


Seasonal variation in Arctic marine mammal acoustic detection in the northern Bering Sea

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Abstract

Declines in Arctic sea ice cover are influencing the distribution of protected endemic marine mammals, many of which are important for local Indigenous Peoples, and increasing the presence of potentially disruptive industrial activities. Due to increasing conservation concerns, we conducted the first year-round acoustic monitoring of waters off Gambell and Savoonga (St. Lawrence Island, Alaska), and in the Bering Strait to quantify vocalizing presence of bowhead whales, belugas, walruses, bearded seals, and ribbon seals. Bottom-mounted archival acoustic recorders collected data for up to 10 months per deployment between 2012 and 2016. Spectrograms were analyzed for species-typical vocalizations, and daily detection rates and presence/absence were calculated. Generalized additive models were used to model call presence as a function of time-of-year, sea surface temperature, and sea ice concentration. We identified seasonality in call presence for all species, corroborating previous acoustic and distribution studies, and identified finer-scale spatiotemporal distribution via occurrence of call presence between different monitoring sites. Time-of-year was the strongest significant effect on call presence for all species. These data provide

important information on Arctic endemic species' spatiotemporal distributions in biologically and culturally important areas within a rapidly changing Arctic region.

KEYWORDS

acoustics, Arctic, Bering Sea, generalized additive models, marine mammals

1 | INTRODUCTION

The Arctic has experienced substantial changes in climate, expressed both atmospherically and oceanographically, with greater and more rapid warming observed in the Arctic than other regions across the globe (ACIA, 2005; Serreze & Francis, 2006; Wood et al., 2015; Zhang, 2005). Increasing temperatures, as well as changes in atmospheric and ocean circulation are expected to drive declines in perennial and summer sea ice such that the Arctic sea ice system becomes seasonal rather than perennial (Douglas, 2010; Haine & Martin, 2017; Stewart, Kunkel, Stevens, Sun, & Walsh, 2013; Wang, Overland, & Stabenro, 2012).

Declines in sea ice cover have resulted in earlier and longer seasons of open water, facilitating access and navigation of Arctic waters for both human activities and nonendemic temperate species (Stafford, 2019; Stephenson, Smith, Brigham, & Agnew, 2013). In conjunction with increased global economic interest in resource-rich offshore Arctic areas, and improved maritime technologies with which to exploit them, there has been growth in both industrial and transportation activities in the maritime Arctic (Arctic Council, 2009). This includes expansion of offshore oil and gas activities, as well as vessel traffic among Arctic ports and between the Atlantic and Pacific Oceans. As ice cover continues to diminish, shipping and further expansion of industrial activities is likely to occur, including mining, commercial fishing, and oil and gas development and extraction. These anthropogenic activities can have potential acute and chronic impacts on the environment and species that inhabit Arctic and sub-Arctic regions (Blackwell et al., 2013; Clarke et al., 2013; Reeves et al., 2014; Rolland et al., 2012).

Increases in human maritime activities in this region are of concern from a conservation and local subsistence perspective, in part due to the impacts on the acoustic environment (Gadamas et al., 2015; Hildebrand, 2009). Marine mammals in particular, are highly dependent on sound for basic functions such as foraging, reproduction, and sensing their environment, making them sensitive to changes in the marine soundscape (Southall, 2017). In the Arctic, sea ice can at times greatly reduce ambient noise by isolating the underwater acoustic environment from outside noise such as wind (Innsley, Halliday, & de Jong, 2017). Consequently, the current and projected declines in sea ice will likely result in an overall increase in ambient noise in the Arctic. Additionally, increases in anthropogenic activities, notably chronic low-frequency sources such as ship propulsion and acute sources such as seismic airguns, will increase cumulative noise levels over broad geographic areas. These anthropogenic sounds can disrupt important behaviors by masking communication, causing stress or injury, and can impact both animal health and hinder the ability of local hunters to conduct safe and successful hunts (Blackwell et al., 2013; Hauser, Laidre, & Stern, 2018; Huntington, 2013; Moore et al., 2012; Rolland et al., 2012; Southall, 2017). Communication masking is of particular concern given that human-generated noise generally occurs within similar spectral ranges as the primary communication signals and other biologically important sounds for baleen whales, walrus, and ice seals (Hildebrand, 2009; National Research Council, 2003; Richardson, Greene, Malme, & Thomson, 1995).

Due to these increasing concerns and impacts, it is necessary to understand species distribution in an area that may be affected to further estimate the impacts of increasing anthropogenic activity. This is especially important in the Arctic. Given the relatively quiet natural baseline soundscape in the Arctic, marine mammal species endemic to the Arctic and sub-Arctic regions may be more vulnerable to noise pollution impacts (Innsley et al., 2017; Moore et al., 2012; Reeves

et al., 2014). These include bowhead whales (*Balaena mysticetus*), beluga whales (*Delphinapterus leucas*), Pacific walrus (*Odobenus rosmarus divergens*), bearded seals (*Erignathus barbatus*), and ribbon seals (*Histiophoca fasciata*). Each of these species can be identified by species-specific vocalizations (Table 1). Bowhead whale song, walrus knocks, and bearded seal trills are produced mainly by males in a reproductive context, whereas beluga vocalizations analyzed here are generally produced in a nonreproductive social context (Sjare, Stirling, & Spencer, 2003; Stirling, Calvert, & Spencer, 1987; Ray, Watkins, & Burns, 1969; Stafford, Castellote, Guerra, & Berchok, 2018; Van Parijs, Kovacs, & Lydersen, 2001; Würsig & Clark, 1993). It is uncertain whether ribbon seal vocalizations are made solely by males or in a reproductive context, as vocalizations have been recorded during the nonbreeding season (Frouin-Muoy, Mouy, Berchok, Blackwell, & Stafford, 2019; Mizuguchi, Mitani, & Kohshima, 2016).

Arctic endemic marine mammal species are protected through various statutes, including the U.S. Marine Mammal Protection Act (MMPA) and Endangered Species Act (ESA), and the International Whaling Commission (IWC). These species are also important for local food security and cultural well-being in the Arctic and sub-Arctic regions (e.g., Ashjian et al., 2010; Gadamus et al., 2015; Huntington, Quakenbush, & Nelson, 2017; Noongwook, The Native Village of Savoonga, The Native Village of Gambell, Huntington, & George, 2007). In the Pacific Arctic, marine mammals rely on habitat provided by the Bering Strait and surrounding waters. The Bering Strait, as the only gateway between the Pacific and the Arctic, is an obligatory shipping route between the Pacific and Arctic Oceans, and is a key area of interest for industrial activities (Hartsig, Frederickson, Yeung, & Senner, 2012). The expansion of shipping activity in the Bering Strait could substantially increase noise levels and the risk of whale-vessel collisions. These concerns are further complicated by the fact that efficient implementation of mitigation measures, such as traffic separation schemes to spatially and temporally restrict ships from the whales' migratory routes, are compromised by both the relatively narrow width (80 km) and shared jurisdiction of the Bering Strait by the United States and the Russian Federation.

Given the significance of the Arctic seascape, and increasing human impact, noninvasive passive acoustic monitoring (PAM) is an ideal method to better understand species occurrence and distribution. PAM uses feature recognition of species-specific signals and is a useful and cost-effective tool to obtain long-term information about the seasonal occurrence and distribution of vocal species. This is especially valuable for relatively remote areas such as Arctic and sub-Arctic waters, where ice cover, meteorological, and logistical conditions make it difficult and

TABLE 1 Summary of species-typical call types for the five focal species.

Species	Call type	References
Bowhead whale (<i>Balaena mysticetus</i>)	Low frequency (<500 Hz), frequency-modulated calls lasting from 0.5 to 5 sec. Commonly produced in song sequences (see Figure 2a).	Clark & Johnson, 1984; Cummings & Holliday, 1987; Ljunbglad et al., 1982; Stafford et al., 2012
Beluga (<i>Delphinapterus leucas</i>)	Highly variable whistles, or narrow-band, frequency modulated vocalizations and pulsed sounds (400 Hz–20 kHz) (see Figure 2b).	Karlsen et al., 2002; Sjare & Smith, 1986; Stafford et al., 2018
Pacific walrus (<i>Odobenus rosmarus divergens</i>)	Loud, repetitive and highly stereotypic series of pulses ("knocks" or "taps"), occasionally punctuated with ringing bell sounds (<1 kHz) (see Figure 2c).	Ray & Watkins, 1975; Schevill et al., 1966; Stirling et al., 1983, 1987
Bearded seal (<i>Erignathus barbatus</i>)	Frequency-modulated underwater calls generally ranging from 130 Hz to 4.8 kHz. Predominately long and elaborate frequency modulated trills produced by males (see Figure 2d).	Ray et al., 1969; Risch et al., 2004, 2007; Stirling et al., 1983; Van Parijs et al., 2004
Ribbon seal (<i>Histiophoca fasciata</i>)	Underwater calls include roars, grunts, and frequency modulated down-sweeps (<3.5 kHz) (see Figure 2e).	Jones et al., 2014; Miksis, Olds, & Parks, 2011; Mizuguchi et al., 2016; Watkins & Ray, 1977

expensive to conduct shipboard and aerial surveys (Mellinger, Stafford, Moore, Dziak, & Matsumoto, 2007; Moore, Stafford, Mellinger, & Hildebrand, 2006; Moore et al., 2012; Stafford et al., 2018).

The ability to detect species' vocalizations relies on the species being vocally active in the area of interest. Detection is also influenced by the distance between vocalizing animals and acoustic recorders, the frequency and amplitude of the vocalizations, vocal behavior, and ambient noise levels. Given these considerations, species presence and patterns of habitat use can be evaluated by long-term monitoring via autonomous acoustic recorders (Mellinger et al., 2007; Moore et al., 2012).

In this study, PAM was conducted within the Bering Strait region spanning four years (2 September 2012–1 July 2016) to examine the seasonal presence of vocalizing bowhead whales, belugas, Pacific walrus, bearded seals, and ribbon seals. Year-round monitoring, in conjunction with statistical modeling techniques, provides key information on the occurrence and spatiotemporal distribution of these species within a region important for biological, cultural, conservation, and management reasons.

2 | METHODS

Passive acoustic monitoring was conducted at three locations in the Bering Strait region over a 4-year period (Figure 1). Information on recorder deployments, including sample rate, deployment period, duty cycle, and deployment location, is summarized in Table 2. These recorders were attached to a subsurface mooring consisting of a

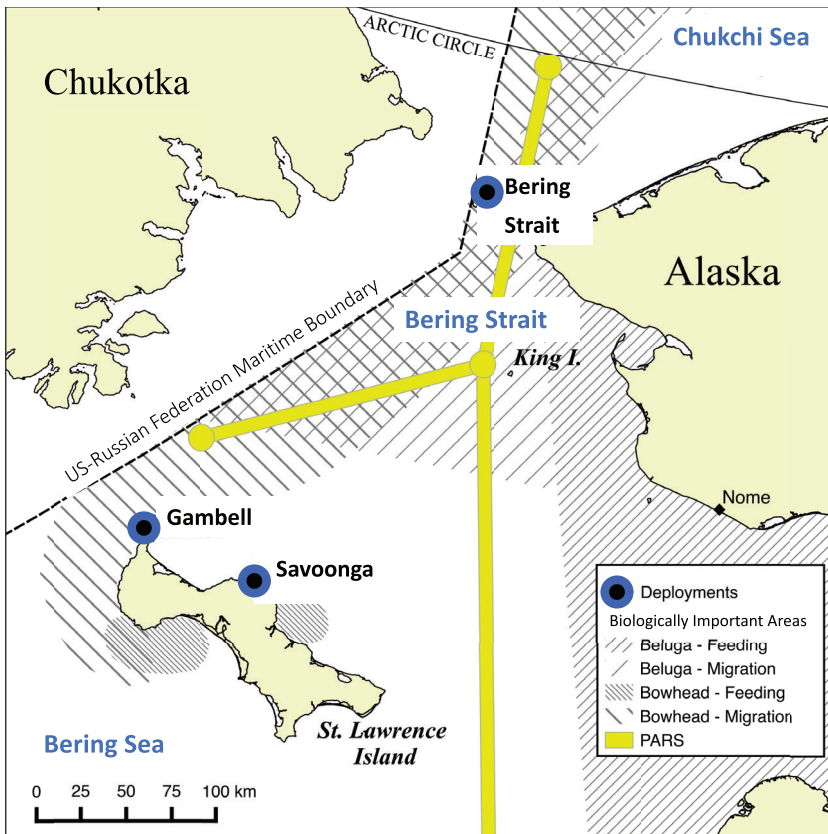


FIGURE 1 Location of acoustic monitoring stations. Also shown are feeding and migration Biologically Important Areas for bowhead whale and beluga from Ferguson et al. (2015) and the U.S. Coast Guard Port Access Route Study (PARS) proposed vessel routing system.

TABLE 2 Summary of sound recorder deployments used in the analysis.

Location	Deployment ID	Sample rate	Recording period	Total days	Duty cycle on/off (minutes)	Total recordings	Total minutes	Recorder/depth	Deployment position
Bering Strait	A2W-12 ^a	16.384 kHz	2 September 2012–14 May 2013	254	10/50	6,168	61,680	AURAL-M2 5.5 m	65.8005°N 168.8010°W
Gambell	2014.1	20 kHz	1 October 2014–21 June 2015	262	5/55	5,657	28,372	DSG ^b 20–30 m	63.8178°N 171.6915°W
	2015.2	20 kHz	21 June 2015–14 October 2015	114	5/55	3,287	22,969	DSG ^b 20–30 m	63.8227°N 171.6756°W
	2015.11	48 kHz	15 October 2015–1 July 2016	260	10/50	6,240	62,167	DSG-ST ^b 20–30 m	63.8222°N 171.6654°W
Savoonga	2014.2	20 kHz	1 October 2014–21 June 2015	262	5/55	5,642	28,301	DSG ^b 20–30 m	63.6636°N 170.2257°W

^aWoodgate et al. (2015).

^bLoggerhead Instruments, Sarasota, FL, with HTI-96-MIN hydrophone (High Tech Inc., Gulfport, MS).

bottom metal weight (30–40 kg) connected to either one 35 cm or two 20 cm diameter plastic floats by a 2-m-long nylon rope. Deployment locations were selected to best evaluate differences in habitat usage for different comparative areas around St. Lawrence Island and the Bering Strait. Deployment locations were also selected based on local features that favored successful deployment and recovery of moorings.

2.1 | Acoustic analysis

All sound recordings were manually inspected by visualizing spectrograms (FFT size 2,048 samples, Hann window, 90% overlap) using Raven (Bioacoustics Research Program, 2014) or Ishmael (Mellinger, 2001) to detect vocalizations of the five focal species: bowhead whale, beluga, Pacific walrus, bearded seal, and ribbon seal. Recordings were duty cycled (either 5/55 min or 10/50 min on/off, see Table 2) and spectrograms were analyzed by experienced analysts to identify vocalizations from target species, which included species-typical vocalizations such as bowhead whale song (Figure 2a), beluga whistles and pulsed/noisy calls (Figure 2b; Chmelnitsky & Ferguson, 2012), series of knocks and bell calls typically produced by male Pacific walruses (Figure 2c; Stirling et al., 1987), trill sounds produced by male bearded seals (Figure 2d; Risch et al., 2007), and ribbon seal frequency down-sweeps (Figure 2e; Miksis-Olds & Parks, 2011).

While sea ice cover strongly reduces ambient noise, especially at low frequencies, we currently do not fully understand how it influences the detection range of these species-typical vocalizations. For bowhead whale calls, for which the detection range is likely the farthest among the five focal species given their source level and relatively low frequency (Blackwell et al., 2013), the detection range is estimated to be several 10s of km given signal characteristics and the sensitivity of the hydrophones used in this study. The source level for the other species' calls are likely lower than the bowhead whale calls and not known for all the different call types, though they are generally low frequency, which would suggest that the calls should be detectable up to 10 km. There is likely variance in detection ranges within the context of these recordings, given ice cover, which will influence noise propagation as well as detection, given the highly variable nature of sea ice noise (Milne & Ganton, 1964). We were unable to directly measure how these variables interact and could not quantitatively account for its influence on detection range and probability.

While searching for marine mammal vocalizations, analysts kept the frequency and time resolution of the spectrograms constant during call detection; these were adjusted during more detailed inspections required for species

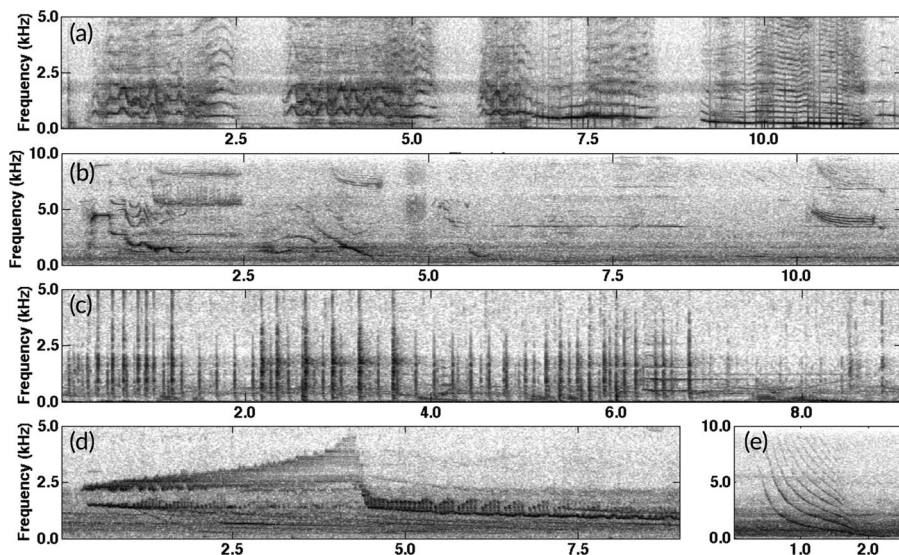


FIGURE 2 Example spectrograms (1,024 FFT points, 90% overlap, Hann window) of detected marine mammal vocalizations. a: bowhead whale; b: beluga; c: walrus; d: bearded seal; e: ribbon seal.

assignment and call count determination. Every individual vocalization was recorded even if the species was previously identified within that hour. When a possible vocalization was detected, the vocalization was ranked on certainty (from low "1" to high "3") that the correct species was identified. Low certainty vocalizations were cross-checked by another analyst to verify species identifications. When a species identification was confirmed by a second analyst, that vocalization was ranked as a 3 (or high certainty of correct species identification) on the certainty scale. If the analysts could not confidently identify the species, the detected vocalization was subsequently removed from further analysis. From the detected vocalizations, daily presence/absence was used for further analysis. Daily detection rates were also calculated as the proportion of recordings within a day that contained any detection of the target species.

2.2 | Statistical analyses

Temporal variation in marine mammal call presence from the five focal species was modeled using generalized additive models (GAM; Hastie & Tibshirani, 1990; Wood, 2011). A binomial response corresponding to the detection of vocalizations within days and weighted by the number of recording periods was modeled as a function of time of year (the number of days between the recording date and the first day of the year) and of an (tensor product) interaction between sea surface temperature (*sst*) and sea ice concentration (*ice*). Monitoring location (Bering Strait, Gambell, or Savoonga) was used as a random effect. The model selection criterion was based on minimizing the generalized cross-validation (GCV), which measures the predictive squared error of the model; low values show the best compromise between model complexity and fit to the observed data (Wood, 2001). Model fitting was carried out separately for each species using R (R Core Team, 2017) and the *mgcv* package (Wood, 2001).

Satellite-derived sea surface temperatures collected by the Group for the High-Resolution Sea Surface Temperature (GHR SST), were obtained as daily (L4) rasters with 0.25° (~12 km) spatial resolution from NOAA's National Centers for Environmental Information Long Term Stewardship and Reanalysis Facility. Cell values corresponding to the monitoring locations were extracted using custom Matlab scripts. Sea ice concentration was estimated from measurements by the Advanced Microwave Scanning Radiometer 2 (AMSR2) instrument aboard the Global Change Observation Mission 1st-Water "SHIZUKU" satellite (Spren, Kaleschke, & Haygster, 2008). Daily rasters of sea ice concentration with 3.125 km spatial resolution were downloaded from the Institute of Environmental Physics, University of Bremen, Germany, and cell values within 20 km from each monitoring location were extracted and averaged using custom Matlab (Mathworks, Natick, MA) scripts.

3 | RESULTS

Monitoring at the Bering Strait (RUSALCA deployment; Woodgate, Stafford, & Prah, 2015) resulted in a total of 6,168 recordings, totaling 1,028 hr of sound recording and covering 254 days from September 2012 to May 2013 (Table 2). A total of 15,184 recordings were obtained from the monitoring station at Gambell, totaling 1,892 hr of sound recordings covering 636 days from October 2014 to June 2016. At Savoonga 5,642 recordings were obtained, totaling 472 hr of sound recordings, covering 262 days from October 2014 to June 2015. The total data set represents 3,392 hr from 894 days within these discrete recording periods from 2012 to 2016 (Table 2).

Sea ice coverage data extracted from AMSR2 daily rasters showed seasonal presence of sea ice (defined here as occurring between first and last day with average sea concentration >15%; Rogers, Walsh, Rupp, Brigham, & Sfraga, 2013) during the winter at all monitoring stations (Bering Strait: 3 December 2012–1 June 2013; Gambell: 16 December 2014–22 April 2015, and 9 December 2015–9 May 2016; Savoonga: 20 December 2014–12 May 2015). Ice concentration at Gambell showed variation between the winters during which acoustic monitoring was conducted at this location. Using this 15% average sea ice criterion, the 2014/2015 winter (130 days) was shorter

TABLE 3 The total number of individual vocalizations detected per recording and species.

Location	Deployment ID	Bowhead whale	Beluga	Walrus	Bearded seal	Ribbon seal	Total
Bering Strait	A2W-12	2,046	510	1,749	4,375	0	8,680
Gambell	2014.1	2,186	1,053	1,402	1,817	113	6,571
	2015.2	0	1	0	4,375	0	4,376
	2015.11	2,471	788	2,675	2,193	1	8,128
Savoonga	2014.2	1,410	254	1,420	2,259	121	5,464
	Total	8,113	2,606	7,246	15,019	235	33,219

than in 2015/2016 (150 days). The proportion of winter days with average sea ice concentration >15% at Gambell was also less in 2014/2015 (59%) than in 2015/2016 (97%).

A total of 33,219 individual vocalizations from focal marine mammal species were detected (Table 3): bowhead whale (8,113), beluga (2,606), Pacific walrus (7,246), bearded seal (15,019), and ribbon seal (235). Temporal variation in detection rates for each target species is presented below.

3.1 | Bering Strait monitoring site

Bowhead whale call presence at Bering Strait occurred in two main periods 44 days apart. The first period (5 November 2012–27 January 2013) started 27 days before the onset of seasonal sea ice coverage, and no bowhead whale vocalizations were detected during February or the first half of March in 2013 at Bering Strait (Figure 3). The second period

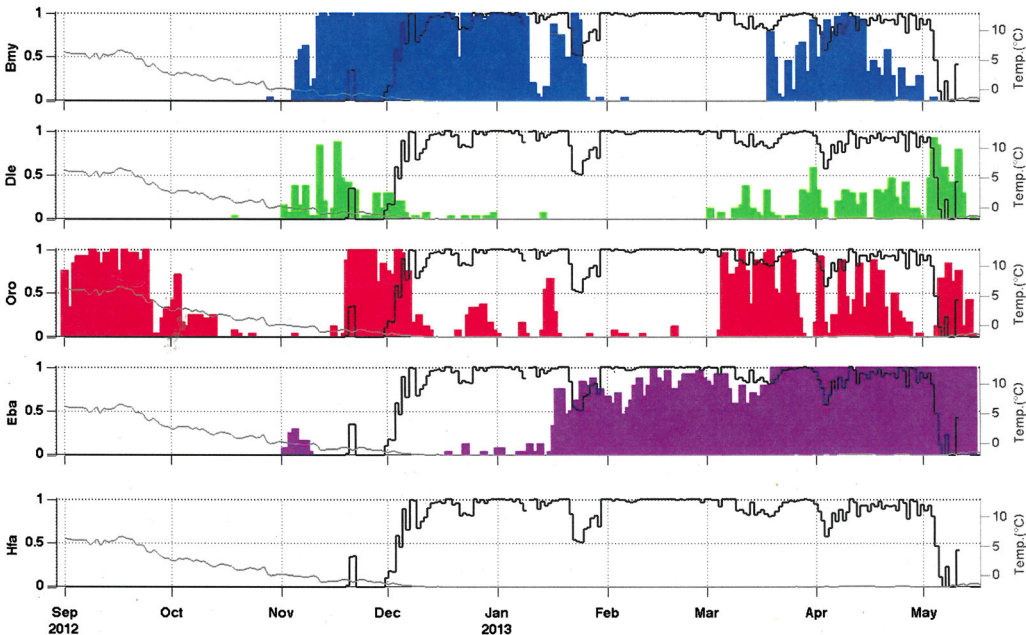


FIGURE 3 Temporal variation in daily detection rates of bowhead whale (Bmy), beluga (Dle), walrus (Oro), bearded seal (Eba) and ribbon seal (Hfa) at A2W Bering Strait monitoring station. Color bars indicate the proportion of recordings within a day that contain detections for each species. Black lines indicate sea ice concentration within a 20 km circle centered at the recorder's location, estimated from measurements by the Advanced Microwave Scanning Radiometer 2 (AMSR2) instrument aboard the Global Change Observation Mission 1st-Water "SHIZUKU" (GCOM-W1) satellite (Spreen et al., 2008). Gray line shows sea surface temperature as derived by the Group for the High-Resolution Sea Surface Temperature (GHRSSST).

of bowhead call presence at Bering Strait (19 March 2013–4 May 2013) began during the presence of seasonal ice coverage and ended with recession of seasonal sea ice (Figure 3).

Two periods of beluga call presence were also observed at Bering Strait: the first period of call presence was detected between 2 November 2012 and 31 December 2012 before the onset of seasonal ice coverage. This period consisted of 59 days with a mean daily detection rate of 0.11 (*SD*: 0.18; Figure 3). A second period of call presence occurred, during which beluga vocalizations were detected with a mean daily detection rate of 0.18 (*SD*: 0.21), from 2 March 2013 during seasonal ice coverage until 12 May 2013 after seasonal sea ice recession (Figure 3).

Relatively high walrus call presence at Bering Strait occurred during multiple periods of consecutive days with daily detection rates >0.5 (periods of call presence ranged from 26 to 61 days) interspersed with periods of 6–25 days with only a single or no detection (Figure 3). Periods of high daily detection rates occurred throughout the entire recording period at Bering Strait.

Bearded seal call presence at Bering Strait occurred from early November until 14 May 2013. There were no vocalizations detected in September or October (Figure 3). A first period of bearded seal call presence with low daily detection rates (<0.25) started in early November and lasted 7 days, during which no sea ice was detected. Following a period of 40 days with no call presence at this station, a peak of bearded seal call presence occurred from mid-December 2012 through May 2013 (Figure 3). The onset of this period occurred 28 days after sea ice coverage was detected at this station. Bearded seal daily detection rates at Bering Strait gradually increased from December to mid-March, after which time daily detection rates were higher than 0.9 (Figure 3).

Ribbon seal vocalizations were less abundant than calls from the other focal species. No ribbon seal calls were detected at Bering Strait (Figure 3).

3.2 | Gambell monitoring site

At Gambell, bowhead whale call presence was seasonal, with the first calls detected in October of 2014 and 2015 (Figure 4). Onset of call presence at these locations (11 October 2014 and 15 October 2015) occurred in advance of seasonal sea ice coverage. Daily detection rates remained relatively low (<0.5) until the first week of December of both years, at which time bowhead calls were detected in almost all recordings. These high daily detection rates were sustained until the first half of April (5 April 2015 and 14 April 2016) at Gambell (Figure 4). Bowhead whale call presence was not detected 20 days after the recession of seasonal sea ice in 2015, and 15 days prior to the recession of sea ice in 2016 (Figure 4).

Beluga call presence was detected at Gambell between 18 December 2014 and 1 May 2015 with a mean daily detection rate of 0.42 (*SD*: 0.33; Figure 4). Beluga call presence the following year was detected for a period of 112 days, between 9 December 2015 and 20 March 2016, with mean daily detection rates of 0.27 (*SD*: 0.31; Figure 4).

Pacific walrus call presence was seasonal at Gambell, and occurred mainly between early December (16 December 2014 and 9 December 2015) and the end of April (25 April 2015 and 8 May 2016; Figure 4). The onset of calling was abrupt at Gambell: daily detection rates transitioned from zero to >0.5 within three days of the first detection in both 2015 and 2016. Call presence declined throughout April at Gambell, from detections in nearly every recording at the end of March to no detections beyond mid-May in both 2015 and 2016 (Figure 4).

Bearded seal call presence appeared to be seasonal at Gambell, where the onset of bearded seal call presence occurred from 17 January 2015 to 10 June 2015, and from 20 January 2016 to 6 June 2016 (Figure 4). The first detected calls occurred 33 days and 42 days after the first day with sea ice concentration $>15\%$ in 2015 and 2016, respectively. Daily detection rates were variable and increased gradually during January and February and remained >0.9 until early June (Figure 4). Cessation of call presence in both 2015 and 2016 was sudden, transitioning from calls detected in all recordings, to no detected vocalizations in 14 and 9 days, respectively. This sudden halt occurred 34 and 18 days after seasonal sea ice recession in 2015 and 2016, respectively.

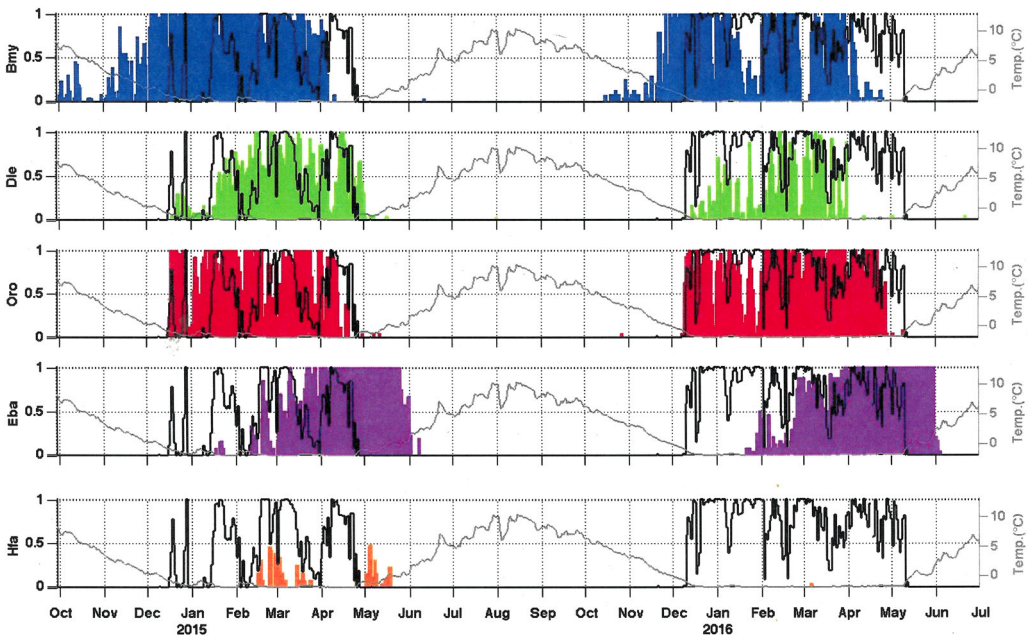


FIGURE 4 Temporal variation in daily detection rates of bowhead whale (Bmy), beluga (Dle), walrus (Oro), bearded seal (Eba) and ribbon seal (Hfa) at Gambell monitoring station. Color bars indicate the proportion of recordings within a day that contain detections for each species. Black lines indicate sea ice concentration within a 20 km circle centered at the recorder's location, estimated from measurements by the Advanced Microwave Scanning Radiometer 2 (AMSR2) instrument aboard the Global Change Observation Mission 1st-Water "SHIZUKU" (GCOM-W1) satellite (Spreen et al., 2008). Gray line shows sea surface temperature as derived by the Group for the High-Resolution Sea Surface Temperature (GHRSSST).

Ribbon seal daily detection rates at Gambell differed between the 2014/2015 and 2015/2016 late winter periods, as there were sporadic periods of call presence between 15 February 2015 and 24 March 2015, and 24 April 2015 to 18 May 2015 (Figure 4). The latter period coincided with the last days of sea ice coverage. However, during the 2015/2016 season, only a single vocalization was detected during the equivalent period of seasonal sea ice coverage (Table 3, Figure 4).

3.3 | Savoonga monitoring site

The first bowhead whale vocalizations at Savoonga were detected 11 October 2014, also before seasonal sea ice coverage (Figure 5). Daily detection rates >0.5 were generally sustained from December until the second week of March 2015 at Savoonga, 61 days prior to the recession of seasonal sea ice (Figure 5).

At Savoonga, beluga whale call presence lasted a period of 88 days with mean daily detection rates of 0.11 (SD : 0.21) was observed between 21 December 2014 and 19 March 2015 (Figure 5). Compared to other monitoring locations, beluga vocalizations were detected less frequently at Savoonga (Figure 5).

Walrus call presence was also seasonal at Savoonga, with an abrupt onset of calling (daily detection rates from zero to >0.5 within 5 days of the first detection) that occurred 16 December 2014. Relatively high daily detection rates of >0.5 lasted until 8 May 2015 (Figure 5). First detected calls were identified one day prior to the onset of the seasonal sea ice coverage, and call presence also declined throughout April 2015 at Savoonga until early summer when there were no vocalizations detected (Figure 5).

At Savoonga, the first bearded seal vocalizations were detected 7 days after first sea ice coverage, on 27 December 2014. Daily detection rates were also variable at first but increased throughout January and February

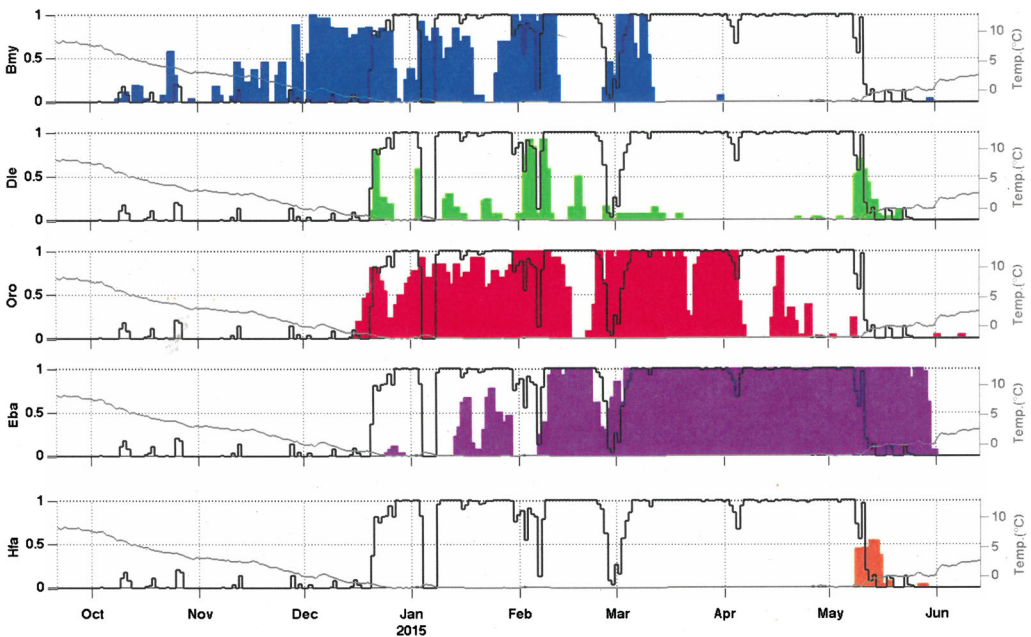


FIGURE 5 Temporal variation in daily detection rates of bowhead whale (Bmy), beluga (Dle), walrus (Oro), bearded seal (Eba) and ribbon seal (Hfa) at Savoonga monitoring station. Color bars indicate the proportion of recordings within a day that contain detections for each species. Black lines indicate sea ice concentration within a 20 km circle centered at the recorder's location, estimated from measurements by the Advanced Microwave Scanning Radiometer 2 (AMSR2) instrument aboard the Global Change Observation Mission 1st-Water "SHIZUKU" (GCOM-W1) satellite (Spreen et al., 2008). Gray line shows sea surface temperature as derived by the Group for the High-Resolution Sea Surface Temperature (GHRSSST).

until >0.9 from March to June 2015 (Figure 5). Another abrupt cessation of call presence occurred 1 June 2015, when vocalizations went from being detected in all recordings to none in a period of 4 days. This occurred 16 days after seasonal sea ice recession.

Only one period of ribbon seal call presence was detected at Savoonga, between 9 May 2015 and 18 May 2015, which also coincided with the last days of seasonal sea ice coverage (Figure 5).

3.4 | Statistical modeling

Time-of-year had the strongest significant effect on the probability of call presence within a day of monitoring for all focal species compared to sea surface temperature and sea ice concentration (Table 4, Figures 6–8). The time-of-year effect appeared to account for much of the seasonality in call presence of all five focal species. The model identified bowhead whale call presence at Gambell between October and the end of April, between December and March at Savoonga, and two peaks of call presence at the Bering Strait monitoring station (Figure 6). Seasonal call presence of belugas was identified between December and April at Gambell and Savoonga, and between October and January, and between March and May at Bering Strait (Table 4, Figure 6). Sea ice concentration and sea surface temperature also had significant effects on predicted beluga call presence, though at lower magnitudes than time-of-year (Table 4, Figure 7 and Figure 8).

Models indicated seasonal occurrence of walrus call presence off Gambell and Savoonga between December and the end of April (Table 4, Figure 6). In the Bering Strait, the model predicted more variability in call presence between November and May (Figure 6). Sea ice concentration and sea surface temperature effects were lower than that of

TABLE 4 Summary of GAM model fitting for each detected species.

Bmy: Bowhead whale				
Parametric coefficients	Estimate	SE	t	p
(Intercept)	-2.924	0.305	-9.604	<.0001
location2	-6.094	1.744	-3.495	.0005
location3	-13.057	8.553	-1.527	.1269
Smooth terms	edf	Ref. df	F	p
s(ice):location1	6.312	9	392.171	<.0001
s(ice):location2	3.892	9	60.335	<.0001
s(ice):location3	6.263	9	108.014	<.0001
s(sst):location1	7.878	9	214.310	<.0001
s(sst):location2	8.751	9	146.089	<.0001
s(sst):location3	2.954	8	46.500	<.0001
s(yrday):location1	13.256	18	1,183.255	<.0001
s(yrday):location2	12.415	16	283.692	<.0001
s(yrday):location3	9.421	14	888.077	<.0001
IQ (adj) = 0.831, deviance explained = 8 L.6%, fREML = 1,607				
Dle: Beluga				
Parametric coefficients	Estimate	SE	t	p
(Intercept)	-6.695	1.230	-5.443	<.0001
location2	-25.117	6 L.175	-0.411	.681
location3	0.101	1.769	0.057	.955
Smooth terms	edf	Ref. df	F	p
s(ice):location1	5.156	9	105.072	<.0001
s(ice):location2	1.260	9	15.756	<.0001
s(ice):location3	4.058	9	61.312	<.0001
s(sst):location1	1.167	9	5.346	.015
s(sst):location2	4.759	9	106.504	<.0001
s(sst):location3	1.674	9	27.367	<.0001
s(yrday):location1	11.536	18	748.872	<.0001
s(yrday):location2	9.008	14	141.251	<.0001
s(yrday):location3	9.364	16	190.554	<.0001
R ² (adj) = 0.546, deviance explained = 66.0%, fREML = 3,532.4				
Oro: Walrus				
Parametric coefficients	Estimate	SE	t	p
(Intercept)	-9.312	5.839	-1.595	.111
location2	-0.329	6.885	-0.048	.962
location3	6.586	5.934	1.110	.267
Smooth terms	edf	Ref. df	F	p
s(ice):location1	6.930	9	332.911	<.0001
s(ice):location2	3.782	9	119.123	<.0001

(Continues)

TABLE 4 (Continued)

Oro: Walrus				
Parametric coefficients	Estimate	SE	t	p
s(ice):location3	6.465	9	69.365	<.0001
s(sst):location1	5.886	9	198.625	<.0001
s(sst):location2	2.448	9	23.246	<.0001
s(sst):location3	7.310	9	45.999	<.0001
s(yrday):location1	9.075	18	699.978	<.0001
s(yrday):location2	9.949	15	558.916	<.0001
s(yrday): location3	14.383	16	722.626	<.0001
R ² (adj) = 0.789, deviance explained = 78.5%, fREML = 4,864.8				
Eba: Bearded seal				
Parametric coefficients	Estimate	SE	t	p
(Intercept)	-11.655	4.340	-2.685	.007
location2	-12.265	17.865	-0.687	.492
location3	7.316	8.569	0.854	.393
Smooth terms	edf	Ref. df	F	p
s(ice):location1	1.898	9	80.781	<.0001
s(ice):location2	3.314	9	67.952	<.0001
s(ice):location3	4.165	9	13.329	.007
s(sst):location1	0.000	9	0.000	1
s(sst):location2	4.010	9	26.222	<.0001
s(sst): location3	0.000	7	0.000	.863
s(yrday):location1	8.111	18	1310.981	<.0001
s(yrday):location2	8.649	15	436.671	<.0001
s(yrday):location3	10.456	15	557.387	<.0001
R ² (adj) = 0.964, deviance explained = 95.2%, fREML = 2,604.8				

time-of-year (Figures 6–8) but were significant in explaining vocal presence (Table 4). Seasonality in bearded seal call presence was identified between February and May at Gambell and Savoonga, and between March to April and November to January at Bering Strait (Figure 6). Time-of-year was significant only at Gambell for modeling ribbon seal call presence between March and May (Table 4, Figure 6).

4 | DISCUSSION

Patterns of PAM detections of focal Arctic marine mammal species were used to characterize the seasonal presence of vocalizing individuals at locations in the northern Bering Sea, an important wintering area for these species, through which shipping is expected to increase. This is the first study to conduct year-round acoustic monitoring off St. Lawrence Island, and provides systematic, fine-scale data about temporal patterns of Arctic marine mammal call occurrence, including species and areas important to Indigenous subsistence. The patterns seen here generally mirror what is known of the occurrence of these species based on observations of local residents and scientific studies

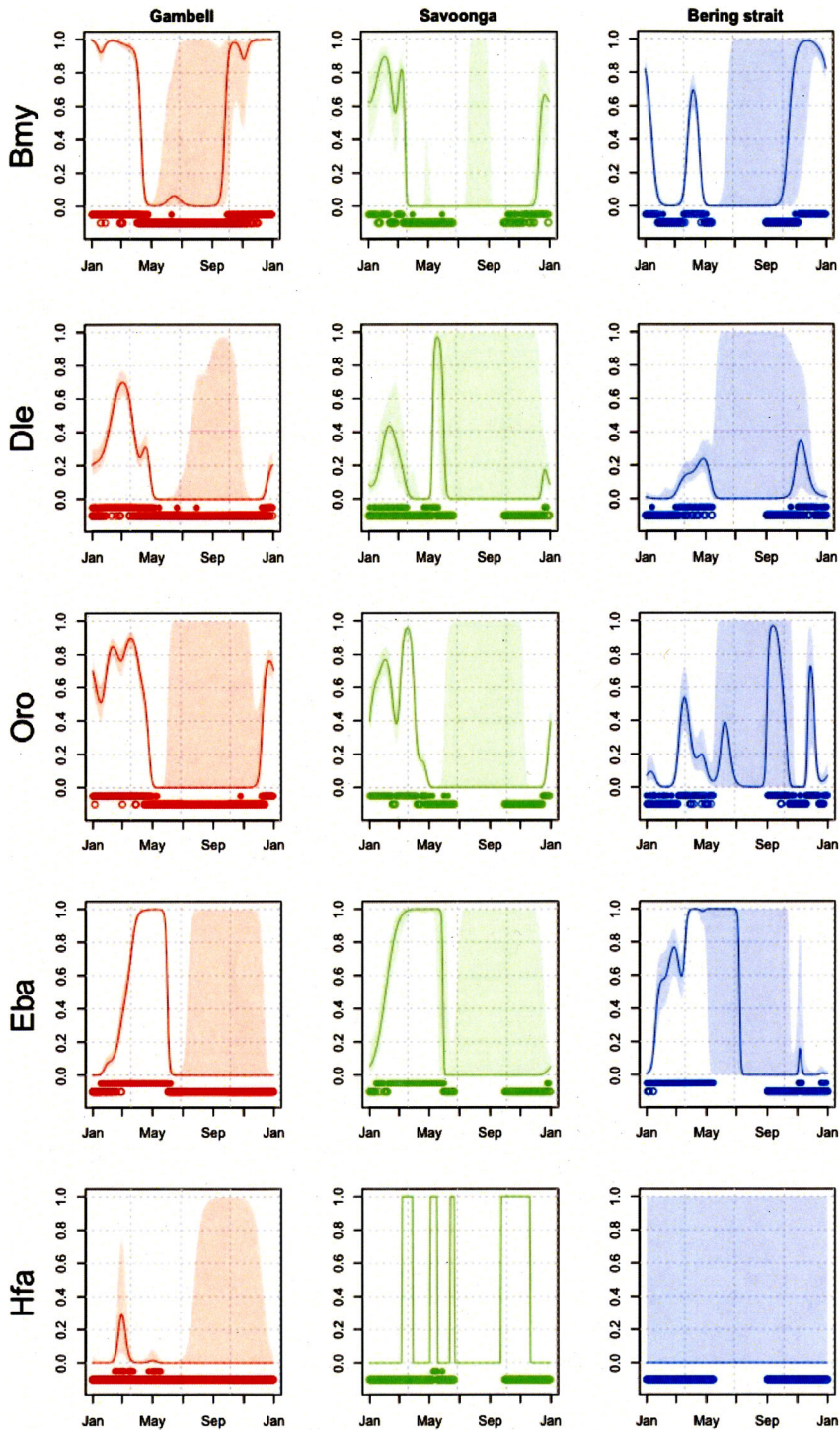


FIGURE 6 Effect of time-of-year on detection of calling presence of bowhead whales (Bmy), belugas (Dle), walrus (Oro), bearded seals (Eba), and ribbon seals (Hfa). Colored area indicates 95% confidence intervals of fitted GAM smooth. Filled circles (top row) indicate values for observations with species detections and empty circles (bottom row) indicate observations without detections.

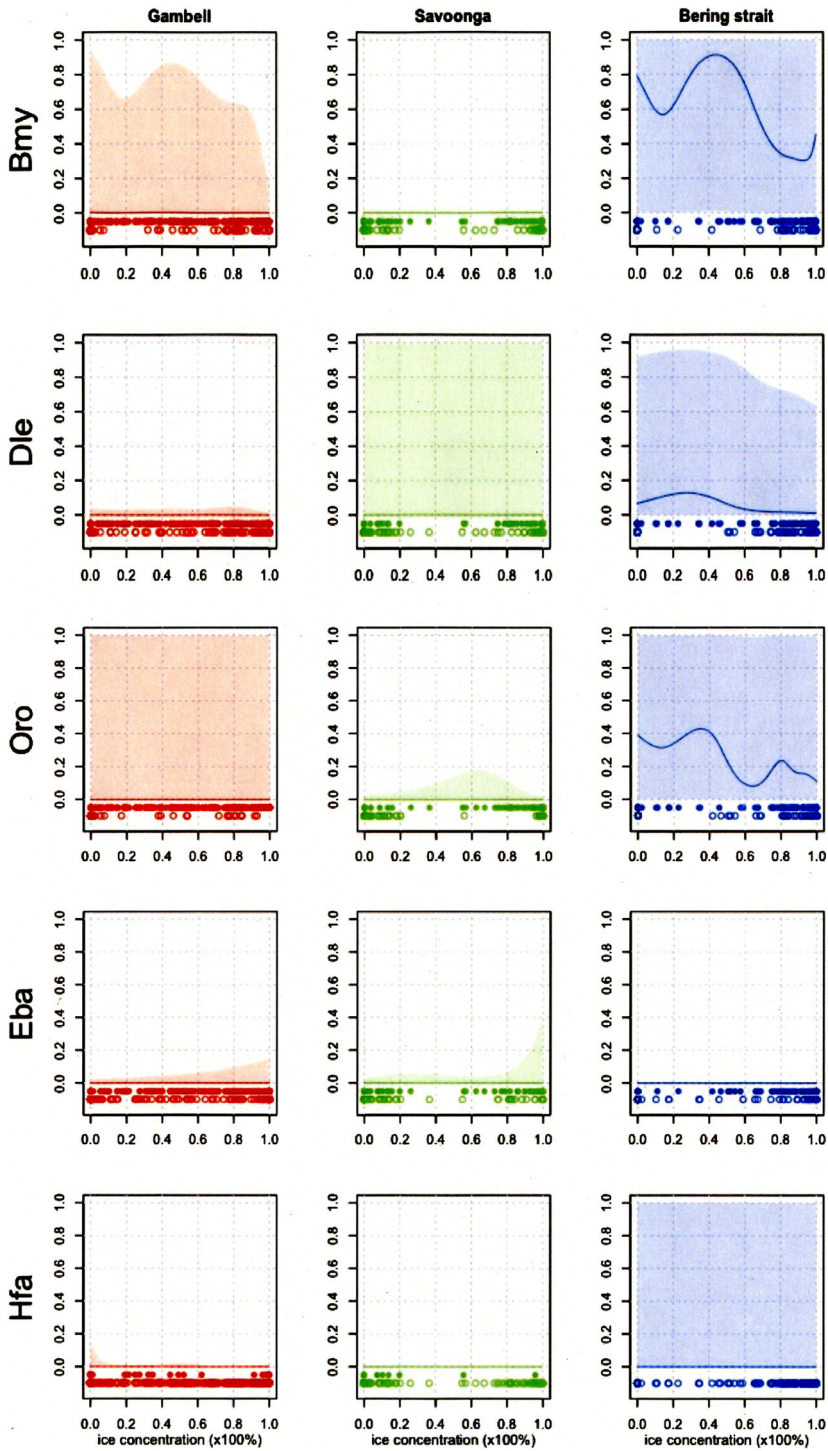


FIGURE 7 Effect of sea ice concentration on the detection of calling presence of bowhead whales (Bmy), belugas (Dle), walrus (Oro), bearded seals (Eba), and ribbon seals (Hfa). Colored area indicates 95% confidence intervals of fitted GAM smooth. Filled circles (top row) indicate values for observations with species detections and empty circles (bottom row) indicate observations without detections.

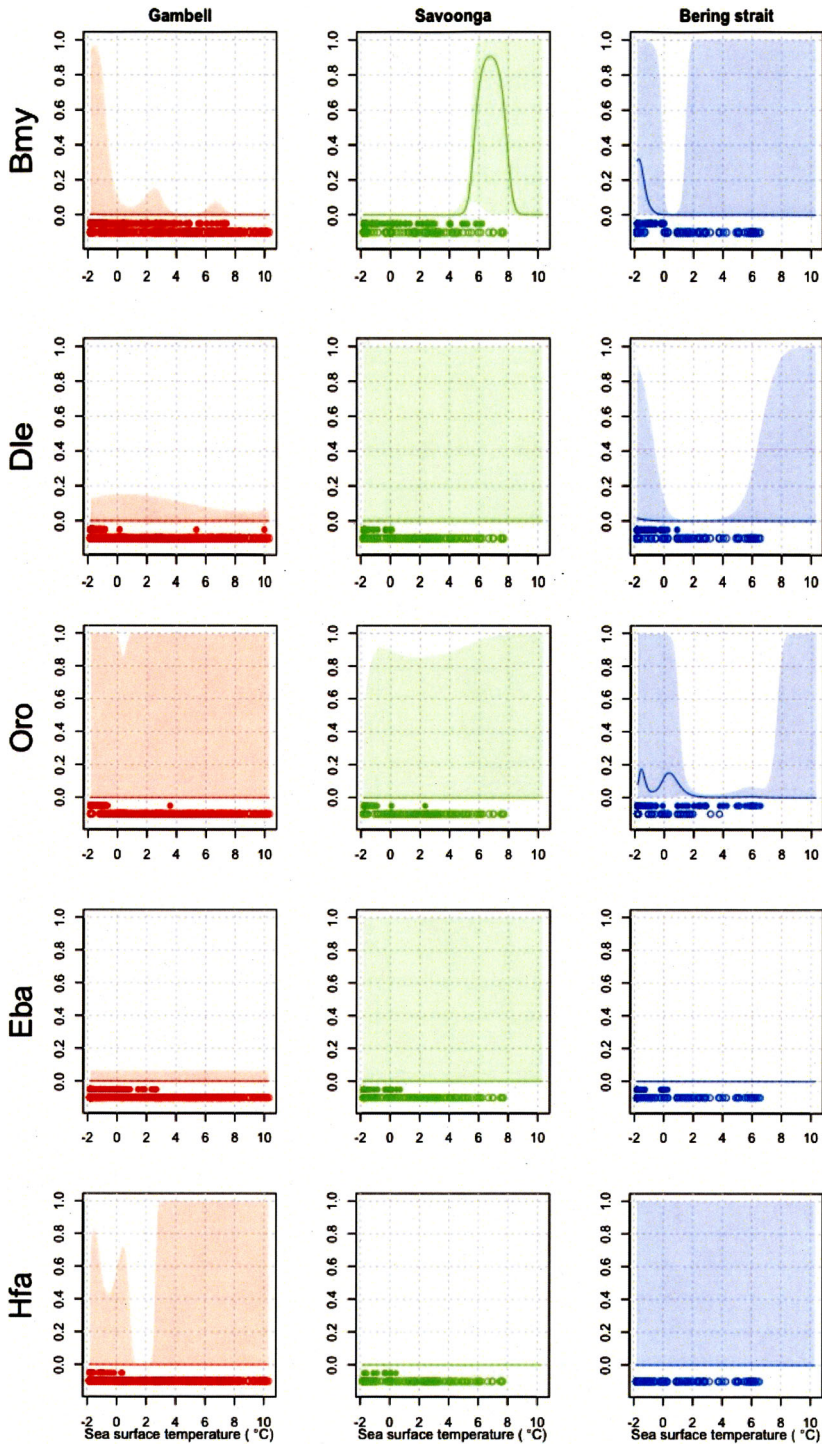


FIGURE 8 Effect of sea surface temperature on the detection of calling presences of bowhead whales (Bmy), belugas (Dle), walrus (Oro), bearded seals (Eba), and ribbon seals (Hfa). Colored area indicates 95% confidence intervals of fitted GAM smooth. Filled circles (top row) indicate values for observations with species detections and empty circles (bottom row) indicate observations without detections.

(Huntington et al., 2017; Myrvin, The Communities of Novoe Chaplino, Sireniki, Uelen, and Yanrakinnot, & Huntington, 1999; Noongwook et al., 2007).

Acoustic detections of Arctic marine mammals in the northern Bering Sea showed clear and consistent seasonal patterns for most species, with call presence coinciding with the seasonal presence of sea ice. While there is likely within- and between-site variance in call detection ranges, we were unable to directly measure these for this study but we do not believe that the spatial extent of call detections is greater than the spatial scale of the environmental variables used. While many of the species-typical calls use similar frequency ranges, bowhead whale calls may be detectable over greater distances and could therefore bias the detection of their call presence slightly. Despite this caveat, patterns of call presence for all species complemented observed winter displacement of marine mammals southward from the Beaufort and Chukchi Seas following sea ice advance and subsequent reoccupation of northern feeding areas in the spring (e.g., Citta et al., 2012; Frouin-Mouy, Mouy, Martin, & Hannay, 2016; Hauser et al., 2015). Modeled effects demonstrated a strong time-of-year correlation with species' call presence/absence. This appears to indicate strong seasonal forces, underscoring the importance of sea ice in the distribution and call presence for these marine mammals, albeit in different patterns for different species.

4.1 | Bowhead whale occurrence

Bowhead whales of the Bering-Chukchi-Beaufort stock primarily spend the winter months (December–March) in the northern Bering Sea (Citta et al., 2012). After wintering in the Bering Sea, they migrate through the Bering Strait into the Chukchi Sea in the spring (April–May), moving towards summering (June–September) areas in the eastern Beaufort Sea before returning to the Bering Sea wintering grounds from October through December (Braham, Fraker, & Krogman, 1980; Citta et al., 2012; Quakenbush et al., 2012). The near-continuous bowhead whale call presence at Savoonga and Gambell between December and April is consistent with Indigenous knowledge regarding whales wintering off the north coast of St. Lawrence Island (Noongwook et al., 2007). Bowhead whale calls have also been detected during the summer months in the Chukchi and Beaufort Seas (Clark et al., 2015; Hannay et al., 2013) and are absent in acoustic recordings at Bering Strait between May and November, supporting their winter seasonal occurrence in the Bering Sea (Citta et al., 2015).

Moreover, the two main periods of call presence at Bering Strait are consistent with southward migration through the Bering Strait from November through February and a northward spring migration into the Chukchi Sea during March and April (Figure 3; Citta et al., 2012, 2015). The autumn call presence period at the Bering Strait monitoring station was also consistent with satellite tracking studies that reported peak use of a Chukotka/Bering Strait core-use area between October 2012 and January 2013 (Citta et al., 2018; Figure 3). Additionally, the detection of call presence at Bering Strait in spring complements the northward spring migration through the same region (Citta et al., 2018; Figure 3). Further, bowhead whale call presence at Gambell in both years were consistent with reports of winter core-use areas adjacent to Gambell and west of St. Lawrence island in the Anadyr Strait and the Gulf of Anadyr between November and May (Citta et al., 2018).

Previous studies of satellite-tracked animals that examined areas of high occupancy did not identify bowhead whale presence in waters off Savoonga; however, call presence of bowhead whales in this study was observed with relatively high daily detection rates between December and March (Citta et al., 2018; Figure 5). Additionally, Indigenous hunters have reported bowhead whales feeding on the northern side of St. Lawrence Island during December, westward migratory movements off Savoonga during December and January, and sightings off St. Lawrence Island during May and June (Ferguson, Waite, Curtice, Clarke, & Harrison, 2015; Noongwook et al., 2007). Acoustic detections in this study are consistent with Indigenous knowledge of bowhead whales in the area, indicating presence of calling bowhead whales and areas of importance around St. Lawrence Island and migratory routes through the Bering Strait.

4.2 | Beluga whale occurrence

Five identified beluga whale stocks are known to winter in the Bering Sea: Bristol Bay, Anadyr, Eastern Chukchi Sea, and Eastern Beaufort Sea, although only the last two stocks migrate north through Bering Strait (Citta et al., 2017; Laidre et al., 2015). There is little overlap among the stocks' traditional home ranges, and although beluga seasonal variation in vocal behavior is unknown, belugas are soniferous and migration patterns can be distinguished by presence of vocalizing animals (Citta et al., 2017; Garland, Berchok, & Castellote, 2015; Stafford et al., 2016). Beluga whale vocalizations were detected seasonally at all stations, with call presence detected only between November and May (Figures 3–5). Detections from the Bering Strait monitoring station showed two periods with beluga call presence: one in early November to late December 2012 and another in early March to mid-May 2013, and detected vocalizations farther south into the Bering Sea at Gambell and Savoonga stations occurred in winter (Figures 3–5). These patterns complement observed beluga migration patterns, in which belugas move southward to winter in the Bering Sea and begin their northern migration to summer feeding areas in early spring (March–April). However, it is possible that the two periods of beluga call presence at Bering Strait may represent the different migratory timing of the two populations that migrate north to the Chukchi Sea (Eastern Chukchi Sea and Eastern Beaufort Sea; Hauser, Laidre, Suydam, & Richard, 2014).

Beluga vocalizations detected off Gambell indicated presence from mid/early December to early May 2015 and March 2016, respectively, and are consistent with satellite tracking studies that also showed foraging presence along the northwestern shore of St. Lawrence Island, as well as in Anadyr Strait between December and March (Citta et al., 2017; Hauser et al., 2015). Daily detection rates of belugas off Savoonga were lower than those at Gambell, and may provide insight into the spatiotemporal movement patterns of different beluga populations (Hauser et al., 2014).

4.3 | Pacific walrus occurrence

The majority of Pacific walrus are present over the continental shelf throughout the Bering and Chukchi Seas, wintering, breeding (January–February) and calving (April–June) in the Bering Sea, and migrating north into the Chukchi Sea during late spring following the receding ice pack (Fay, 1982; MacCracken, Beatty, Garlich-Miller, Kissling, & Snyder, 2017; Robards, Kitaysky, & Burns, 2013). While a large proportion of the population (primarily females, calves, and juveniles) migrates north into the Chukchi Sea, groups of animals, mostly males, aggregate near coastal haul outs in the Gulf of Anadyr, Bering Strait, and Bristol Bay. As sea ice expands southward in autumn, females and young walrus summering in the Chukchi Sea return to the Bering Sea, followed by males in late autumn and winter (Fay, 1982; Jay & Hills, 2005).

While the first detected calls appeared to coincide with the onset of the seasonal sea ice coverage at Gambell and Savoonga in 2015 and 2016, the same was not observed at Bering Strait in 2012. Walrus call presence was detected at Bering Strait during September and October 2012, several months before the onset of seasonal ice coverage (Figure 3). A subsequent period of walrus call presence then occurred in March 2012, several months after the onset of ice coverage (Figure 3). Cessation of walrus call presence at Gambell and Savoonga corresponded with the recession of seasonal sea ice; however, at Bering Strait, walrus vocalizations were still detected in the last recorded day (14 May 2013), 8 days after sea ice recession (Figures 3–5).

Detections of vocalizations off Gambell and Savoonga suggest that at least some male walrus winter off the northern coast of St. Lawrence Island between mid-December and the end of April (Figure 4 and Figure 5). The main peak of call presence at Bering Strait with daily detection rates >0.5 occurred during November 2012, prior to the onset of call presence at St. Lawrence Island monitoring stations, which occurred in late December (Figures 3–5). This appears consistent with the paradigm of southward migration from summering grounds in the Chukchi Sea to wintering grounds in the Bering Sea.

Between-year comparisons across monitoring locations need to be interpreted with some caution as there is variability in monitoring coverage across years and between monitoring stations. Additionally, adult female Pacific

walrus and their young have different migratory habits from males (Fay, 1982; Ray & Watkins, 1975) that cannot be derived through detection of male-produced acoustic signals. Walrus signals were frequently detected in the northeast Chukchi Sea during July, August, and September (Hannay et al., 2013), indicating that this species vocalizes during the summer months and not just during the presumed breeding season. The combination of the lack of sounds at Gambell or Savoonga during the summer months and those detected early summer (June) at Bering Strait corresponds to the known northward migration of walrus into the Chukchi Sea, complementing Hannay et al. (2013) observations, though full coverage of summer months at Bering Strait is lacking (Figures 3–5).

4.4 | Bearded seal occurrence

Bearded seals of the Beringia Distinct Population Segment (DPS) occur in the waters of the Bering, Chukchi, Beaufort, and East Siberian Seas. Many bearded seals of the Beringia DPS winter in the Bering Sea, and move north through the Bering Strait from late April through June to summer in the Chukchi Sea (Boveng, Cameron, Goodwin, & Whiting, 2012; Burns, 1970, 1981b; Heptner, Chapskii, Arsen'ev, & Sokolov, 1976). During autumn and winter, the southward advance of sea ice displaces most bearded seals from the Chukchi Sea, through the Bering Strait into the Bering Sea by December, where they spend the winter and early spring (Boveng et al., 2012; Frouin-Mouy et al., 2016).

Call presence of bearded seals at Bering Strait, Gambell, and Savoonga seem to be consistent with this southward displacement pattern, with first detected vocalizations at Bering Strait in mid-December, and first detections at Gambell and Savoonga in mid-January and late December, respectively, and peak detections at all stations in spring (Figures 3–5). Nuances among these monitoring stations allow potential insight into more fine-scale occurrence and distribution, as call presence during winter occurred first at Bering Strait in mid-December, indicating southward movement through the Bering Strait and then Savoonga, reaching Gambell monitoring station in mid-January. This suggests that bearded seals may occupy the northern central coast of St. Lawrence Island before moving to the Northwest coast.

However, determining the finer-scale patterns in bearded seal movements is more complicated. The spring season is thought to be the peak of that mating season, potentially explaining the peak in vocalizations detected during spring at all monitoring stations. Additionally, call presence of bearded seals at Gambell and Savoonga extended beyond the recession of seasonal sea ice, contrasting with Jones et al. (2014) and MacIntyre, Stafford, Conn, Laidre, and Boveng (2015), who found that the majority of bearded seal calls in the northern Chukchi Sea were detected during periods when sea ice cover was >83% (Figure 4 and Figure 5). While winter and spring presence in the Bering Sea is evident in this study, no autumn southward migration was evident, apart from the small week-long period of call presence at the Bering Strait in November (Figure 3). This likely results from seasonal differences in calling rates, which are higher during the spring reproductive season (Van Parijs, 2010). Finally, recent PAM studies have detected calls from this species nearly year-round in both Beaufort and Chukchi Seas, contrasting with previous studies and acoustic detections in this study (MacIntyre et al., 2015).

4.5 | Ribbon seal occurrence

Ribbon seals occasionally occur in the Chukchi Sea, but most occur in waters of the Bering Sea, where they spend winter and spring hauled out on seasonal pack ice for breeding, giving birth and molting. Summer and autumn are spent in open waters from the North Pacific to the Chukchi Sea (Boveng et al., 2008, 2013; Burns, 1981a, Laidre et al., 2008). In this study, only short periods of ribbon seal vocalization presence were detected during late winter and early spring near Gambell and Savoonga, respectively. Higher daily detections rates off St. Lawrence Island compared to farther north in the Bering Strait support the notion that the Bering Sea is the primary habitat for ribbon seals (Figures 3–5).

While ribbon seal vocalization detections were scarce, they were generally consistent with previously described occupancy in the Bering Sea from mid-March to mid-July (Boveng et al., 2008). Previous PAM studies of ribbon seals found peaks in ribbon seal detections in the Bering Sea from February to June (Frouin-Mouy et al., 2019; Miksis-Olds & Parks, 2011), and between the Chukchi and Beaufort Seas, north of Point Barrow, during the autumn open water season (Frouin-Mouy et al., 2019; Jones et al., 2014). Additionally, no ribbon seal vocalizations were detected outside of the winter/spring seasons in the Bering Sea (Frouin-Mouy et al., 2019; Miksis-Olds & Parks, 2011). While ribbon seals range from the North Pacific to the Chukchi Sea, including a subpopulation in the Sea of Okhotsk, finer-scale distribution of this species is poorly understood in the Pacific Arctic. Because the ribbon seal population has apparently rebounded since being extensively hunted by the Soviet Union in the 1960s (Boveng & Lowry, 2018), it is possible that acoustic monitoring stations in this study and previous studies were not located in high-use areas for these seals. It is also possible that the relative scarcity of ribbon seal calls in this study may either result from this species occurring in fewer numbers in the areas monitored than the other species discussed, lower calling rates in animals present, or different vocal behavior in these areas. Satellite-tracked ribbon seals spent the summer and autumn throughout the waters of the Bering Sea, Aleutian Islands, Bering Strait, Chukchi Sea, and Arctic Basin (Boveng et al., 2013), highlighting their large distribution range. Interestingly, Miksis-Olds and Parks (2011) reported ribbon seal down-sweeps in the Bering Sea when sea ice coverage exceeded 80%; however, of all the days with ribbon seal detections off Gambell, only 25% exceeded the 80% sea ice concentration threshold in this study (Figure 4).

4.6 | Modeled effects and implications

For all focal species, time-of-year had the strongest significant effect on the occurrence of vocalization detections. Models explained over 66% of the variance in calling patterns for belugas, 78.5% of the variation in Pacific walrus calling patterns, and over 80% of the variance for the other three species (Table 4). Sea surface temperature and sea ice concentration are clearly related to one another and are highly seasonally dependent, with lower sea surface temperatures and higher sea ice concentrations in winter months (Figures 3–5). Significant time-of-year results suggest that species call occurrence is influenced by seasonal patterns in these key environmental parameters. Additionally, while sea ice was statistically significant for most species, the modeled effects of sea ice on call presence were limited and were only found statistically significant in predicting call presence for bowheads, belugas, and walrus at Bering Strait (Figure 7).

Future sea ice scenarios predict a northward shift of the southern (winter) boundary of sea ice in the Bering Sea during the 21st century (Douglas, 2010; Wang et al., 2012), although no significant trends in spring and autumn sea ice transition dates between 1979 and 2013 for the Bering Sea were found (Laidre et al., 2015). Because time of year was the most significant variable in modeling marine mammal occurrence in the Bering Sea, changes in the timing, extent, and thickness of sea ice during advance and retreat may cause shifts in marine mammal distributions and migration timing in the northern Bering Sea, including shortening of the periods in which certain marine mammal species occur off St. Lawrence Island and other wintering areas in the Bering Sea. These changes can arise directly through variation in the relative exclusion effect of sea ice, particularly for cetaceans who are subject to the risk of ice entrapment (Heide-Jørgensen, Richard, Ramsay, & Akeagok, 2002; Nerini, Braham, Marquette, & Rugh, 1984), or for pinnipeds that are dependent on sea ice as a platform for hunting, breeding, and resting (Moore & Huntington, 2008). However, site fidelity, such as has been observed for ringed seal breeding sites (Kelly et al., 2010), general locations of walrus summer haul-out sites (Jay & Hills, 2005), and bearded seal winter foraging areas (Boveng et al., 2012), may be a limiting factor in distribution shifts for some species.

Indirect changes may also occur via shifts in availability and partitioning of prey (Moore & Huntington, 2008). For example, the Eastern Chukchi Sea stock belugas' migration occurred significantly later when sea ice freeze-up shifted later in the Beaufort, Chukchi, and Bering Seas. However, the same was not found for belugas from the Eastern Beaufort Sea stock (Hauser et al., 2017). Also, extended presence of walrus in the Chukchi Sea occurred during earlier retreat and later freeze-up of sea ice compared to past conditions (Jay, Fischbach, & Kochnev, 2012).

4.7 | Variability in acoustic detections

Marine mammal calling rates can vary over time (e.g., Baumgartner & Fratantoni, 2008; Matthews et al., 2001), by sex, and depend on behavioral context (e.g., Barrett-Lennard, Ford, & Heise, 1996; Panova, Belikov, Agafonov, & Bel'Kovich, 2012), influencing the detectability of animal presence through PAM (Mellinger et al., 2007). For example, while bowhead song, walrus knocks, and bearded seal trills are typically only produced by males, beluga vocalizations can occur within groups of animals of both sexes (Ray et al., 1969; Sjare et al., 2003; Stirling et al., 1987; Van Parijs et al., 2001; Würsig & Clark, 1993). Furthermore, beluga calling rates vary as a function of group behavioral state (Panova et al., 2012; Sjare & Smith, 1986), although seasonal variation in vocal behavior is unknown. Ribbon seal calls may be produced by males in reproductive and/or territorial activities (Otsuki, Akamatsu, Nobetsu, Mizuguchi, & Mitani, 2018; Watkins & Ray, 1977), although less is known about this species' vocal behavior. Therefore, females, young animals, and nonvocalizing individuals are likely missed by PAM, which is premised on the detection of these call types. Because PAM provides information only on vocally active animals, and for some signals, only for adult males, estimates of occurrence or residency must be considered minimum estimates. Despite these acknowledged limitations, PAM allowed for the detection of seasonal presence and migration periods for bowhead and beluga whales, walrus, and bearded and ribbon seals on relatively fine temporal scales.

PAM is also particularly relevant for assessing the impact of masking of communication signals (Erbe, Reichmuth, Cunningham, Lucke, & Dooling, 2016). The detection of vocalizations indicates when animals are actively using acoustic signals for conspecific communication and mediation of biologically important functions, and is therefore when the potential impact from communication masking is most problematic. This study reinforces traditional Indigenous knowledge and western science which indicate that during winter and early spring, between November and May, several protected and culturally important marine mammal species intensively use the environment around St. Lawrence Island and the Bering Strait in reproductive and social cohesion contexts. They could therefore be subject to reduced fitness if masking from introduced anthropogenic noise interferes with these key functions.

As further environmental changes unfold, sustained and dedicated monitoring of key habitat areas in this biologically and culturally important region are required to understand how such changes may interact with anthropogenic activities to cause shifts in marine mammal spatiotemporal distributions. Acoustic monitoring provides a useful tool to detect these changes of endemic marine mammals, as well as seasonal migrants, in the northern Bering Sea. These tools also provide insight into the relationship between detected marine mammal vocalizations and anthropogenic disturbances within the environment, including industrial activities such as offshore oil and gas and commercial shipping. Due to the extensive seasonal migration of marine mammals, impacts localized in the northern Bering Sea, such as those caused by increases in industrial activity and reduction in sea ice, may have spatially dispersed effects. Consequently, international cooperation and inclusion of Indigenous stakeholders in decision making is of vital importance for management and population level assessment of impacts on marine mammals wintering in the Bering Sea.

4.8 | Conclusions

This study provides a continuously monitored quantitative basis to describe the seasonal and inter-annual presence and behavioral patterns of bowhead and beluga whales, walrus, and bearded and ribbon seals within biologically and culturally important locations in the northern Bering Sea. This is the first study to conduct such coastal year-round acoustic monitoring off St. Lawrence Island, providing important repeatable and relatively fine-scale data on the temporal patterns of marine mammal vocal occurrence, including species of subsistence value for Indigenous peoples. These results constitute an important baseline of information in the context of a rapidly transforming Arctic ecosystem that is increasingly exposed to anthropogenic activities. Sustained monitoring and future work on detection ranges in similar conditions, will provide evidence of climate-driven phenological changes and will enable informed assessment of potential behavioral and acoustic disturbance, including masking, from industrial activities that are likely to continue to increase with increases in navigable areas and seasons for maritime vessel traffic (Reeves et al.,

2014). Sustained, dedicated monitoring should be maintained at strategic locations within this region to help discriminate among baseline inter-annual variability and trends caused by long-term changes in environmental conditions and anthropogenic activities.

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REFERENCES

- ACIA. (2005). *Arctic climate impact assessment*. Cambridge, UK: Cambridge University Press.
- Arctic Council. (2009). *Arctic marine shipping assessment, 2009*. Retrieved from https://www.pmel.noaa.gov/arctic-zone/detect/documents/AMSA_2009_Report_2nd_print.pdf
- Ashjian, C. J., Braund, S. R., Campbell, R. G., George, J. C., Kruse, J., Maslowski, W., ... Spitz, Y. H. (2010). Climate variability, oceanography, bowhead whale distribution, and Inupiat subsistence whaling near Barrow, Alaska. *Arctic*, 63, 179–194.
- Barrett-Lennard, L. G., Ford, J. K., & Heise, K. A. (1996). The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behavior*, 51, 553–565.
- Baumgartner, M. F., & Fratantoni, D. M. (2008). Diel periodicity in both sei whale vocalization rates and the vertical migration of their copepod prey observed from ocean gliders. *Limnology and Oceanography*, 53, 2197–2209.
- Bioacoustics Research Program. (2014). *Raven Pro: Interactive sound analysis software (Version 1.5)* [Computer software]. Ithaca, NY: Cornell Lab of Ornithology. Available from: <http://www.birds.cornell.edu/raven>
- Blackwell, S. B., Nations, C. S., McDonald, T. L., Greene, C. R., Jr., Thode, A. M., Guerra, M., & Macrander, A. M. (2013). Effects of airgun sounds on bowhead whale calling rates in the Alaskan Beaufort Sea. *Marine Mammal Science*, 29, E342–E365.
- Boveng, P. L., & Lowry, L. (2018). Ribbon seal: *Histiophoca fasciata*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 811–813). New York, NY: Academic Press.
- Boveng, P. L., Bengtson, J. L., Cameron, M. F., Dahle, S. P., Logerwell, E. A., London, J. M., ... Ziel, H. L. (2013). *Status review of the ribbon seal*. U.S. Department of Commerce, NOAA Technical Memorandum NMFS AFSC-255.
- Boveng, P. L., Bengtson, J. L., Buckley, T. W., Cameron, M. F., Dahle, S. P., Megrey, B. A., ... Williamson, N. J. (2008). *Status review of the ribbon seal (Histiophoca fasciata)*. U.S. Department of Commerce, NOAA Technical Memorandum NMFS AFSC-191.
- Boveng, P. L., Cameron, M. F., Goodwin, J., & Whiting, A. (2012). Seasonal migration of bearded seals between intensive foraging patches. Poster presented at the Alaska Marine Science Symposium (AMSS), Anchorage, AK.
- Braham, H. W., Fraker, M. A., & Krogman, B. S. (1980). Spring migration of the western Arctic population of bowhead whales. *Marine Fisheries Review*, 42, 36–46.
- Burns, J. J. (1970). Remarks on the distribution and natural history of pagophilic pinnipeds in the Bering and Chukchi Seas. *Journal of Mammalogy*, 51, 445–454.
- Burns, J. J. (1981a). Ribbon seal – *Phoca fasciata*. In S. H. Ridgway & R. J. Harrison (Eds.), *Handbook of marine mammals*. Vol. 2. *Seals* (pp. 89–109). New York, NY: Academic Press.
- Burns, J. J. (1981b). Bearded seal – *Erignathus barbatus*. In S. H. Ridgway & R. J. Harrison (Eds.), *Handbook of Marine Mammals*. Vol. 2. *Seals* (pp. 145–170). New York, NY: Academic Press.
- Chmelnitsky, E. G., & Ferguson, S. H. (2012). Beluga whale, *Delphinapterus leucas*, vocalizations from the Churchill River, Manitoba, Canada. *Journal of the Acoustical Society of America*, 131, 4821–4835.

- Citta, J. J., Quakenbush, L. T., George, J. C., Small, R. J., Heide-Jørgensen, M. P., Brower, H., ... Brower, L. (2012). Winter movements of bowhead whales (*Balaena mysticetus*) in the Bering Sea. *Arctic*, 65, 13–34.
- Citta, J. J., Quakenbush, L. T., Okkonen, S. R., Druckenmiller, M. L., Maslowski, W., Clement-Kinney, J., ... Heide-Jørgensen, M. P. (2015). Ecological characteristics of core-use areas used by Bering–Chukchi–Beaufort (BCB) bowhead whales, 2006–2012. *Progress in Oceanography*, 136, 201–222.
- Citta, J. J., Richard, P., Lowry, L. F., O’Corry-Crowe, G., Marcous, M., Suydam, R., ... Druckenmiller, M. L. (2017). Satellite telemetry reveals population specific winter ranges of beluga whales in the Bering Sea. *Marine Mammal Science*, 33, 236–250.
- Citta, J. J., Okkonen, S. R., Quakenbush, L. T., Maslowski, W., Osinski, R., George, J. C., ... Harwood, L. A. (2018). Oceanographic characteristics associated with autumn movements of bowhead whales in the Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 152, 121–131.
- Clark, C. W., & Johnson, J. H. (1984). The sounds of the bowhead whale, *Balaena mysticetus*, during the spring migrations of 1979 and 1980. *Canadian Journal of Zoology*, 62, 1436–1441.
- Clark, C. W., Berchok, C. L., Blackwell, S. B., Hannay, D. E., Jones, J., Ponirakis, D., & Stafford, K. M. (2015). A year in the acoustic world of bowhead whales in the Bering, Chukchi and Beaufort seas. *Progress in Oceanography*, 136, 223–240.
- Clarke, J., Stafford, K. M., Moore, S. E., Rone, B., Aerts, L., & Crance, J. (2013). Subarctic cetaceans in the southern Chukchi Sea: Evidence of recovery or response to a changing ecosystem. *Oceanography*, 26, 136–149.
- Cummings, W. C., & Holliday, D. V. (1987). Sounds and source levels from bowhead whales off Pt. Barrow, Alaska. *Journal of the Acoustical Society of America*, 82, 814–821.
- Douglas, D. C. (2010). *Arctic sea ice decline: Projected changes in timing and extent of sea ice in the Bering and Chukchi Seas*. US Geological Survey Open-File Report 2010–1176.
- Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., & Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine Pollution Bulletin*, 103, 15–38.
- Fay, F. H. (1982). Ecology and biology of the Pacific walrus *Odobenus rosmarus divergens* Illiger. *North American Fauna*, 74, 1–279.
- Ferguson, M. C., Waite, J. M., Curtice, C., Clarke, J. T., & Harrison, J. (2015). Biologically important areas for cetaceans within U.S. waters: Aleutian Islands and Bering Sea region. *Aquatic Mammals*, 41, 79–93.
- Frouin-Mouy, H., Mouy, X., Berchok, C. L., Blackwell, S. B., & Stafford, K. M. (2019). Acoustic occurrence and behavior of ribbon seals (*Histiophoca fasciata*) in the Bering, Chukchi, and Beaufort Seas. *Polar Biology*, 42, 657–674.
- Frouin-Mouy, H., Mouy, X., Martin, B., & Hannay, D. (2016). Underwater acoustic behavior of bearded seals (*Erignathus barbatus*) in the northeastern Chukchi Sea, 2007–2010. *Marine Mammal Science*, 32, 141–160.
- Gadamus, L., Raymond-Yakoubian, J., Ashenfelter, R., Ahmasuk, A., Metcalf, V., & Noongwook, G. (2015). Building an indigenous evidence-base for tribally-led habitat conservation policies. *Marine Policy*, 62, 116–124.
- Garland, E. C., Berchok, C. L., & Castellote, M. (2015). Temporal peaks in beluga whale (*Delphinapterus leucas*) acoustic detections in the northern Bering, northeastern Chukchi, and western Beaufort Seas: 2010–2011. *Polar Biology*, 38, 747–754.
- Haine, T. W. N., & Martin, T. (2017). The Arctic-Subarctic sea ice system is entering a seasonal regime: Implications for future Arctic amplification. *Scientific Reports*, 7, 4618.
- Hannay, D. E., Delarue, J., Mouy, X., Martin, B. S., Leary, D., Oswald, J. N., & Vallarta, J. (2013). Marine mammal acoustic detections in the northeastern Chukchi Sea, September 2007–July 2011. *Continental Shelf Research*, 67, 127–146.
- Hartsig, A., Frederickson, I., Yeung, C., & Senner, S. (2012). Arctic bottleneck: Protecting the Bering Strait Region from increased vessel traffic. *Ocean and Coastal Law Journal*, 18, 35–87.
- Hastie, T. J., & Tibshirani, R. J. (1990). Generalized additive models. In *Monographs on Applied Statistics and Applied Probability* (Vol. 43). Boca Raton, FL: Chapman & Hall/CRC.
- Hauser, D. D. W., Laidre, K. L., Parker-Stetter, S. L., Horne, J. K., Suydam, R. S., & Richard, P. R. (2015). Regional diving behavior of Pacific Arctic beluga whales *Delphinapterus leucas* and possible associations with prey. *Marine Ecology Progress Series*, 541, 245–264.
- Hauser, D. D. W., Laidre, K. L., Stafford, K. M., Stern, H. L., Suydam, R. S., & Richard, P. R. (2017). Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation. *Global Change Biology*, 23, 2206–2217.
- Hauser, D. D. W., Laidre, K. L., & Stern, H. L. (2018). Vulnerability of Arctic marine mammals to vessel traffic in the increasingly ice-free Northwest Passage and Northern Sea Route. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 7617–7622.
- Hauser, D. D. W., Laidre, K. L., Suydam, R. S., & Richard, P. R. (2014). Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). *Polar Biology*, 37, 1171–1183.
- Heide-Jørgensen, M. P., Richard, P., Ramsay, M., & Akeagok, S. (2002). Three recent ice entrapments of Arctic cetaceans in West Greenland and the eastern Canadian High Arctic. *NAMMCO Scientific Publications*, 4, 143–148.

- Heptner, L. V. G., Chapskii, K. K., Arsen'ev, V. A., & Sokolov, V. T. (1976). Ribbon (banded) seal. *Phoca (Histriophoca) fasciata* Zimmermann, 1783. In L. V. G. Heptner, N. P. Naumov, & J. Mead (Eds.), *Mammals of the Soviet Union. Volume II, Part 3 – Pinnipeds and toothed whales, Pinnipedia and Odontoceti* (pp. 436–452). Moscow, Russia: Vysshaya Shkola Publishers. (Translated from Russian by P. M. Rao, 1996, Science Publishers, Inc., Lebanon, NH).
- Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, 395, 5–20.
- Huntington, H. P. (2013). *Traditional knowledge regarding bowhead whales and Camden Bay, Beaufort Sea, Alaska* (Final report to the North Slope Borough Department of Wildlife Management). Barrow, AK: North Slope Borough.
- Huntington, H. P., Quakenbush, L. T., & Nelson, M. (2017). Evaluating the effects of climate change on Indigenous marine mammal hunting in northern and western Alaska using traditional knowledge. *Frontiers in Marine Science*, 4, 40.
- Insley, S. J., Halliday, W. D., & de Jong, T. (2017). Seasonal patterns in ocean ambient noise near Sachs Harbour, Northwest Territories. *Arctic*, 70, 239–248.
- Jay, C. V., & Hills, S. (2005). Movements of walrus radiotagged in Bristol Bay, Alaska. *Arctic*, 58, 192–202.
- Jay, C. V., Fischbach, A. S., & Kochnev, A. A. (2012). Walrus areas of use in the Chukchi Sea during sparse sea ice cover. *Marine Ecology Progress Series*, 468, 1–13.
- Jones, J. M., Thayre, B. J., Roth, E. H., Mahoney, M., Sia, I., Mercuri, K., ... Hildebrand, J. A. (2014). Ringed, bearded, and ribbon seal vocalizations north of Barrow, Alaska: Seasonal presence and relationship with sea ice. *Arctic*, 67, 203–222.
- Karlsen, J. D., Bisther, A., Lydersen, C., Haug, T., & Kovacs, K. M. (2002). Summer vocalizations of adult male white whales (*Delphinapterus leucas*) in Svalbard, Norway. *Polar Biology*, 25, 808–817.
- Kelly, B. P., Badajos, O. H., Kunnsaranta, M., Moran, J. R., Martinez-Bakker, M., Wartzok, D., & Boveng, P. (2010). Seasonal home ranges and fidelity to breeding sites among ringed seals. *Polar Biology*, 33, 1095–1109.
- Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., ... Ugarte, F. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology*, 29, 724–737.
- Laidre, K. L., Stirling, I., Lowry, L. F., Wiig, Ø., Heide-Jørgensen, M. P., & Ferguson, S. H. (2008). Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications*, 18, S97–S125.
- Ljungblad, D. K., Thompson, P. O., & Moore, S. E. (1982). Underwater sounds recorded from migrating bowhead whales, *Balaena mysticetus*, in 1979. *Journal of the Acoustical Society of America*, 71, 477–482.
- MacCracken, J. G., Beatty, W. S., Garlich-Miller, J. L., Kissling, M. L., & Snyder, J. A. (2017). *Final species status assessment for the Pacific walrus (Odobenus rosmarus divergens), May 2017 (Version 1.0)*. Anchorage, AK: U.S. Fish and Wildlife Service.
- MacIntyre, K. Q., Stafford, K. M., Conn, P. B., Laidre, K. L., & Boveng, P. L. (2015). The relationship between sea ice concentration and the spatio-temporal distribution of vocalizing bearded seals (*Erignathus barbatus*) in the Bering, Chukchi, and Beaufort Seas from 2008 to 2011. *Progress in Oceanography*, 13, 241–249.
- Matthews, J. N., Brown, S., Gillespie, D., Johnson, M., McLanaghan, R., Moscrop, A., ... Tyack, P. (2001). Vocalisation rates of the North Atlantic right whale (*Eubalaena glacialis*). *Journal of Cetacean Research and Management*, 3, 271–282.
- Mellinger, D. K. (2001). *Ishmael 1.0 User's Guide*. U. S. Department of Commerce, NOAA Technical Memorandum OAR PMEL-120. Available from NOAA/PMEL/OERD, 2115 SE OSU Drive, Newport, OR.
- Mellinger, D. K., Stafford, K. M., Moore, S. E., Dziak, R. P., & Matsumoto, H. (2007). An overview of fixed passive acoustic observation methods for cetaceans. *Oceanography*, 20, 36–45.
- Miksis-Olds, J. L., & Parks, S. E. (2011). Seasonal trends in acoustic detection of ribbon seal (*Histriophoca fasciata*) vocalizations in the Bering Sea. *Aquatic Mammals*, 37, 464–471.
- Milne, A. R., & Ganton, J. H. (1964). Ambient noise under Arctic-Sea ice. *Journal of the Acoustical Society of America*, 36, 855–863.
- Mizuguchi, D., Mitani, Y., & Kohshima, S. (2016). Geographically specific underwater vocalizations of ribbon seals (*Histriophoca fasciata*) in the Okhotsk Sea suggest a discrete population. *Marine Mammal Science*, 32, 1138–1151.
- Moore, S. E., & Huntington, H. P. (2008). Arctic marine mammals and climate change: Impacts and resilience. *Ecological Applications*, 8, S157–S165.
- Moore, S. E., Stafford, K. M., Mellinger, D. K., & Hildebrand, J. A. (2006). Listening for large whales in offshore waters of Alaska. *BioScience*, 56, 49–55.
- Moore, S. E., Stafford, K. M., Melling, H., Berchok, C., Wiig, Ø., Kovacs, K. M., ... Richter-Menge, J. (2012). Comparing marine mammal acoustic habitats in Atlantic and Pacific sectors of the High Arctic: Year-long records from Fram Strait and the Chukchi Plateau. *Polar Biology*, 35, 475–480.
- Mymrin, N., The Communities of Novoe Chaplino, Sireniki, U., Yanrakinnot, & Huntington, H. P. (1999). Traditional knowledge of the ecology of beluga whales (*Delphinapterus leucas*) in the northern Bering Sea, Chukotka, Russia. *Arctic*, 52, 62–70.
- National Research Council. (2003). *Ocean noise and marine mammals*. Washington, DC: The National Academies Press.

- Nerini, M. K., Braham, H. W., Marquette, W. M., & Rugh, D. J. (1984). Life history of the bowhead whale, *Balaena mysticetus* (Mammalia: Cetacea). *Journal of Zoology (London)*, 204, 443–468.
- Noongwook, G., The Native Village of Savoonga, The Native Village of Gambell, Huntington, H. P., & George, J. C. (2007). Traditional knowledge of the bowhead whale (*Balaena mysticetus*) around St. Lawrence Island, Alaska. *Arctic*, 60, 47–54.
- Otsuki, M., Akamatsu, T., Nobetsu, T., Mizuguchi, D., & Mitani, Y. (2018). Diel changes in ribbon seal *Histiophoca fasciata* vocalizations during sea ice presence in the Nemuro Strait, Sea of Okhotsk. *Polar Biology*, 41, 451–456.
- Panova, E. M., Belikov, R. A., Agafonov, A. V., & Bel'Kovich, V. M. (2012). The relationship between the behavioral activity and the underwater vocalization of the beluga whale (*Delphinapterus leucas*). *Oceanology*, 52, 79–87.
- Quakenbush, L., Citta, J., George, J. C., Heide-Jørgensen, M. P., Small, R., Brower, H., ... Pokiak, J. (2012). *Seasonal movements of the Bering-Chukchi-Beaufort stock of bowhead whales: 2006–2011 satellite telemetry results*. International Whaling Commission Scientific Committee Paper SC/64/BRG1.
- Core Team, R. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ray, G. C., & Watkins, W. A. (1975). Social function of underwater sounds in the walrus *Odobenus rosmarus*. *Rapports et Proces-verbaux des Réunions. Conseil International pour l'Exploration de la Mer*, 169, 524–526.
- Ray, G. C., Watkins, W. A., & Burns, J. J. (1969). The underwater song of *Erignathus* (bearded seal). *Zoologica*, 54, 79–83.
- Reeves, R. R., Ewins, P. J., Agbayani, S., Heide-Jørgensen, M. P., Kovacs, K. M., Lydersen, C., ... Blijleven, R. (2014). Distribution of endemic cetaceans in relation to hydrocarbon development and commercial shipping in a warming Arctic. *Marine Policy*, 44, 375–389.
- Richardson, W. J., Greene, C. R., Jr., Malme, C. I., & Thomson, D. H. (1995). *Marine mammals and noise*. New York, NY: Academic Press.
- Risch, D., Clark, C. W., Corkeron, P. J., Elepfandt, A., Kovacs, K. M., Lydersen, C., ... Van Parijs, S. M. (2007). Vocalizations of male bearded seals, *Erignathus barbatus*: Classification and geographical variation. *Animal Behavior*, 73, 747–762.
- Robards, M. D., Kitaysky, A. S., & Burns, J. J. (2013). Physical and sociocultural factors affecting walrus subsistence at three villages in the northern Bering Sea: 1952–2004. *Polar Geography*, 36, 65–85.
- Rogers, T. S., Walsh, J. E., Rupp, T. S., Brigham, L. W., & Sfraga, M. (2013). Future Arctic marine access: Analysis and evaluation of observations, models, and projections of sea ice. *Cryosphere*, 7, 321–332.
- Rolland, R. M., Parks, S. E., Hunt, K. E., Castellote, M., Corkeron, P. J., Nowacek, D. P., ... Kraus, S. D. (2012). Evidence that ship noise increases stress in right whales. *Proceedings of the Royal Society B: Biological Sciences*, 279, 2363–2368.
- Schevill, W. E., Watkins, W. A., & Ray, C. (1966). Analysis of underwater *Odobenus* calls with remarks on the development and function of pharyngeal pouches. *Zoologica*, 51, 103–106.
- Serreze, M. C., & Francis, J. A. (2006). The Arctic amplification debate. *Climatic Change*, 76, 241–264.
- Sjare, B. L., & Smith, T. G. (1986). The relationship between behavioral activity and underwater vocalizations of the white whale, *Delphinapterus leucas*. *Canadian Journal of Zoology*, 64, 2824–2831.
- Sjare, B., Stirling, I., & Spencer, C. (2003). Structural variation in the songs of Atlantic walruses breeding in the Canadian High Arctic. *Aquatic Mammals*, 29, 297–318.
- Southall, B. L. (2017). Noise. In B. Würsig & H. Thewissen (Eds.), *Encyclopedia of marine mammals* (3rd ed.). New York, NY: Academic Press.
- Spreen, G., Kaleschke, L., & Heygster, G. (2008). Sea ice remote sensing using AMSR-E 89 GHz channels. *Journal of Geophysical Research*, 113, C02S03.
- Stafford, K. M. (2019). Increasing detections of killer whales (*Orcinus orca*), in the Pacific Arctic. *Marine Mammal Science*, 35, 696–706.
- Stafford, K. M., Castellote, M., Guerra, M., & Berchok, C. L. (2018). Seasonal acoustic environments of beluga and bowhead whale core-use regions in the Pacific Arctic. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 152, 108–120.
- Stafford, K. M., Ferguson, M. C., Hauser, D. D. W., Okkonen, S. R., Berchok, C. L., Cita, J. J., ... Suydam, R. S. (2016). Beluga whales in the western Beaufort Sea: Current state of knowledge on timing, distribution, habitat use and environmental drivers. *Deep Sea Research Part II: Topical Studies in Oceanography*, 152, 182–194.
- Stephenson, S. R., Smith, L. C., Brigham, L. W., & Agnew, J. A. (2013). Projected 21st-century changes to Arctic marine access. *Climatic Change*, 118, 885–899.
- Stewart, B. C., Kunkel, K. E., Stevens, L. E., Sun, L., & Walsh, J. E. (2013). *Regional climate trends and scenarios for the U.S. National Climate Assessment. Part 7. Climate of Alaska*. U.S. Department of Commerce, NOAA Technical Report NESDIS 142–147.
- Stirling, I., Calvert, W., & Cleator, H. (1983). Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the High Arctic. *Arctic*, 36, 262–274.
- Stirling, I., Calvert, W., & Spencer, C. (1987). Evidence of stereotyped underwater vocalizations of male Atlantic walruses, *Odobenus rosmarus rosmarus*. *Canadian Journal of Zoology*, 65, 2311–2321.

- Van Parijs, S. M. (2010). Aquatic mating in pinnipeds: A review. *Aquatic Mammals*, 29, 214–226.
- Van Parijs, S. M., Kovacs, K. M., & Lydersen, C. (2001). Spatial and temporal distribution of vocalising male bearded seals: Implications for male mating strategies. *Behavior*, 138, 905–922.
- Wang, M., Overland, J. E., & Stabeno, P. (2012). Future climate of the Bering and Chukchi Seas projected by global climate models. *Deep-Sea Research Part II: Topical Studies in Oceanography*, 65–70, 46–57.
- Watkins, W. A., & Ray, G. C. (1977). Underwater sounds from ribbon seal, *Phoca (Histriophoca) fasciata*. *Fisheries Bulletin*, 75, 450–453.
- Wood, K. R., Bond, N. A., Danielson, S. L., Overland, J. E., Salo, S. A., Stabeno, P. J., & Whitefield, J. (2015). A decade of environmental change in the Pacific Arctic region. *Progress in Oceanography*, 136, 12–31.
- Wood, S. N. (2001). mgcv: GAMs and generalized ridge regression for R. *R News*, 1, 20–25.
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society*, B73, 3–36.
- Woodgate, R., Stafford, K. M., & Prah, F. (2015). A synthesis of year-round interdisciplinary mooring measurements in the Bering Strait (1990–2014) and the RUSALCA years (2004–2011). *Oceanography*, 28, 46–67.
- Würsig, B., & Clark, C. (1993). Behavior. In J. J. Burns, J. J. Montague, & C. J. Cowles (Eds.), *The bowhead whale*. Society for Marine Mammalogy Special Publication Number 2.
- Zhang, J. (2005). Warming of the arctic ice-ocean system is faster than the global average since the 1960s. *Geophysical Research Letters*, 32, L19602.

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