Both in the Canadian Arctic (Cleator *et al.* 1989) and in Svalbard (Van Parijs *et al.* 2001), during the mating

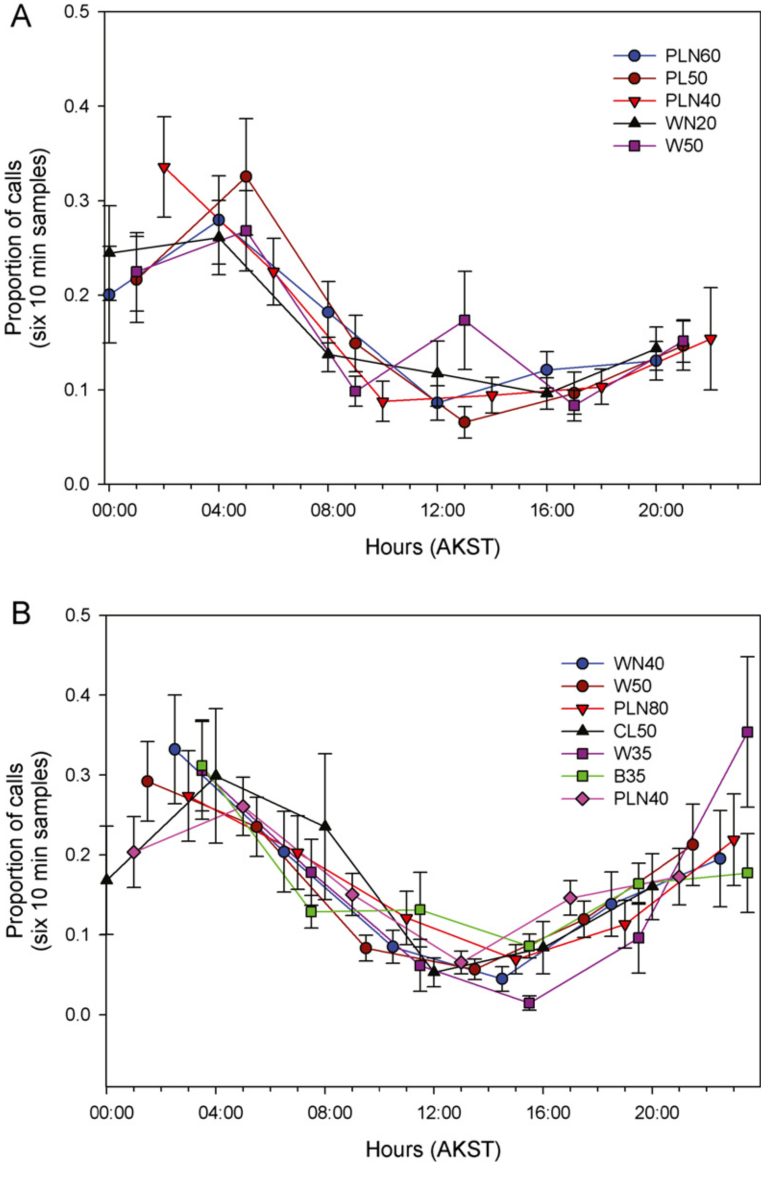

Figure 7. Proportion of bearded seal calls for all overwinter 2007–2008 (A) and overwinter 2008–2009 (B) recording stations (samples were 10 min long and recorded every 10th day).

period bearded seal calls also followed a 24 h cycle, with a similar increase in calls in the afternoon and a peak in the late night/early morning. For males, it might be more advantageous to advertise their presence over longer periods during the mating season, which might create a trade-off between the hourly call rate and the total period over which a male can energetically afford to be vocally active. Consequently, males might vocalize mainly during the hours that most females are in the water. In spring

1982 in the Canadian Arctic, bearded seals hauled out in the late morning or afternoon and returned to the water in early evening (Cleator *et al.* 1989). By mid-May 1982, seals were hauling out earlier in the morning and staying up on the ice until later in the evening (Cleator *et al.* 1989). In Svalbard, female bearded seals spend the greatest proportion of their time in the water between 2100 and 0800 (local time; Central European Time) (Krafft *et al.* 2000), coinciding with the increase in male calls (Van Parijs *et al.* 2001). These patterns of haul out and presence of females in the water at night likely explain the daily peak in calling rate in early morning in the spring (mating period); however, the reason for the diel cycle of calls outside the mating period is still unclear.

Interannual changes in the timing of sea-ice formation and retreat, as observed between 2008–2009 and 2009–2010 (earlier retreat), may affect habitat availability and stability for ice-obligate species. There are serious concerns for the future of the two circumpolar phocid seals endemic to the high Arctic, the bearded seal and the ringed seal (*Phoca hispida*). Ringed seals, which rely on suitable ice substrate for resting, pupping, and molting similarly to bearded seals, suffer continued low pup survival in western Hudson Bay potentially due to an earlier spring breakup of ice together with lower snow depths (Ferguson *et al.* 2005). Changes in sea-ice extent also have the potential to modify temporal availability of habitat for the bearded seals during the pupping season and, consequently, to impact pup survival. Later ice formation and reduced sea ice extent may also cause changes in reproductive timing (breeding occurring earlier in the season) or northward shifts in bearded seal habitat (Cooper *et al.* 2009).

To understand potential impacts of a changing environment, knowledge of how this species uses acoustic signals and the factors that shape acoustic behavior is essential. Acoustic techniques form an important tool for management and conservation of this species in a region undergoing rapid changes. PAM can be an effective method to document the spatial and temporal distribution of marine mammals in the Arctic (Hannay *et al.* 2013) instead of, or in combination with, visual surveys (Bengston *et al.* 2005, Day *et al.* 2013). The results of this study show that, in the Chukchi Sea, bearded seals produce underwater calls almost year round, thereby making PAM a valuable tool for studying them, especially in winter when poor weather, heavy ice cover, and little or no daylight make traditional visual methods unfeasible. The vocal activity of bearded seals decreases during summer when they are more easily studied using boat-based surveys during the open-water season (Aerts *et al.* 2013). Consequently, a combination of both acoustic monitoring and visual surveys can provide year-round data on bearded seal distribution in the Chukchi Sea (or elsewhere) and improve our knowledge of the biology of this species. Finally, as presented in this study, PAM can also provide information on the acoustic behavior of this species including the diel pattern and seasonal variation in the acoustic repertoire.

Acknowledgments

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Supporting Information

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12246/suppinfo.

Table S1. Call types for bearded seals annotated during manual analysis of the overwinter 2007–2008, 2008–2009, and 2009–2010 data sets. Call types are modified from Risch *et al.* (2007). Abbreviations: AL = Alaska, T = trill, M = moan, A = ascent. See Figure 2 for example spectrograms of each call type.

Table S2. Bearded seal vocal repertoire descriptive statistics for 2007–2010 recordings (overwinter data sets, one 20 min file every third day; n = 115,739), 2008–2009 recordings from 120 km north-northwest of Barrow, Alaska (Jones *et al.* 2014; n = 1,228) and 1985–2001 recordings from Point Barrow (Risch *et al.*, 2007; n = 2,291).

Table S3. Parametric coefficient results and AIC values of the Gaussian distribution Generalized Additive Models (GAM) of the effect of sea-ice coverage, month, station, latitude, longitude, ice edge distance, depth, and distance to shore on the call counts.

Table S4. Results of 2-way ANOVA for monthly and annual effects on bearded seal call type occurrence. Asterisks indicate significant effects ($P < 0.05$).

Figure S1. Columns are the percentage of roaming (A) and territorial (B) male bearded seals at each station during three overwinter recordings (white: 2007–2008; grey: 2008–2009; black: 2009–2010) using Van Parijs and Clark (2006) classification (roaming males made AL1i(T) longer than 11.9 s, while territorial males had AL1i(T) less than 11.9 s long). Error bars are the mean duration (in seconds) $\pm$ SE.