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Ringed, Bearded, and Ribbon Seal Vocalizations North of Barrow, Alaska: Seasonal Presence and Relationship with Sea Ice

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ABSTRACT. The acoustic repertoires of ringed, bearded, and ribbon seals are described, along with their seasonal occurrence and relationship to sea ice concentration. Acoustic recordings were made between September and June over three years (2006–09) along the continental slope break in the Chukchi Sea, 120 km north-northwest of Barrow, Alaska. Vocalizations of ringed and bearded seals occurred in winter and during periods of 80%–100% ice cover but were mostly absent during open water periods. The presence of ringed and bearded seal calls throughout winter and spring suggests that some portion of their population is overwintering. Analysis of the repertoire of ringed and bearded seal calls shows seasonal variation. Ringed seal calls are primarily barks in winter and yelps in spring, while bearded seal moans increase during spring. Ribbon seal calls were detected only in the fall of 2008 during the open water period. The repertoire of known ribbon seal vocalizations was expanded to include three additional calls, and two stereotyped call sequences were common. Retrospective analyses of ringed seal recordings from 1982 and ribbon seal recordings from 1967 showed a high degree of stability in call repertoire across large spatial and temporal scales.

Key words: ringed seal, bearded seal, ribbon seal, Arctic phocid, call repertoire, seasonality, vocalization, sea ice

RÉSUMÉ. Le répertoire acoustique des phoques annelés, des phoques barbus et des phoques à bandes sont décrits, de même que leur présence saisonnière et leur rapport avec la concentration de glace de mer. Des enregistrements acoustiques ont été effectués entre septembre et juin sur une période de trois ans (2006–2009), le long de la rupture de la pente continentale, dans la mer des Tchouktches, à 120 km au nord-nord-ouest de Barrow, en Alaska. Les vocalisations de phoques annelés et de phoques barbus étaient présentes pendant l'hiver et pendant les périodes où la concentration de glace était de 80 % à 100 %, mais elles se faisaient rares pendant les périodes d'eau libre. La présence des cris de phoques annelés et de phoques barbus tout au long de l'hiver et du printemps suggère qu'une partie de leur population hiverne. L'analyse du répertoire de cris de phoques annelés et de phoques barbus indique une variation saisonnière. L'hiver, le cri du phoque annelé prend principalement la forme d'aboiements, tandis que le printemps, il prend la forme de glapissements. Les gémissements du phoque barbu s'intensifient au printemps. Le cri des phoques à bandes n'a été capté qu'à l'automne 2008, pendant la période des eaux libres. Le répertoire des vocalisations connues du phoque à bandes a été élargi pour inclure trois autres cris, bien que deux séquences de cris stéréotypées étaient courantes. L'analyse rétrospective des enregistrements de cris de phoques annelés de 1982 et de phoques à bandes de 1967 a laissé entrevoir une grande stabilité du point de vue du répertoire des cris, et ce, sur de vastes échelles spatiales et temporelles.

Mots clés : phoque annelé, phoque barbu, phoque à bandes, phocidé de l'Arctique, répertoire des cris, saisonnalité, vocalisation, glace de mer

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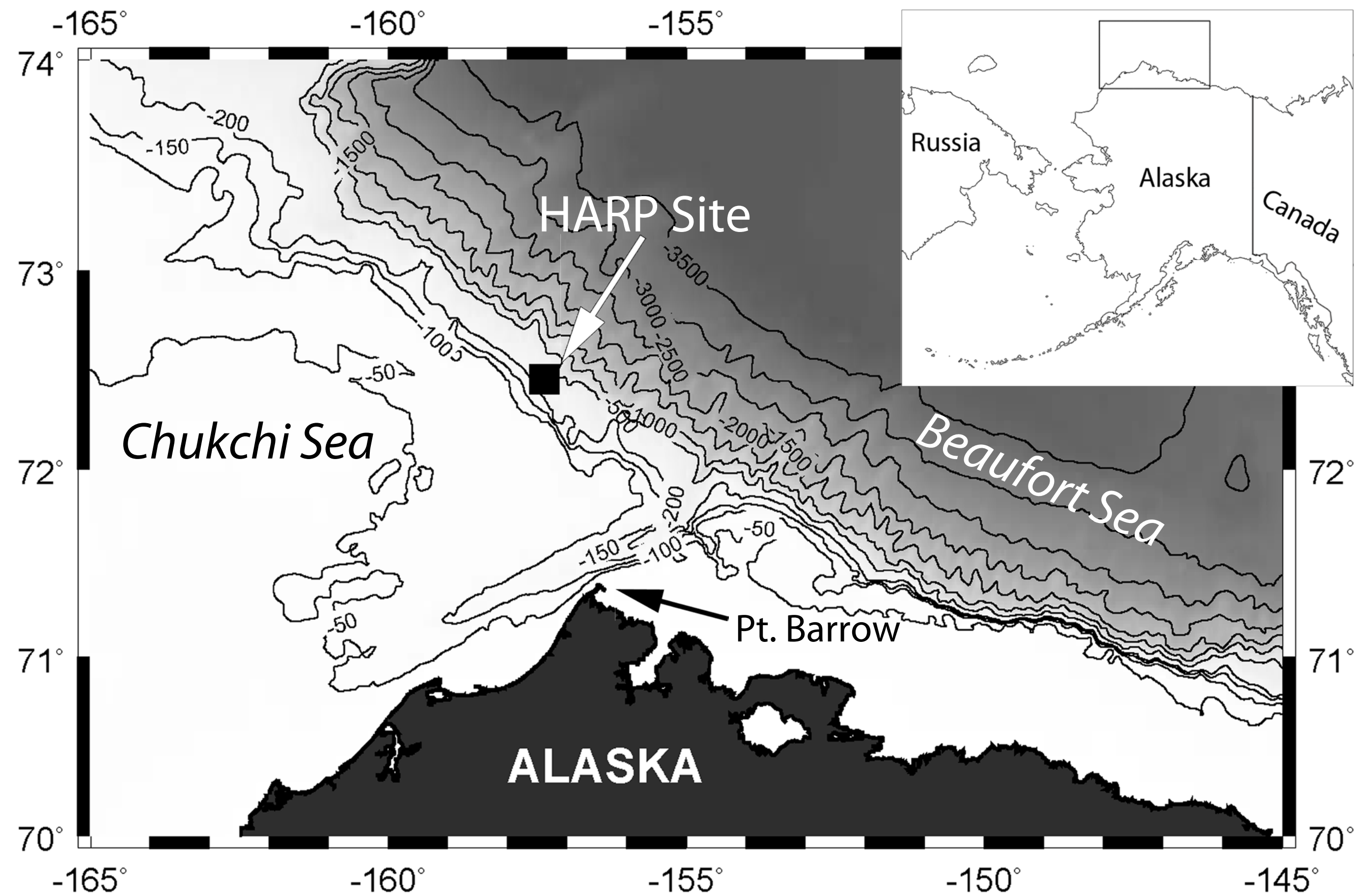

FIG. 1. Site of HARP deployment 120 km NNW of Point Barrow, Alaska, along the continental slope. Contour depths are in meters. HARP was deployed at 240 m depth.

INTRODUCTION

Developments in acoustic monitoring have provided tools for studying marine mammals in polar regions (Stirling et al., 1983; Cleator and Stirling, 1990; Moore et al., 2010; Van Opzeeland et al., 2010; MacIntyre et al., 2013). The availability of long-term acoustic recording devices has enabled investigation of the acoustic behavior and seasonal occurrence of marine mammals in places and at times where ship- and aerial-based or on-ice studies have not been feasible. These acoustic studies provide details on species distributions and movements, reproductive behavior, and population structure (e.g., Širović et al., 2004; Delarue et al., 2011; Risch et al., 2007).

Ringed seals (*Pusa hispida*), bearded seals (*Erignathus barbatus*), and ribbon seals (*Histriophoca fasciata*) are ice-breeding phocid species with ranges that overlap across a large area of the Bering, Chukchi, and Beaufort Seas. However, their seasonal movements and specific preferences for sea ice type and concentration, water depth, and breeding habitat differ substantially between species. Ringed and bearded seals spend most or all of the year in the Arctic and Subarctic and are closely associated with sea ice (Cameron et al., 2010; Kelly et al., 2010), whereas ribbon seals haul out on sea ice in the Bering Sea and Sea of Okhotsk from March through June and occupy open water from the North Pacific to the Arctic Ocean during other months (Burns et al., 1981b; Kelly and Lentfer, 1988; Boveng et al., 2008). Mating, parturition, and molting for all three species occur between March and late June; however, much remains unknown about the habitat preferences, seasonal distributions, and underwater behaviors of each species, mainly because of the difficulty and cost of conducting studies in the extreme environmental conditions of the Arctic and Subarctic. Intraspecific variation in seasonal movements and habitat preferences has been observed in ringed and bearded seals, further complicating the understanding of how and when these species use particular areas within their ranges (Burns et al., 1981a; Finley et al., 1983; Fedoseev, 1997; Crawford et al., 2011). Ringed, bearded, and ribbon seals produce underwater vocalizations that are readily identifiable (Stirling et al., 1983; Miksis-Olds and Parks, 2011) and thus are well suited for passive acoustic monitoring studies.

Autonomous acoustic recordings of ice seals were made during 2006–09 along the continental slope break, 120 km north-northwest of Barrow, Alaska, in the borderlands between the Beaufort and Chukchi Seas (Fig. 1). We compared the descriptions of the recorded acoustic repertoires and seasonal occurrence of the calls of ringed, bearded, and ribbon seals with satellite-based records of sea ice concentrations to provide insights into the seals' relationships with the ice. We also consider the seasonal presence and variation of the calls in relation to known patterns of reproduction, behavior, and movement. Retrospective analyses of ringed and ribbon seal recordings from 1982 and 1967, respectively, and comparison to the 2006–09 recordings show a high degree of stability in the call repertoire, suggesting continuity across large spatial and temporal scales.

Ringed Seals

Ringed seals are the most numerous and widely distributed of the Arctic phocid species (Kelly et al., 2010). Throughout their circumpolar range, they are closely associated with sea ice for most of the year. Their preferred winter habitat is stable ice with ridging or hummocks that facilitate accumulation of snow cover to allow construction of subnivean lairs—conditions that commonly occur in landfast ice (Smith and Stirling 1975, 1978; Hammill and Smith, 1989; Smith et al., 1991). However, several studies have also found ringed seals overwintering and breeding in drifting pack ice (Fedoseev 1975, 1997; Finley et al., 1983; Wiig et al., 1999).

Underwater vocalizations of free-ranging ringed seals have been studied in the Canadian Arctic (Stirling, 1973; Smith and Stirling, 1978; Stirling et al., 1983; Calvert and Stirling, 1985), and descriptions of their acoustic repertoire have included yelps, barks, growls, and woofs, with the suggestion of "low," "medium," and "high-pitched" call subtypes (Stirling, 1973; Stirling et al., 1983). Most of these vocalizations are less than one half-second in duration. Ringed seals commonly produce alternating barks and yelps in rapid succession. The behavioral context of ringed seal calls has not been confirmed; however, on the basis of their presence in winter and spring, Stirling et al. (1983) hypothesized that the calls are involved in intraspecific competition to maintain social structure around breathing holes and that they may also serve a reproductive purpose.

Bearded Seals

Bearded seals spend most or all of the year in drifting pack ice or in polynyas (Burns et al., 1981a). They are usually found over the continental shelf at depths less than 100 m (Lowry et al., 1980; Kingsley et al., 1985). They whelp, mate, and molt on sea ice between March and late June (Burns et al., 1981a). During that period, males also produce several types of vocalizations that are associated with breeding and probably serve as a fitness display (Cleator et al., 1989; Van Parijs et al., 2001). Extensive studies of bearded seal vocalizations have identified four main call categories (trills, moans, ascents, and sweeps), geographic variation in call characteristics, and a high degree of interannual stability in call types within each region (Stirling et al., 1983; Cleator et al., 1989; Van Parijs et al., 2001, 2003; Van Parijs and Clark, 2006; Risch et al., 2007).

Ribbon Seals

Ribbon seals are primarily a subarctic species. They whelp, mate, and molt on seasonal pack ice in the Bering Sea and the Sea of Okhotsk from mid-March to mid-July (Boveng et al., 2008). From summer through late winter, ribbon seals live in open water, are not associated with sea ice, and rarely haul out (Burns, 1970; Burns et al., 1981b; Braham et al., 1984; Kelly and Lentfer, 1988; Lowry and Boveng, 2009). While in open water, ribbon seals range from the North Pacific to the Chukchi Sea (Shustov, 1965; Moore and Barrowclough, 1984; Boveng, 2008), although knowledge of their distribution during this part of the year is limited. Ribbon seals are well adapted to deep diving (Burns et al., 1981b). Studies of stomach contents indicate that ribbon seals may feed in deeper water (> 300 m) than either ringed seals or bearded seals, and that they prefer to forage near the bottom on the continental slope (Deguchi et al., 2004).

Ribbon seals produce distinct vocalizations that have been described from recordings made during the spring breeding season in the Bering Sea, including three call types: downsweeps, roars, and grunts (Watkins and Ray, 1977; Miksis-Olds and Parks, 2011).

METHODS

Acoustic Recording and Analysis

Between early September and late June of 2006–09, a High-frequency Acoustic Recording Package (HARP; Wiggins and Hildebrand, 2007) recorded underwater sounds at a depth of 240 m in the Chukchi Sea, 120 km north-northwest of Barrow, Alaska (Fig. 1). The HARP sampled at 32 kHz continuously during the 2006–07 deployment, and with a recording schedule of 7 min out of every 14 min in subsequent deployments. Acoustic recordings from the 2006–07 and 2007–08 deployments had an effective bandwidth of 10 Hz–2.5 kHz, but for the 2008–09 deployment, the hydrophone bandwidth was extended to 10 Hz–16 kHz. During the first two recording periods, the hydrophone consisted of six cylindrical transducers (Benthos AQ-1) wired in series for a hydrophone sensitivity of −187 dB re: V/μPa and with 55 dB of preamp gain. In 2008–09, a two-stage hydrophone was used. It included the low-frequency stage from previous years with six cylindrical transducers and approximately 50 dB of preamplifier gain. The additional, high-frequency stage consisted of a spherical omni-directional transducer (ITC-1042, www.itc-transducers.com) with a relatively flat (± 2 dB) sensitivity response of −200 dB re: V/μPa from 1 Hz to 100 kHz and about 80 dB of preamplifier gain. Combined sensitivity of the two stages was consistent with published HARP specifications (Wiggins and Hildebrand, 2007). All acoustic recordings were converted into an adapted wav file format (XWAV) for analysis. XWAV files were decimated using an eighth-order

Chebyshev type I filter to reduce the data to 10.67 k samples/s (new bandwidth: 10 – 5333 Hz), minimizing further computational requirements. Analyses were conducted using the Triton program, based on MATLAB (MathWorks Inc., Natick, MA), to calculate and display long-term spectral averages (LTSA) and standard spectrograms, to perform audio playbacks, and to log call detections (Wiggins and Hildebrand, 2007).

Call Detection and Species Identification

Trained analysts visually scanned 15 min LTSA windows with 3 s temporal and 5 Hz frequency resolution for the characteristic calls of the three species. We compared previously described vocalizations for ringed, bearded, and ribbon seals (Stirling, 1973; Watkins and Ray, 1977; Stirling et al., 1983, Risch et al., 2007; Miksis-Olds and Parks, 2011) with calls detected in the HARP recordings. To avoid misidentification, we accepted only alternating sequences of barks and yelps of ringed seals, published call types for bearded seals, and characteristic downsweeps of ribbon seals as initial evidence for their presence (Fig. 2). When likely calls were detected in the LTSA, a corresponding 60 s spectrogram (1000 point FFT, Hanning windows, 30% overlap) was inspected to verify and log their presence. While analyzing the 2006 – 07 and 2007 – 08 recordings, we logged two representative call detections for each hour when seal vocalizations were present, thereby providing acoustic presence or absence at a temporal resolution of one hour. For the 2008 – 09 recordings, one detected call was logged for every minute of acoustic presence observed in the LTSA. The higher temporal resolution for detected call logging was adopted to facilitate subsequent repertoire analyses based on the broader bandwidth recordings from the 2008 – 09 deployment. One-minute XWAV time series and JPEG graphical files were saved for all logged calls, beginning 5 s prior to the start of each log entry. Each JPEG image showed the 15 min LTSA window from which the call was detected and a 60 s spectrogram of the call detection, often with additional calls. In the final step, an experienced independent analyst (J.M. Jones) visually inspected the JPEG files of all logged detections to check for identification errors. Any misidentifications were reassigned to the correct species or removed from the detection database.

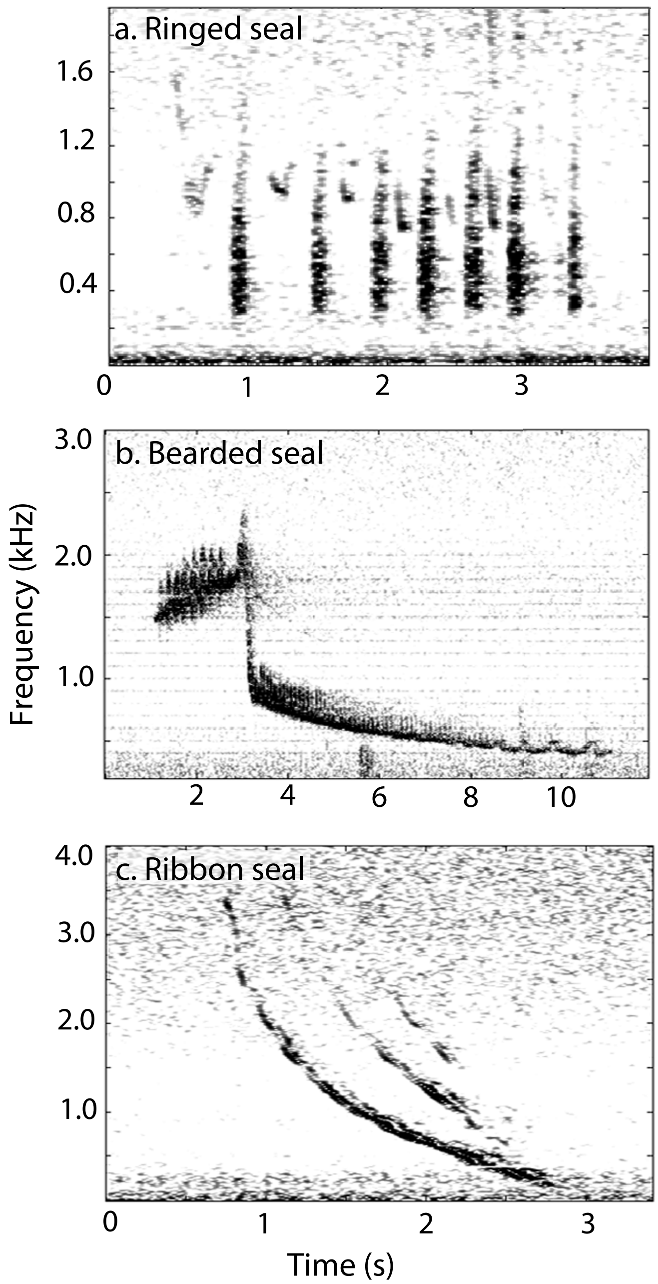

FIG. 2. Spectrograms of characteristic calls used for initial detection of (a) ringed seal (bark-yelp sequence), (b) bearded seal (AL1i trill), and (c) ribbon seal (downsweep). Sampling rate: 10.67 kHz, FFT length: 800, overlap: 90%.

Acoustic Repertoire Analysis

We analyzed all 60 s XWAV call detections from the 2008 – 09 recordings to describe the repertoire of each species and to look for seasonal variation in calling behavior. The key parameters of start and end times and minimum, maximum, start, and end frequencies were logged for each call. Only vocalizations with each of these parameters clearly shown in the spectrograms were included for repertoire and seasonal analysis. Vocalizations corresponding to published call types were identified by type. Key parameters were also logged for unidentified calls occurring within the detection windows, and these vocalizations were designated as “unknown.”

We attributed unknown calls to a species on the basis of repeated co-occurrence with characteristic vocalizations in the same 60 s XWAV and absence of the sounds of other marine mammal species in the same hour. Calls not previously described, but showing clear co-occurrence with known calls for a species, were identified as new call types if they showed consistent duration, start frequency, frequency range, and degree of tonality. To analyze seasonal variation in calling behavior, we calculated the monthly proportion of total calls for each call type.

Retrospective Analysis and Geographic Comparison

We also applied call detection and repertoire analysis to archived recordings from other studies of ringed and ribbon seal vocalizations. We included 8 h of ringed seal recordings that were collected on a recording schedule of 20 min out of every two hours from 23 to 26 April 1982, 8 km SW of Griffith Island in the Canadian High Arctic (CHA; Calvert and Stirling, 1985) and 15 min of ribbon seal vocalizations recorded opportunistically by G. Carleton Ray near St. Lawrence Island, Alaska, from 16 to 23 May 1967 (Watkins and Ray, 1977). Archival recordings of ringed and ribbon seals were digitized from the original magnetic tapes at sample rates of 96 and 64 kHz, respectively. The authors of these studies attributed previously undescribed vocalizations to ringed and ribbon seals by relating perceived intensity of the sounds to the visually observed proximity of those species during the recordings. During retrospective repertoire analysis, we assigned call types to individual vocalizations from the completed repertoire analysis of the Chukchi Sea HARP recordings. Additionally, to help identify the presence of spotted seals and further avoid misidentification, we obtained and analyzed recordings of two captive breeding spotted seals made by Doug Wartzok from 1973 to 1977 (Beier and Wartzok, 1979). No spotted seal vocalizations were detected in the present study.

Correction for Scheduled vs. Continuous Recordings

To assess potential differences in detection rates between scheduled and continuous recordings, we performed call detection analysis on the 2006–07 recordings over a two-week period in winter, during which the calls of ringed seals were dominant, and over two weeks in spring that contained mainly bearded seal calls. The start and end times of all recorded calls were logged during these periods. A series of simulated seven-minute recordings scheduled every 14 min was imposed on these time series of vocalizations. The start of each simulation was randomly assigned to a minute in the first day of the two-week period. The number of hours with vocalizations that would have fallen within the scheduled recording period for each simulation run was tallied from the winter recordings for ringed seals and from the spring recordings for bearded seals. This process was repeated 100 times. The mean number of hours with calls in the scheduled recording period for each day was compared with the number of hours containing calls from the continuous recordings. The correction factor for each species was the average of all of the ratios of continuous to mean daily scheduled detections. This factor was applied to the time series of acoustic presence for ringed and bearded seals during the 2007–08 and 2008–09 deployments to account for the likely number of missed detections from periods with no recording. This process yielded a mean correction factor of 1.45 for ringed seal calls, which was applied to the number of daily hours with call detections. We calculated less than 10% difference in bearded seal call detection rates between scheduled and continuous recordings, so a correction factor was not applied for that species. Ribbon seals were recorded only during scheduled recording deployments; therefore, a correction factor was not estimated.

Sea Ice Measurements

Data from the Advanced Microwave Scanning Radiometer–Earth Observing System (AMSR-E) were processed to produce a three-year time series of mean daily sea ice concentration. A spatial resolution of approximately 6 km × 4 km was provided using the Special Sensor Microwave/Imager (SSM/I) at 89 GHz (Spreen and Kaleschke, 2008). Daily mean values were extracted for an area extending from 68˚ to 76˚ N and from 180˚ to 130˚ W.

To obtain mean daily sea ice concentrations near the recording site, we performed time-series analysis using Windows Image Manager (WIM) and WIM Automation Module (WAM) software (Kahru, 2000). WAM computes the arithmetic mean, variance, and median for each day using the extent of sea ice coverage as a percentage of the total mask area. We used a circular mask area with a 20 km radius centered on the instrument site, with linear interpolation applied to days without data because of periodic spatial gaps in polar-orbit satellite passes. The 20 km mask radius was selected for statistical comparisons of daily acoustic presence with sea ice cover on the basis of two previous observations of maximum detection range for bearded seals in water less than 100 m deep (Stirling et al., 1983; Cleator and Stirling, 1990). This estimate of maximum detection range for what we assume to be the highest amplitude vocalizations produced near the study site was intended to be conservative.

RESULTS

Ringed Seal Vocalizations

We analyzed the vocal repertoire of ringed seals using more than 900 calls from the 2008–09 recording period (Table 1, Fig. 3). A distinguishing characteristic of ringed seal vocalizations is their short duration, with 82% of calls lasting less than 0.3 s. We found that ringed seal vocalizations separate into three call types: *yelps*, *barks*, and *growls*, which is consistent with the results of previous studies. Most calls occurred within rapid alternating sequences of barks and yelps (Fig. 2a) or in sequences containing only yelps. Call subtypes suggested by Stirling et al. (1983), such as "high-pitched yelp" and "medium- and low-pitched barks" were not clearly distinguishable from the main call types. Similarly, "woofs" and "descending chirps" were not readily separable from barks and yelps, respectively, so those call types were not included in this repertoire.

Yelps are tonal calls that sound similar to dog yelps or yips. These calls usually lack harmonics or sidebands. Yelps are more variable in duration and frequency than

TABLE 1. Ringed seal vocal repertoire descriptive statistics for 2008–09 recordings from the Chukchi Sea (HARP; N = 928) and 1982 recordings from the Canadian High Arctic (CHA; N = 601).

				Frequency (Hz)			
Call type	Source	N	Duration (s)	Start	End	Min	Max
Bark	HARP	380	0.10 ± 0.06 (0.04–0.47)	245 ± 92 (94–801)	248 ± 93 (82–787)	245 ± 92 (94–801)	702 ± 246 (138–1438)
Bark	CHA	228	0.12 ± 0.05 (0.02–0.28)	248 ± 100 (78–597)	253 ± 126 (73–991)	248 ± 100 (78–597)	714 ± 228 (158–1440)
Yelp	HARP	521	0.14 ± 0.18 (0.02–1.93)	725 ± 210 (196–1411)	686 ± 198 (126–1322)	648 ± 181 (126–1098)	763 ± 215 (196–1494)
Yelp	CHA	356	0.17 ± 0.13 (0.01–0.9)	917 ± 234 (161–1745)	781 ± 215 (151–1588)	770 ± 211 (151–1588)	927 ± 244 (161–2185)
Growl	HARP	27	0.69 ± 0.57 (.12–2.29)	235 ± 120 (65–599)	233 ± 151 (79–719)	188 ± 161 (60–927)	399 ± 249 (156–1240)
Growl	CHA	17	0.49 ± 0.26 0.17–0.95	169 ± 51 (69–281)	143 ± 44 (89–266)	107 ± 79 (41–348)	317 ± 162 (131–676)

other ringed seal call types. Although we do not define subtypes of this call type, we note that there are some common variations. About half (49%) of all yelps decreased rapidly in frequency (~900 Hz/s) from the start to the end of the call, sometimes with a very short upsweep at the beginning or end (Fig. 3a), while 17% of yelps increased in frequency throughout the call, often with a short (~0.02 s) downsweep at the end (Fig. 3b). The remaining yelps shared frequency parameters and qualitative characteristics with all other yelps, but ranged from constant in frequency to modulated (e.g., Fig. 3c).

Barks are lower in frequency than yelps, often with harmonic bands or energy spread across a range of frequencies, and usually with a raspy quality. In duration, barks are similar to yelps, but less varied (Table 1). In frequency, however, barks exhibit more variation. Most have a guttural, grunt-like quality, with energy distributed across a range of frequencies, and weak or indistinguishable non-harmonic frequency banding (Fig. 3d). Overall, barks are reminiscent of the voiced pharyngeal fricative in human speech. However, 37% of barks had clear harmonic bands and often a rise and fall of 10–100 Hz in the fundamental frequency during the call (Fig. 3e). This harmonic quality was present to a lesser degree in many barks, so subtypes were not defined.

Growls (Fig. 3f) have longer durations than barks, but share a similar range of frequencies and overall sound quality. Growls often have two or three harmonic bands, a lower fundamental frequency than barks, and often they are slightly frequency-modulated. Unlike barks and yelps, growls occur individually and not in alternating sequences of calls.

We reanalyzed recordings of ringed seal vocalizations collected in 1982 from the Canadian High Arctic (Calvert and Stirling, 1985) and performed repertoire analysis with the same method used for 2008–09 Chukchi Sea HARP recordings (Table 1). All CHA vocalizations corresponded closely to call types identified in the Chukchi Sea recordings. Yelps were the most common, followed by barks and growls. The durations of yelp, bark, and growl vocalizations were very similar between the two sites (Table 1). Frequency parameters were also very similar for barks and growls. However, yelps recorded in the CHA had slightly higher start and end frequencies, compared to those recorded in the Chukchi Sea.

Bearded Seal Vocalizations

The majority of bearded seal vocalizations were received at relatively low intensities (~6–10 dB above background). However, more than 1200 calls in the 2008–09 recording period had received intensity levels that allowed all parameters to be clearly identified, and these calls were included in repertoire analysis (Table 2, Fig. 4). Vocalizations were categorized as trills, moans, and ascents, consistent with previous studies. Nearly all corresponded to call types in the repertoire of bearded seals off Point Barrow, described by Risch et al. (2007). Trills matched the AL1, AL1i, AL2, AL4, and AL5 call types from that study. Moans and ascents matched the AL3 and AL7 call types, respectively. AL6 and AL2i call types were not detected in the 2008–09 recordings. Descriptive statistics from the Risch et al. (2007) study are included in Table 2 to facilitate comparison with results of this analysis.

Ribbon Seal Vocalizations

We performed repertoire analysis on a large sample of ribbon seal calls detected during fall 2008 and found six types of vocalizations (Fig. 5). *Downsweeps*, *grunts*, and *roars* were present, matching previously described calls (Watkins and Ray, 1977; Miksis-Olds and Parks, 2011). We attribute three additional call types to ribbon seals: *yowls*, *growls*, and *hisses*. These calls were detected only in the presence of one or more of the previously described call

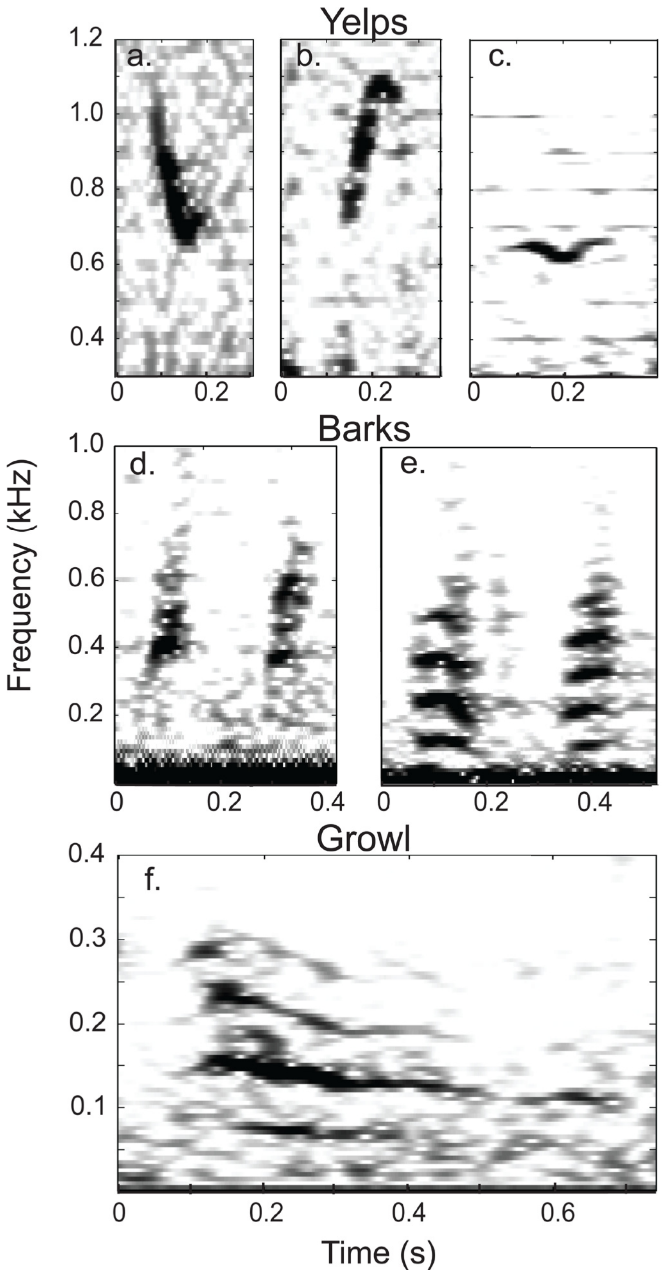

FIG. 3. Spectograms of ringed seal vocalizations (yelps, barks, and growls) detected and recorded in the Chukchi Sea in 2008–09 and the Canadian High Arctic in 1982. Sampling rate: 10.67 kHz, FFT: 600, overlap: 90%. Yelps commonly (a) decrease or (b) increase rapidly in frequency, but also (c) exhibit varying degrees of frequency modulation. Barks also vary from (d) more broadband to (e) exhibiting clear harmonics. Growls (f) are longer in duration and lower in frequency than other calls.

types (i.e., downsweeps, grunts, and roars). None of these additional calls matched those described for any other Arctic marine mammal species, including the spotted seal (*Phoca largha*), harp seal (*Pagophilus groenlandicus*), and walrus (*Odobenus rosmarus*) (Beier and Wartzok, 1979; Terhune, 1994; Sjare et al., 2003). Furthermore, there was no temporal overlap between ribbon seal calls and those of other marine mammal species. Ribbon seal calls generally occurred in bouts lasting from five minutes to about one hour. From the beginning to the end of a calling bout, the intensity and number of vocalizations detected often increased to a peak level before falling off again toward the end of the bout. Ribbon seal calls were found only during the open water season of 2008 and were not detected at any other time. Descriptive statistics for the ribbon seal repertoire are shown in Table 3.

Downsweeps (Fig. 5a) are the most identifiable of ribbon seal vocalizations and made up about 20% of total calls. We did not find discrete categories of downsweeps based on duration and frequency range as reported by Watkins and Ray (1977). Instead, duration varied continuously. We found a strong relationship between duration and frequency range in downsweeps, with a consistent rate of frequency change of about 0.9 kHz/s.

Ribbon seal roars (Fig. 5b) are non-tonal sounds that span a broad range of frequencies, lasting about one second. These vocalizations are variable in the frequency of peak energy during the call: some show steady non-harmonic frequency banding, and others have a more even distribution of energy across the bandwidth of the call. Often, the frequency emphasis shifts slightly downward during the call, giving the impression of a screeching, “yeow” sound.

Yowls (Fig. 5c) were the most commonly detected ribbon seal vocalization, representing 37% of total calls included in repertoire analysis. They are narrow-band, slightly modulated calls that lack harmonics. Yowls are reminiscent of some longer-duration ringed seal yelps, but with a raspier, hoot-like quality.

Ribbon seal grunts (Fig. 5d) are shorter on average than yowls and made up 27% of total calls. Like many ringed seal barks, these calls lack harmonics and have a guttural quality, with energy spread across a range of frequencies. However, ribbon seal grunts are distinguished from ringed seal barks by their longer duration (0.40 ± 0.17 s vs. 0.10 ± .06 s for ringed seal barks).

Hisses (Fig. 5e) were the least common ribbon seal call detected and were found only during periods when the received level of their other calls was high. These calls have long durations (4.71 ± 2.77 s) and are characterized by sustained high-frequency hissing that produces a scream-like sound. Unlike other calls, hisses had a slow onset, with the intensity steadily rising to its maximum level over periods of one second or more.

Low-frequency growls (Fig. 5g) are also uncommon. Growls are calls of short duration (0.46 ± 0.15 s) that often have clear harmonic bands. They are the lowest-frequency ribbon seal vocalizations and have little frequency variation from start to end.

Ribbon seal calls occurred in highly stereotyped sequences. The most common of these included a grunt followed by a yowl then another grunt (Fig. 5f), occasionally concluding with a growl. The grunt-yowl-grunt sequence was detected 83 times in 2008. All growls occurred at the end of a grunt-yowl-grunt sequence. Another common pattern was a roar followed immediately by a grunt. Both of these sequences were encountered multiple times per minute during the most intense calling bouts. Downsweeps and hisses did not occur in stereotyped sequences.

TABLE 2. Bearded seal vocal repertoire descriptive statistics for 2008–09 recordings (HARP; N = 1228) and 1985–2001 recordings from Point Barrow, Alaska (Risch et al., 2007; N = 2274).

Call type	Source	N	Duration (s)	Frequency (Hz) Start	End	Min	Max
AL1 (T)	HARP	2	45.88 ± 2.5 (44.29–47.47)	2.84 ± 0.28 (2.64–3.03)	1.02 ± 0.33 (0.79–1.25)	0.25 ± 0.07 (0.12–0.29)	3.26 ± 0.87 (2.64–3.87)
AL1 (T)	Risch et al., 2007	93	40.79 ± 11.26 (7.78–59.51)	2.87 ± 0.72 (0.87–3.80)	1.39 ± 0.53 (0.51–2.58)	0.23 ± 0.05 (0.13–0.34)	4.32 ± 0.91 (1.83–5.35)
AL1i (T)	HARP	238	7.57 ± 5.71 (3.15–48.26)	1.17 ± 0.36 (0.66–2.73)	0.40 ± 0.11 (0.15–0.82)	0.40 ± 0.11 (0.15–0.82)	1.59 ± 0.50 (0.94–3.90)
AL1i (T)	Risch et al., 2007	264	11.69 ± 8.71 (3.61–45.29)	1.58 ± 0.62 (0.86–3.78)	0.42 ± 0.15 (0.23–1.24)	0.42 ± 0.14 (0.23–1.24)	2.59 ± 0.87 (1.38–5.20)
AL2 (T)	HARP	84	35.13 ± 12.23 (3.69–58.12)	2.25 ± 0.69 (0.46–3.76)	0.41 ± 0.12 (0.15–0.82)	0.41 ± 0.12 (0.15–0.82)	2.25 ± 0.69 (0.46–3.76)
AL2 (T)	Risch et al., 2007	83	53.42 ± 11.04 (13.18–73.53)	3.72 ± 1.36 (1.64–11.32)	0.32 ± 0.11 (0.21–0.83)	0.32 ± .010 (0.21–0.80)	3.73 ± 1.35 (1.72–11.32)
AL3 (M)	HARP	386	2.45 ± 1.21 (0.53–7.47)	0.65 ± 0.24 (0.22–1.26)	0.49 ± 0.19 (0.20–1.25)	0.50 ± 0.19 (0.20–1.25)	0.65 ± 0.24 (0.22–1.26)
AL3 (M)	Risch et al., 2007	633	2.14 ± 0.87 (0.76–6.50)	0.37 ± 0.08 (0.19–0.74)	0.29 ± 0.05 (0.16–0.61)	0.29 ± 0.05 (0.16–0.61)	0.37 ± 0.08 (0.19–0.74)
AL4 (T)	HARP	15	5.86 ± 1.68 (4.41–11.29)	0.94 ± 0.42 (0.39–2.25)	0.95 ± 0.40 (0.56–2.14)	0.60 ± 0.26 (0.19–1.35)	1.03 ± 0.43 (0.57–2.36)
AL4 (T)	Risch et al., 2007	209	5.77 ± 1.65 (3.37–10.50)	1.75 ± 0.78 (0.76–4.06)	2.02 ± 1.00 (0.80–4.56)	1.10 ± 0.56 (0.39–2.41)	2.04 ± 1.00 (0.83–4.56)
AL5 (T)	HARP	335	4.27 ± 2.58 (0.80–19.23)	1.05 ± 0.37 (0.44–2.81)	0.70 ± 0.26 (0.26–1.99)	0.68 ± 0.25 (0.26–1.99)	1.07 ± 0.37 (0.44–2.84)
AL5 (T)	Risch et al., 2007	614	4.76 ± 2.54 (0.82–18.71)	0.73 ± 0.30 (0.32–3.75)	0.42 ± 0.13 (0.22–1.81)	0.41 ± 0.13 (0.20–1.81)	0.73 ± 0.30 (0.32–3.75)
AL7 (A)	HARP	168	3.04 ± 1.37 (0.56–8.54)	0.39 ± 0.29 (0.09–1.77)	0.69 ± 0.32 (0.20–1.95)	0.39 ± 0.29 (0.09–1.77)	0.69 ± 0.32 (0.20–1.95)
AL7 (A)	Risch et al., 2007	378	3.48 ± 1.52 (0.86–8.70)	0.22 ± 0.06 (0.12–0.93)	0.65 ± 0.22 (0.26–1.59)	0.22 ± 0.06 (0.12–0.81)	0.65 ± 0.23 (0.26–1.59)

Repertoire analysis was performed on a large sample of ribbon seal calls recorded by G. Carleton Ray in the Bering Sea in 1967 (Table 3). All six call types we attribute to ribbon seals recorded in the Chukchi Sea were also present in the Bering Sea recordings. Start and end frequencies and durations for ribbon seal calls were very similar between the two locations, 41 years apart. The grunt-yowl-grunt sequence was observed 27 times in the 1967 recordings, occasionally concluding with a growl. Roar-grunt sequences were also present.

Seasonal Occurrence and Variation in Repertoire

Ringed seal vocalizations were found only between mid-December and late May of each year (Fig. 6b), with the exception of a single bark-yelp sequence in the fall of 2007. The annual peak in call detections occurred between January and February, with another two or three peaks from March through late May. Average monthly acoustic occurrence (Fig. 7a) generally decreased from January/February through May. Although vocalizations were detected in up to 20 hours of some days, monthly averaged call occurrence was less than 2.2 hours per day for all months.

All call types were detected in most months of ringed seal acoustic presence, yet there was a seasonal difference in the daily proportion of total calls for each type (Table 4, Fig. 8). Barks were the most common type in January and February, and yelps were predominant from March through the end of May. The growl was the least common call type in all months.

Bearded seal vocalizations were detected between December and the end of recording in June for each year (Fig. 6c), except for three occasions on which a small number of trills were detected in October and November. Monthly average acoustic presence generally increased from December through June, with annual peaks in April of all years (Fig. 7b). Although there was a general increase in bearded seal detections from December to June, these events were sporadic, and their timing and magnitude varied widely within and between years. It is also noteworthy

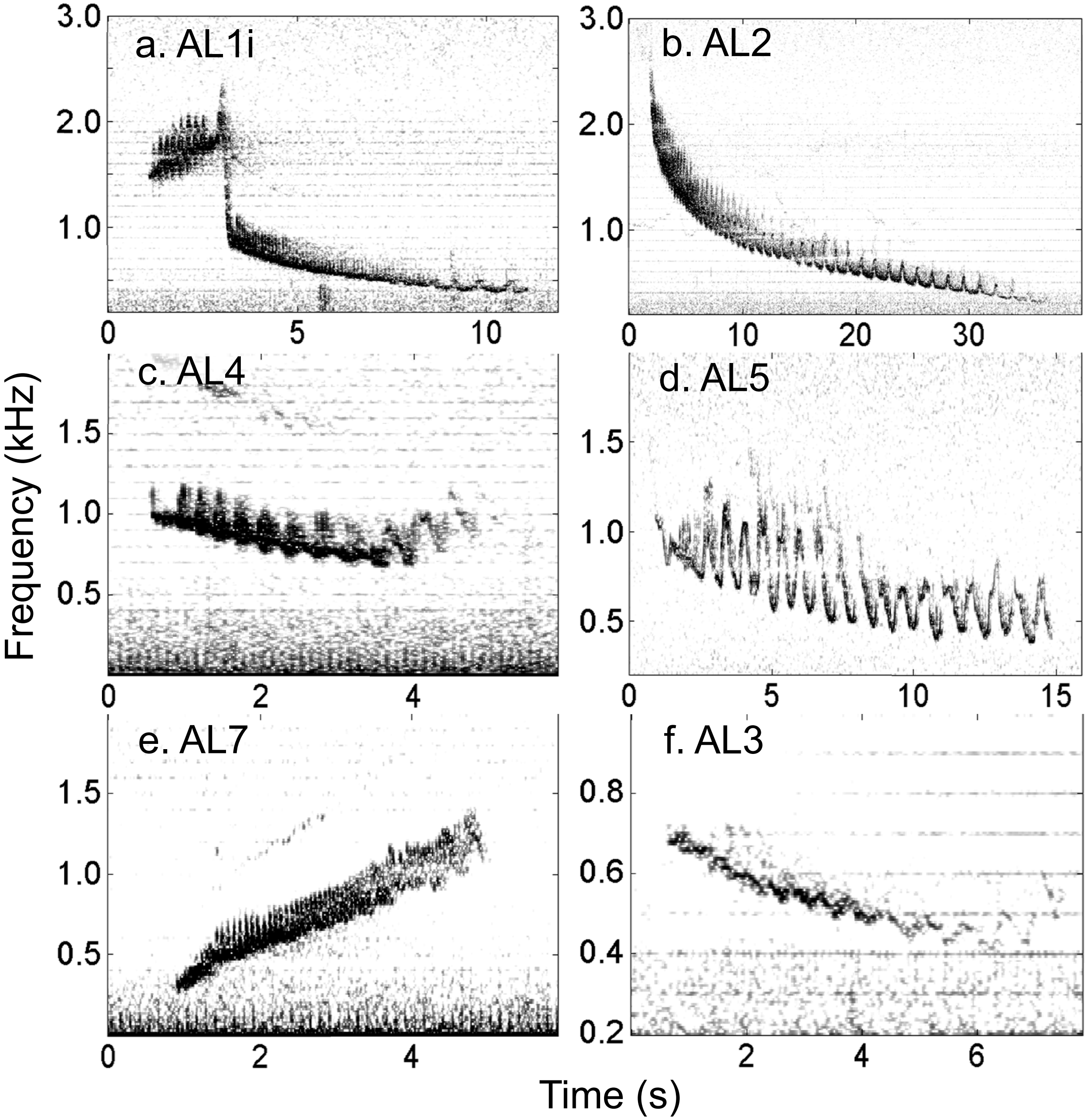

FIG. 4. Bearded seal call spectrograms representing the major call types found in Chukchi Sea 2008–09 recordings. Call types match previous descriptions of vocalizations from near Point Barrow, Alaska (Risch et al., 2007), so the same classification and naming are used. Sampling rate: 10.67 kHz, FFT: 1000, overlap: 80%.

that some of the highest received sound levels for bearded seal calls were recorded in January and February.

Seasonal variation was present in bearded seal calls (Table 5). January and April had the greatest number of calls suitable for repertoire analysis, so we compare those months. Moan-type calls (AL3) represented a higher proportion of total calls detected in April than in January. Conversely, the relative proportion of AL1i trills and ascending calls (AL7) decreased from winter to spring.

Ribbon seal calls were detected during the open water period (AMSR-E mean ice cover of 0% within 20 km radius of recording site) on 17 days from 6 September through 24 October 2008, after which there were no further detections through the end of the recording period. We did not detect ribbon seals at any other time from 2006 to 2009.

Since ribbon seal calls were present during fall of only one year, we were unable to assess seasonal variation in calling behavior for this species. Within the 17 days during which ribbon seal calls were present, there were differences in daily detection ratios between calls. However, these were most likely due to variation in the distance to calling animals, with some calls detected over longer distances than others.

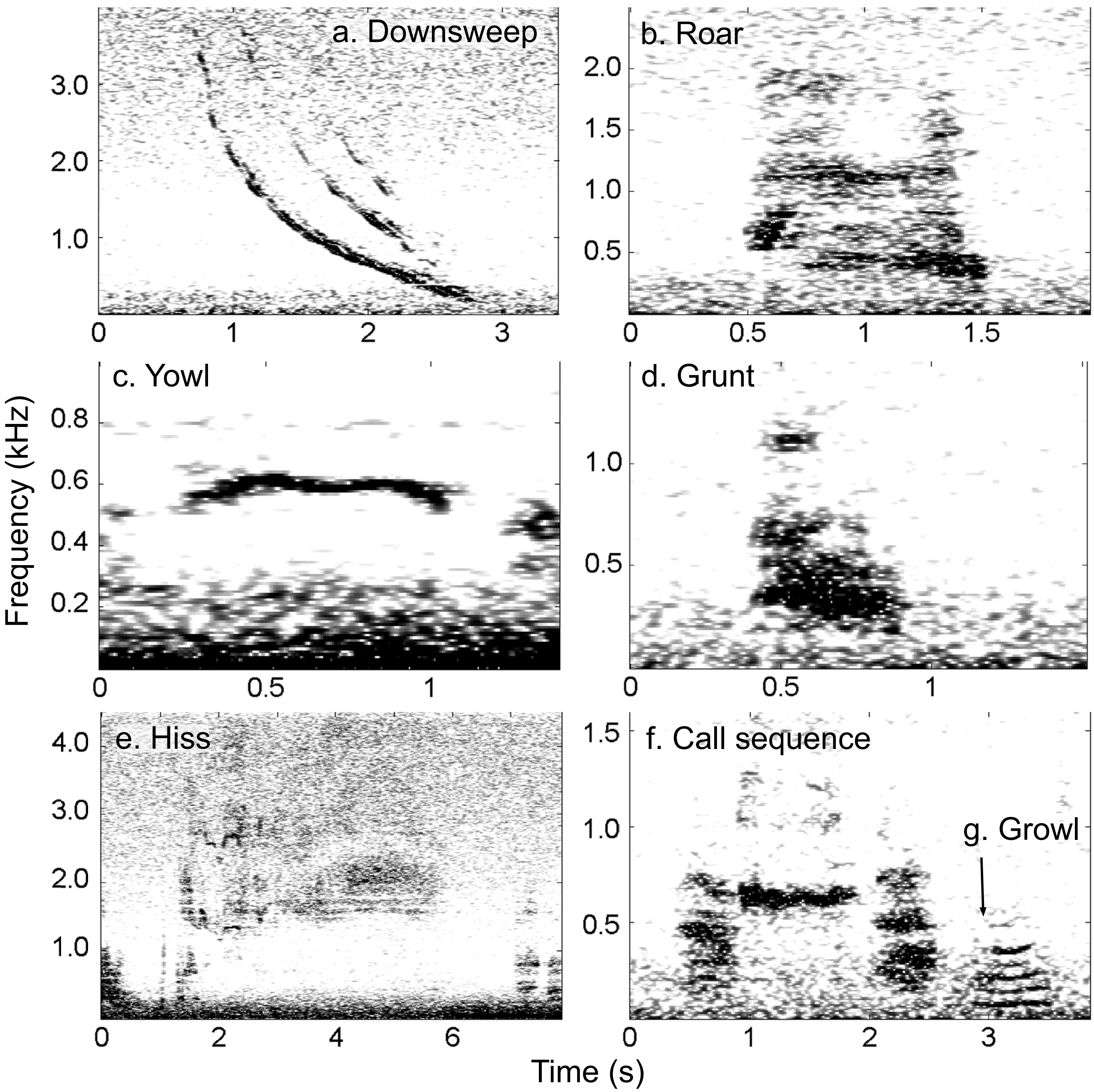

FIG. 5. Ribbon seal call spectrograms recorded in the Chukchi Sea during fall 2008. Call types are (a) downsweep, (b) roar, (c) yowl, (d) grunt, (e) hiss, (f) stereotyped sequence of calls, and (g) growl. Yowl, hiss, and growl calls are newly described. The grunt-yowl-grunt sequence (f) was often detected during periods of ribbon seal acoustic presence. Sampling rate: 10.67 kHz, FFT: 800, overlap: 90%.

Comparison with Mean Daily Sea Ice Concentration

Nearly all ringed seal calls were detected during periods when sea ice cover was greater than 95%. Chi-squared tests were conducted to compare the sea ice concentration with the number of days that contained ringed seal calls during winter (January through March) and spring (April through June) for 2007–09. Ice concentration was separated into three bins (from 90% to 100%) for the winter months and six bins (from 73% to 100%) for the spring months. Chi-squared results showed a strong relationship between sea ice cover and call detections during winter, with significantly more calling days than expected during periods of 99%–100% ice cover (χ^2 = 8.96, df = 2, N = 99 days, p = 0.01). During spring, there was no statistically significant relationship between sea ice cover and ringed seal call detections (χ^2 = 17.19, df = 5, N = 73 days, p = 0.15).

Bearded seal calls were detected during periods when sea ice cover was more than 83%, with the exception of a small number of vocalizations detected during open water.

TABLE 3. Ribbon seal vocal repertoire descriptive statistics for the Chukchi Sea in fall 2008 (HARP; N = 748) and St. Lawrence Island in spring 1967 (Bering; N = 401).

Call type	Source	N	Duration (s)	Frequency (Hz) Start	End	Min	Max
Downsweep	HARP	146	1.42 ± 0.41 (0.57–2.94)	1659 ± 622 (770–4074)	355 ± 195 (127–1370)	355 ± 195 (127–1370)	1659 ± 622 (770–4074)
Downsweep	Bering	112	1.53 ± 0.97 (0.53–6.38)	2686 ± 1420 (707–9779)	552 ± 689 (26–2326)	551 ± 683 (18–2326)	2684 ± 1446 (707–10231)
Grunt	HARP	204	0.40 ± 0.17 (0.11–1.06)	403 ± 164 (199–1123)	379 ± 136 (170–1006)	26 ± 111 (71–738)	1069 ± 528 (285–2569)
Grunt	Bering	173	0.38 ± 0.17 (0.03–1.30)	427 ± 194 (176–1554)	361 ± 184 (138–1271)	300 ± 154 (36–844)	707 ± 290 (270–1629)
Yowl	HARP	273	0.57 ± 0.30 (0.11–1.88)	653 ± 185 (232–2170)	607 ± 124 (199–1274)	571 ± 116 (186–1204)	710 ± 250 (244–2568)
Yowl	Bering	54	0.51 ± 0.32 (0.06–1.04)	703 ± 115 (299–873)	613 ± 101 (318–741)	596 ± 110 (221–741)	740 ± 117 (350–995)
Roar	HARP	98	0.87 ± 0.31 (0.26–1.61)	626 ± 278 (211–1464)	360 ± 131 (147–796)	274 ± 109 (85–583)	1592 ± 552 (466–2995)
Roar	Bering	38	0.80 ± 0.30 (0.28–1.34)	447 ± 141 (262–942)	359 ± 153 (82–800)	300 ± 133 (66–641)	629 ± 168 (318–979)
Hiss	HARP	10	4.71 ± 2.77 (0.39–7.46)	1787 ± 100 (1655–1934)	1746 ± 145 (1410–1880)	1312 ± 292 (537–1619)	2167 ± 192 (1681–2342)
Hiss	Bering	20	4.40 ± 5.60 (0.68–17.54)	1274 ± 1096 (235–3757)	1071 ± 1139 (311–4321)	903 ± 1027 (179–4265)	2271 ± 2269 (556–10403)
Growl	HARP	17	0.46 ± 0.15 (0.24–0.76)	70 ± 23 (42–147)	83 ± 35 (54–214)	68 ± 24 (54–146)	545 ± 203 (269–833)
Growl	Bering	4	0.26± 0.07 (0.17–0.32)	236 ± 114 (112–366)	175 ± 109 (36–340)	165 ± 99 (36–270)	317 ± 174 (130–503)

We performed the same chi-squared analyses used for ringed seals, but divided ice cover in spring (April through June) into eight bins between 73% and 100% to better represent the distribution of sea ice values for bearded seal call detections. Our results show a significant relationship between sea ice cover and call detections during winter (January through March) and significantly more calling days than expected during periods of 99%–100% ice cover (χ^2 = 6.044, df = 2, N = 76 days, p = .049). From April through June, there was no significant relationship between sea ice cover and bearded seal call detections (χ^2= 8.645, df = 7, N = 169 days, p = .279).

DISCUSSION

Acoustic Repertoire and Geographic Variation

Ringed seals produce mostly calls of very short duration (< 0.3 s), a distinguishing characteristic of their vocalizations that will likely aid in future acoustic monitoring studies using autonomously recorded acoustic data. We present a simplified repertoire with three major call types: barks, yelps, and growls. High-resolution spectrograms revealed some common variations in both yelps and barks that were not apparent using previous analysis methods. Including more parameters in future repertoire analyses may help us to determine whether the variation we observed in the frequency and duration of barks and yelps is due to the presence of call subtypes.

Ringed seals occur throughout the High Arctic, and the direct comparison of calls in the Chukchi Sea and Canadian High Arctic demonstrated a remarkable consistency in their vocalizations, both in the call types and their proportions relative to one another. One notable difference in the two areas is the slightly higher frequency of yelps in the CHA compared with the Chukchi Sea. Because of the relatively small sample size of the recordings from the Canadian High Arctic (four days in April 1982), it is difficult to determine if this very small difference in frequency characteristics of yelp calls represents a geographic variation. Analyses of additional ringed seal recordings collected by Stirling in the CHA between 1974 and 1983 may facilitate more quantitative geographic comparisons. The overall similarity of ringed seal calls across spatially and temporally separated samples suggests that little geographic variation exists in the acoustic behavior of this species.

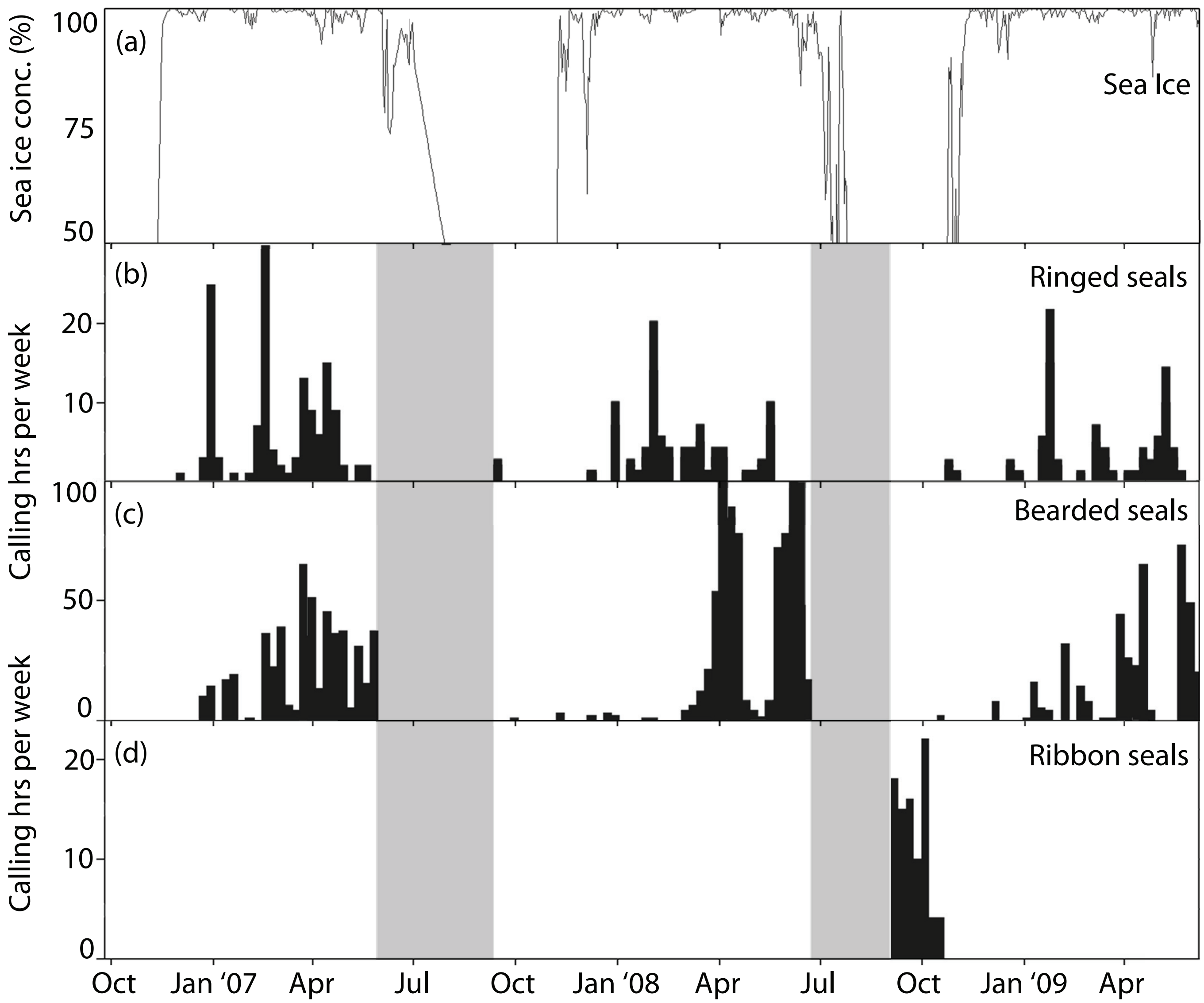

FIG. 6. Ice seal acoustic detections in hourly bins per week from September 2006 to June 2009 plotted against sea ice cover: (a) mean daily percent sea ice cover (AMSR-E 20 km radius), (b) ringed seals, (c) bearded seals, and (d) ribbon seals. Shaded areas indicate periods with no acoustic data. A scheduled recording correction factor of 1.45 was applied to ringed seal detections from September 2007 through June 2009. Note that the scales for calling hours per week differ for each seal species.

Both the simplicity of ringed seal calls and their lack of geographic variation may provide insight into their evolutionary development. Unlike Weddell seals (*Leptonychotes weddelli*), their ecological counterparts in the Antarctic (Smith et al., 1991), ringed seals are subject to predation from polar bears. Stirling and Thomas (2003) hypothesize that strong predation pressure on ringed seals has selected for a smaller number of vocalizations and fainter calls. Ringed seal calls cannot be heard from above the ice (Stirling, 1973; Stirling et al., 1983), unlike those of bearded seals, walrus, and ribbon seals. Satellite telemetry results have shown long-range movements of young ringed seals (Kapel et al., 1998; Teilmann et al., 1999; Crawford et al., 2011), which suggest mixing of the population. Genetic analyses show little diversity and genetic population structure in ringed seals (Davis et al., 2008; Kelly et al., 2009). The lack of geographic variation in acoustic behavior is consistent with both selective pressure due to predation and possible mixing of the ringed seal populations.

Male bearded seals are known to return to the same breeding location year after year, producing uniquely identifiable vocalizations that have been tracked across studies spanning up to 16 years (Van Parijs et al., 2003; Van Parijs and Clark, 2006). These males adopt either "roaming" or "territorial" mating strategies, and trill duration differs between these two tactics (Van Parijs et al., 2003, 2004; Van Parijs and Clark, 2006). Near Point Barrow, roaming males made AL1i and AL4 trills longer than 11.9 s, while territorial males had trills less than 11.9 s long (Van Parijs and Clark, 2006). Conversely, Van Parijs (2003) reported that territorial males in Svalbard had significantly longer trills than roamers.

The proximity between our study site and the Point Barrow study site (Van Parijs et al., 2006) encourages a comparison of trills at these two locations. In our study, the mean duration of AL1i and AL4 trill types is substantially less than 11.9 s (Tables 3 and 4). Therefore, if the same relationship between trill duration and territoriality holds in the offshore environment, the Chukchi Sea bearded seals may have a territorial rather than a roaming strategy.

Sea ice concentration affects vocal patterns in bearded seals, with heavier ice generally resulting in fewer vocalizations and less seasonality in calling among roaming males in both Svalbard and Alaska (Van Parijs, 2004; Jensen, 2005). Differences in ice conditions between offshore and nearshore regions provide an alternative hypothesis for variation in trill durations between these two areas.

The acoustic repertoire of ribbon seals from our study is more varied than previously described. Their calls often occurred in highly stereotyped sequences, containing as many as five calls. All six call types were also present and in similar relative proportions in ribbon seal recordings made in the Bering Sea in 1967, which shows a high degree of similarity across widely separated geographic areas and over 41 years. The presence of the grunt-yowl-grunt-growl call sequence at both sites further indicates that these calls were produced by ribbon seals. The alternating sequences of ribbon seal grunts and yowls are similar in frequency to the barks and yelps of ringed seals. However, we infer that they do not originate from ringed seals from their substantially longer duration, the stereotyped nature of the sequences, and the fact that no ringed seal bark-yelp sequences were detected when ribbon seal calls were present.

The harp seal is a close relative of the ribbon seal (Árnason et al., 1995), shares similar preferences for lower-latitude pack ice during breeding, and occupies open water during large portions of the year. Harp seals also produce rhythmically repeated patterns of vocalizations (Terhune et al., 1987; Moors and Terhune, 2003). It has been suggested that these patterns serve as a means of reducing the effects of masking in a noisy environment due to either environmental noise or calls of conspecifics. Calling rates in harp seal aggregations during the breeding season ranged from 32 to 88 calls per minute (Terhune et al., 1987), with vocalizations usually overlapping each other. We propose that similar factors could be influencing ribbon seal acoustic behavior and note that there were often more than 30 ribbon seal calls per minute in the 1967 recordings and that overlap of those calls was common.

The 1967 ribbon seal recordings we analyzed were collected in April (Watkins and Ray, 1977), a likely month for mating (Burns et al., 1981b). The presence of all call types in recordings made within the breeding range and season for ribbon seals makes it likely that at least some calls are involved in reproduction. It is unknown, however, whether both males and females produce these sounds, and the stability of the repertoire outside the breeding season raises additional questions about the function of these calls.

The size of the vocal repertoire has been related to the mating system in phocid seals. Stirling and Thomas (2003) show that promiscuous and polygamous species are more likely to have a larger acoustic repertoire than monogamous species, and that female gregariousness is positively correlated with size of vocal repertoire. Ribbon seals produce at least six call types, which is comparable to the repertoire of other promiscuous species.

Seasonal Presence and Variation in Acoustic Repertoire

For ringed seals, the presence of calls from December through late May in all years indicates that some portion of the population overwinters in the Chukchi Sea on offshore pack ice, but it leaves open the question of whether this area is used for breeding. Crawford et al. (2011) showed that ringed seals overwintering in offshore waters were more likely to be subadult animals. However, they do breed in other offshore areas, such as Baffin Bay and the Barents Sea (Finley et al., 1983; Wiig et al., 1999).

Male Arctic ringed seals rut from March to mid-May and sometimes into June (McLaren, 1958a). Stirling et al. (1983) found a substantial increase in ringed seal calls detected from March to April in the Canadian High Arctic with no observed influx of animals during that time, suggesting that calling rates increase as the breeding season progresses. Other Arctic and subarctic phocid species that have shown increases in vocal activity during their breeding seasons include hooded seals (*Cystophora cristata*) (Ballard and Kovacs, 1995), harbor seals (*Phoca vitulina*) (Van Parijs et al., 1999), and bearded seals (Van Parijs et al., 2001). Our results indicate a decrease in the three-year monthly averaged call occurrence from January to June (Fig. 7), with annual peaks in January, February, and May. However, daily calling hours and number of calls suitable for repertoire analysis increase somewhat in May 2008 and sharply in May 2009. This increase could indicate breeding, but the limitations of the study do not allow a conclusive interpretation.

We find a substantial change in the ringed seal repertoire from December to May. Barks make up a larger proportion of vocalizations than yelps from December to February, and yelps become the dominant call type from March through May (Table 4). Stirling (1973) observed a similar change in the repertoire of CHA ringed seals, observing that barks and yelps comprised 60% and 40% of winter calls, respectively, but showed the opposite ratio in spring. This finding was consistent with our analysis of spring 1982 data from the CHA. This seasonal variation may be related to defense of underwater territories by adult males during the period of breeding and pupping (Stirling, 1973).

Peaks in call occurrence in January and February may result from different factors. In Weddell seals, nighttime calling rates remained relatively stable from winter to spring (Rouget et al., 2007; Van Opzeeland et al., 2010). Rouget et al. point to reduced foraging in Weddell seals during periods of darkness (Kooyman, 1975) and speculate that wintertime calling in that species may instead be

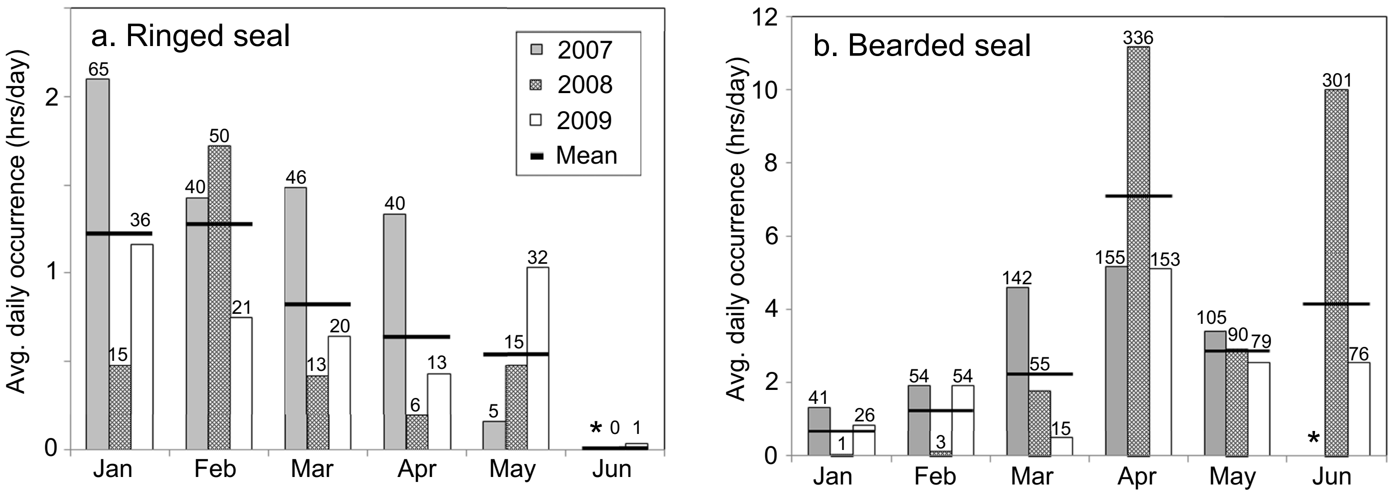

FIG. 7. Monthly average number of hours per day with acoustic occurrence of (a) ringed seals and (b) bearded seals. Ringed seal call detections generally decrease from January through June, except for spikes in February 2008 and May 2008 and 2009. Bearded seal calls show the opposite trend, peaking in April in all three years. Total monthly hours of acoustic presence are above each column bar. The asterisk (*) indicates that no data were recorded in June 2007.

motivated by the need to maintain access to breathing holes when visibility is reduced. Similarly, Stirling et al. (1983) hypothesize that an important function of ringed seal calls is to help maintain social structure around breathing holes.

The bearded seal trill is a breeding call produced exclusively by males (Cleator et al., 1989; Cleator and Stirling, 1990; Davies et al., 2006). Trills were most common from March through June and present as early as December and January. In a multi-year acoustic study in the Alaskan Beaufort, MacIntyre et al. (2013) found that bearded seals called throughout the winter. Our results show similar patterns of presence during winter, increasing through spring. Peak monthly average call occurrence was in April for all three years (Fig. 8). This timing corresponds well with the breeding season for the species in the Arctic, which occurs from March through June (McLaren, 1958b; Burns et al., 1981a). Aerial surveys in the eastern Chukchi Sea during the same period have shown that bearded seal densities can be higher 30 to 160 km offshore than in nearshore waters (Bengtson et al., 2005), indicating that offshore areas in this region provide important breeding habitat. Taken together, these results suggest that bearded seals may be breeding within acoustic detection range of the study area.

There was substantial intra-annual variation in bearded seal call detections. Within each year, detections were sporadic, although monthly averaged call occurrence generally increased from January through June. Even during the peak of the breeding season, when we would expect to record the highest numbers of bearded seal calls, there were periods of days to weeks during which no vocalizations were detected. It is possible that bearded seals were present throughout the study, but not vocalizing. However, acoustic studies nearer to shore have detected trills during most recording days from March to June in Svalbard (Van Parijs et al., 2001) and from December through June in the Alaskan Beaufort Sea (MacIntyre et al., 2013). Two additional factors may be important when evaluating the sporadic nature of bearded seal detections at our site: distance from the hydrophone and movement of sea ice.

During the entire study period, more than 60% of bearded seal calls detected were too faint to include in repertoire analysis, with few acoustically intense bouts of calling over the three years analyzed. We propose that the depth preference of bearded seals is a likely contributing factor. The maximum water depth commonly preferred by bearded seals is 100 m (Lowry et al., 1980; Kingsley et al., 1985), but the HARP was deployed on the continental slope at a depth of approximately 240 m about 40 km away from the nearest 100 m isobath. Detection ranges for bearded seals have been estimated as 25 to 45 km (Stirling et al., 1983; Cleator and Stirling, 1990). Differences in sensitivity of the recording systems and differences in acoustic propagation due to bathymetry make comparison with these estimates uncertain. However, the low received intensity levels suggest that vocalizing animals were at relatively far distances from the instrument and not at high densities near the study site. This interpretation corresponds well with bearded seal depth preferences and suggests that the recorder may have been on the edge of bearded seal habitat.

Winter and spring sea ice motion is variable but predominantly toward the west in the offshore Chukchi Sea, with periodic reversals of direction (Pritchard and Thomas, 1985; Zhao and Liu, 2007; Colony and Thorndike, 2012). This pattern would tend to transport bearded seals away from the recording site, but occasionally toward it. Van Parijs et al. (2003) and Van Parijs and Clark (2006) showed that bearded seals employing a roaming mating strategy maintained stable, albeit relatively large, territories in drifting pack ice. Individuals may also maintain consistent territories in offshore pack ice, but this has yet to be determined, and the degree to which sea ice motion may affect the proximity of bearded seals to the recorder is not known.

Some seasonal variation was observed in bearded seal calls. Comparing January and April, the two months with the

TABLE 4. Ringed seal: Monthly total calls included in repertoire analysis from September 2008 through June 2009 (N = 928).

	Monthly total calls										
	2008				2009						
Call type	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
Bark:											
n	0	5	0	16	172	73	13	2	99	0	380
% total	0	28	–	55	70	53	10	7	29	–	
Yelp:											
n	3	10	0	9	59	65	115	25	235	0	521
% total	100	56	–	31	24	47	89	89	70	–	
Growl:											
n	0	3	0	4	15	1	1	1	2	0	27
% total	0	17	–	14	6	1	1	4	1	–	
Total	3	18	0	29	246	139	129	28	336	0	928

greatest number of calls included in repertoire analysis, we show an increase in the relative proportions of AL3 moans and a decrease in AL7 ascents and AL1i trills (Table 5).

Ribbon seals, as shown by recent satellite telemetry results, spend a significant portion of the year (July through February) in open water and diving (Boveng et al., 2008). Largely because of this aspect of their life history, little is known of their movements during these months. Detections of their vocalizations in the northeastern Chukchi Sea during the open water season provide another glimpse of their distribution and behavior at a time of year when few observations have been made. The presence of vocalizations during September and October is unlikely to be associated with breeding behavior and raises questions about the function of these calls during other times of year. Since ribbon seals were present far from known breeding grounds and well outside of the breeding season, we surmise that they were either feeding in the vicinity of the recorder or moving to or from northern foraging areas. Studies of stomach contents suggest that ribbon seals feed primarily in the midwater, often at the edge of the continental slope (Deguchi et al., 2004), which fits with the depth profile of the recording site. Although little is known about feeding behavior of ribbon seals from July through March, a number of studies have shown that Arctic cod (*Boreogadus saida*) is at least an occasional prey species (e.g., Shustov, 1965; Frost and Lowry, 1980; Dehn et al., 2007). Taken together, the results of this study and a growing body of evidence from other studies suggest that the Chukchi Sea slope waters likely provide foraging habitat for ribbon seals at least during some open water seasons.

Relation of Ice Seal Acoustic Presence and Sea Ice

Ringed seals are arguably the most ice-obligate of all Arctic phocids. From January through March, their calls were significantly more likely to be detected when the ice cover was at or near 100%. In other months, this relationship was not significant. These results are consistent with speculation that ringed seal acoustic behavior is related at least partly to maintenance of social order around breathing holes (Stirling et al., 1983), which are most important to survival during periods of 100% ice cover.

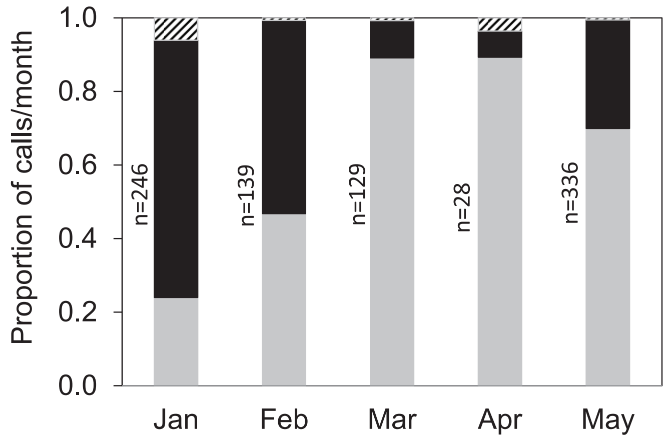

FIG. 8. Ringed seal proportion of monthly total calls for barks (black), yelps (grey), and growls (diagonal stripes) from January through May 2009. Barks decrease as a proportion of total calls and yelps increase, with growls remaining relatively rare in all months.

Bearded seal calls were found in a greater variety of ice conditions than those of the other species. However, their vocalizations were significantly more likely to be detected in 99% to 100% sea ice cover from January through March. This relationship does not exist from April through June. In contrast, heavy ice conditions with reduced open water have been shown to reduce vocalization rates of roaming males occupying pack ice near shore in Svalbard and Alaska (Van Parijs, 2004; Jensen, 2005). Our results correspond with the finding of MacIntyre et al. (2013) that bearded seals offshore in the Beaufort Sea were detected more often in the highest sea ice concentrations. This finding suggests that bearded seals may be overwintering in the offshore environment.

Ribbon seals were detected only during the open water period. The sudden disappearance of their calls in the fall of 2008 coincided with the formation of sea ice, which had increased to about 50% coverage around the recording site two days earlier. This result corresponds well with extralimital records (Moore and Barrowclough, 1984) and satellite telemetry results of movements in open water outside the breeding, pupping, and molting season. Boveng et al. (2008) reported that of 26 ribbon seals fitted with satellite

TABLE 5. Bearded seal: Monthly total calls included in repertoire analysis from September 2008 through June 2009 (N = 1228).

	Monthly total calls										
	2008				2009						
Call type	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Total
AL1 (T)											
n	0	0	0	0	1	0	0	1	0	0	2
% total	–	–	–	–	< 1	–	–	< 1	–	–	
AL1i (T)											
n	0	0	0	16	89	41	3	66	10	13	238
% total	–	–	–	20	23	30	12	14	17	21	
AL2 (T)											
n	0	0	0	1	17	18	1	35	9	3	84
% total	–	–	–	1	4	13	4	7	15	5	
AL3 (M)											
n	0	0	0	4	98	35	22	188	19	20	386
% total	–	–	–	5	26	25	85	39	32	32	
AL4 (T)											
n	0	0	0	4	3	5	0	3	0	0	15
% total	–	–	–	5	1	4	–	1	–	–	
AL5 (T)											
n	0	0	0	31	100	25	0	144	15	20	335
% total	–	–	–	39	26	18	–	30	25	32	
AL7 (T)											
n	0	0	0	23	71	14	0	48	6	6	168
% total	–	–	–	29	19	10	–	10	10	10	
Total	0	0	0	79	379	138	26	485	59	62	1228

transmitters in the central Bering Sea, eight moved into the Chukchi Sea during some portion of the late summer and fall. Ribbon seal vocalizations have also been detected in October and November on the Chukchi Plateau at 75˚ N during the open water period and in the early stage of annual ice formation (Moore et al., 2012).

Limitations of the Study

Using autonomously recorded acoustic data, we do not have the benefit of direct observation of vocalizing animals. Species identification must be made on the basis of previous descriptions, often from other geographic areas, using different analysis methods, and with large temporal separations. Although bearded seals are known to have highly stable and distinctive acoustic repertoires within the geographic areas where their vocalizations have been studied, the temporal stability of ringed and ribbon seal calls and their degree of geographic variation has not been studied previously. To reduce the chances of misinterpreting previous studies, wherever possible, we obtained original recordings and reanalyzed them to ensure uniform methods and facilitate direct comparison of calls. In the case of bearded seals, ample results from recent studies were available and re-analysis was not necessary.

There is still uncertainty about the absence of animals (as opposed to the absence of their calls) because animals may be present but not vocalizing. Seasonal variation in vocalization rates has been observed in ringed seals and bearded seals (Stirling et al., 1983; MacIntyre et al., 2013). Sea ice conditions, predation pressure, and other factors in the offshore environment may affect vocalization rates or types of calls used, so direct comparison of detection rates to those in nearshore areas is difficult.

The source level measurements of vocalizations will help to determine their detection range along with transmission loss estimates due to propagation. Attenuation due to scattering will occur in ice-covered waters and will be frequency-dependent (Roth et al., 2012). Propagation will also vary depending on local bathymetry. All of these factors may change the detection distance and our ability to discern call characteristics. Masking due to ambient noise will also have an effect on detection probability. Ice, wind, and anthropogenic sources may create additional noise that overlaps with the frequencies of ice seal calls. We found that environmental noise was a ubiquitous feature of these recordings. Although we were still able to detect the presence of calls during many types of noise events, this is clearly an important area for additional analyses and warrants future study.

CONCLUSIONS

We have quantitatively described the seasonal use of an offshore area in the Chukchi Sea by bearded seals, ringed seals, and ribbon seals and provided insights into their underwater vocal behavior at times of year and at a location not previously studied. Our results show little variation in the vocalizations of ringed, bearded, and ribbon seals over large spatial and temporal separations. Bearded seal vocalizations closely mirrored those recorded 24 years earlier in an adjacent geographic area near shore. Ringed and bearded seal repertoires were stable over periods spanning 26 and 41 years, respectively, at sites separated by 1900 and 1200 km. Stability in acoustic behavior has been shown on similar time scales in harp seals (Serrano and Terhune, 2002) and bearded seals (Van Parijs and Clark, 2006), suggesting that it may be common among ice-breeding phocids. Ringed and ribbon seals lack geographic variation where compared in this study. The acoustic behavior of ribbon seals is more complex than previously described.

Seasonal presence of ice seal vocalizations shows that Chukchi Sea slope waters more than 100 km offshore provide habitat for ringed and bearded seals from December through June and, at least occasionally, for ribbon seals during fall open water. These results, along with a seasonal change in the repertoire of ringed seals during the breeding season, provide evidence that the offshore northeastern Chukchi Sea is a breeding ground for ringed and bearded seals and at least an occasional destination for foraging ribbon seals. We also show significant relationships from December through March between the ringed and bearded seal acoustic presence and the highest sea ice concentrations. These relationships weaken for both species from April to June. Finally, all three species vocalize at times of year well outside of their breeding seasons. This result is consistent with studies of other phocid seals and raises additional questions about the function of their vocalizations.

The offshore Chukchi shelf and slope represent a combination of seasonal ice conditions, bathymetry, and great distance from shore found in expansive areas of the Chukchi, Kara, Barents, Laptev, and East Siberian Seas. Together, these areas comprise a substantial portion of the distribution of Arctic phocid species that rely on the Marginal Ice Zone and drifting pack ice for key aspects of their life histories. With changes in the seasonal extent of sea ice, it is predicted that northern offshore areas will have ice conditions suitable for mating, molting, and parturition of ice-breeding species for a greater portion of the year than areas nearer to shore, where the most research has occurred to date. Further study of the acoustic behavior, seasonal distributions, and relationships with sea ice may provide insight into how these species are responding to changes in the Arctic and on the importance of offshore areas for their survival.

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