Progress in Oceanography 213 (2023) 103004

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Bowhead whale year-round acoustic presence and habitat associations in the Amundsen Gulf, Western Canadian Arctic, 2018–2019

Nikoletta Diogou [a,b,*], William D. Halliday [a,b], Stan E. Dosso [b], Xavier Mouy [c,d], Andrea Niemi [e], Stephen J. Insley [a,f]

[a] *Wildlife Conservation Society Canada, Whitehorse, Yukon, Canada*
[b] *School of Earth and Ocean Sciences, University of Victoria, Victoria, British Columbia (BC), Canada*
[c] *JASCO Applied Science Ltd, Victoria, BC, Canada*
[d] *Integrated Statistics, Inc., Under Contract to National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA, United States*
[e] *Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, Manitoba, Canada*
[f] *Department of Biology, University of Victoria, Victoria, BC, Canada*

ABSTRACT

Understanding the temporal and spatial distribution of bowhead whales is ecologically and culturally important in the context of a rapidly changing climate. Long-term monitoring can reveal alterations in the bowhead whale distribution range, spatiotemporal patterns, and migration phenology that can be responses to global change. However, Arctic ecosystems are challenging to monitor. Here, we deployed passive acoustic recorders at three locations in the southern Amundsen Gulf (western Canadian Arctic) between September 2018 and September 2019 to detect bowhead whale presence, quantify their seasonal occurrence, and examine the oceanographic conditions that correlate with bowhead occurrence. Results show clear seasonal patterns in the occurrence of bowheads with increased acoustic presence in spring/summer at all sites. In contrast to their typical migratory behavior, bowhead sounds were detected throughout the year at all sites, providing evidence of a number of overwintering animals in what is normally their summer feeding ground. The continuous occupancy of bowheads from May to August at all sites emphasizes the importance of this area as a core foraging ground for this population. Our results indicate a clear selection for the shallowest habitat over an annual cycle. Statistical habitat modeling indicated associations between bowhead occurrence and decreasing sea-ice coverage, wind speed, temperature, and salinity. Positive relationships between bowhead detections and zooplankton density suggest a predator-prey dynamic. These results are the first that cover an entire annual cycle of bowhead presence in the southern Amundsen Gulf, providing new knowledge and current status of bowhead habitat use to support effective management under ongoing Arctic change.

1. Introduction

The Arctic Ocean soundscape is among the most pristine on the planet, relatively unpolluted by anthropogenic noise. The overall ambient sound levels are lower compared to other oceanic regions (Halliday et al., 2020; PAME, 2019) and the endemic marine fauna are acclimatized to a quiet and relatively healthy marine soundscape (Haver et al., 2018; Insley et al., 2017). The Arctic soundscape is mostly dominated by biological (produced by animals) and geophysical (produced by wind, ice and waves) sounds. These contributions are frequency-dependent, and vary temporally (seasonally and interannually) and spatially (geographically and in depth) (PAME, 2019). However, the Arctic is undergoing rapid changes with temperatures rising nearly four times as fast as the rest of the globe (Rantanen et al., 2021). This warming is causing continuously shrinking sea-ice coverage and thickness; models predict that the Arctic will be ice-free during the summer by 2035 (Guarino et al., 2020; Wang and Overland, 2009). Such environmental changes can cause a series of cascading effects through the entire marine ecosystem (Cooper and Grebmeier, 2022; Frey et al., 2021; Lefebvre et al., 2022; Moore et al., 2022). Variability of sea ice can have direct ecological effects on ice-obligated (bearded seals, *Erignathus barbatus,* and ringed seals, *Pusa hispida*) and ice-associated (bowhead whales, *Balaena mysticetus,* and beluga whales, *Delphinapterus leucas*) marine mammals, which may respond by changing their distribution, behavior, spatiotemporal patterns, and migration phenology (Gulland et al., 2022; Hauser et al., 2017; Insley et al., 2021; Stafford et al., 2022). Indirect effects of the sea-ice decline include an unprecedented increase in human activities as the Arctic becomes more accessible (Moore et al., 2012). Oil companies conduct more numerous and geographically-extended seismic surveys in the Arctic during the ice-free periods

---

* Corresponding author at: Wildlife Conservation Society Canada, Whitehorse, Yukon, Canada.
E-mail address: niki.diogou@gmail.com (N. Diogou).

https://doi.org/10.1016/j.pocean.2023.103004
Received 25 May 2022; Received in revised form 15 February 2023; Accepted 1 March 2023

(Moore et al., 2012), although the North American Arctic has recently had a moratorium on offshore oil and gas activity. Commercial shipping has increased (Pizzolato et al., 2016) and vessel traffic has seen a threefold increase between the 1990s and 2015 in the Canadian Arctic (Dawson et al., 2018). Consequently, the underwater Arctic soundscape is experiencing increased anthropogenic noise (mainly from vessels, seismic surveys construction and sonar) (Halliday et al., 2021). As a result, marine mammals are exposed to acoustic disturbance, to increased risk of ship strikes (COSEWIC, 2009) and pollution such as oil spills (Huntington et al., 2015) that compromise their vital functions and the health of their ecosystems.

Bowhead whales, the only endemic baleen whale species in the Arctic, are considered to be the longest living mammal on the planet (~200 years) (George et al., 2021) and have been culturally important for the Inuit for centuries (Huntington et al., 2021b). The Bering-Chukchi-Beaufort (BCB) stock of bowhead whales inhabits the western Canadian Arctic during summer months, and is listed under Canada's Species At Risk Act as *Special Concern* (COSEWIC, 2009). Under the management plan for BCB bowheads (COSEWIC, 2009), acoustic disturbance is listed as the top threat. Whales rely heavily on marine soundscapes. Bowheads are highly vocal and use acoustics, actively or passively, for critical biological functions: they produce a wide variety of sounds for reproduction, group cohesion, socializing and migration (Stafford and Clark, 2021). Bowhead sounds range from low-frequency moans at an almost constant frequency, to calls composed of a series of pulses varying in amplitude, frequency, duration and interpulse interval (Clark and Johnson, 1984). These sounds are roughly classified into two major categories: (a) calls ranging from 25 to 500 Hz, lasting about 1 s (Clark and Johnson, 1984) and with source levels of about 161 dB (for 20–170 Hz calls; Thode et al., 2016); and (b) songs that consist of repetitive and complex moan sequences and range between 50 and 5000 Hz (JASCO, 2009; Delarue et al., 2009; Stafford et al., 2018b; Blackwell et al., 2007; Tervo et al., 2012). Calls are produced during the summer foraging and fall and spring migration periods (Clark and Johnson, 1984; Wursing and Clark, 1993) and are thought to function in mother-calf communication, navigating though ice fields, and coordinating between migrating groups or individuals (George et al., 1989; Ljungblad et al., 1982, 1980). Songs are produced from fall to spring

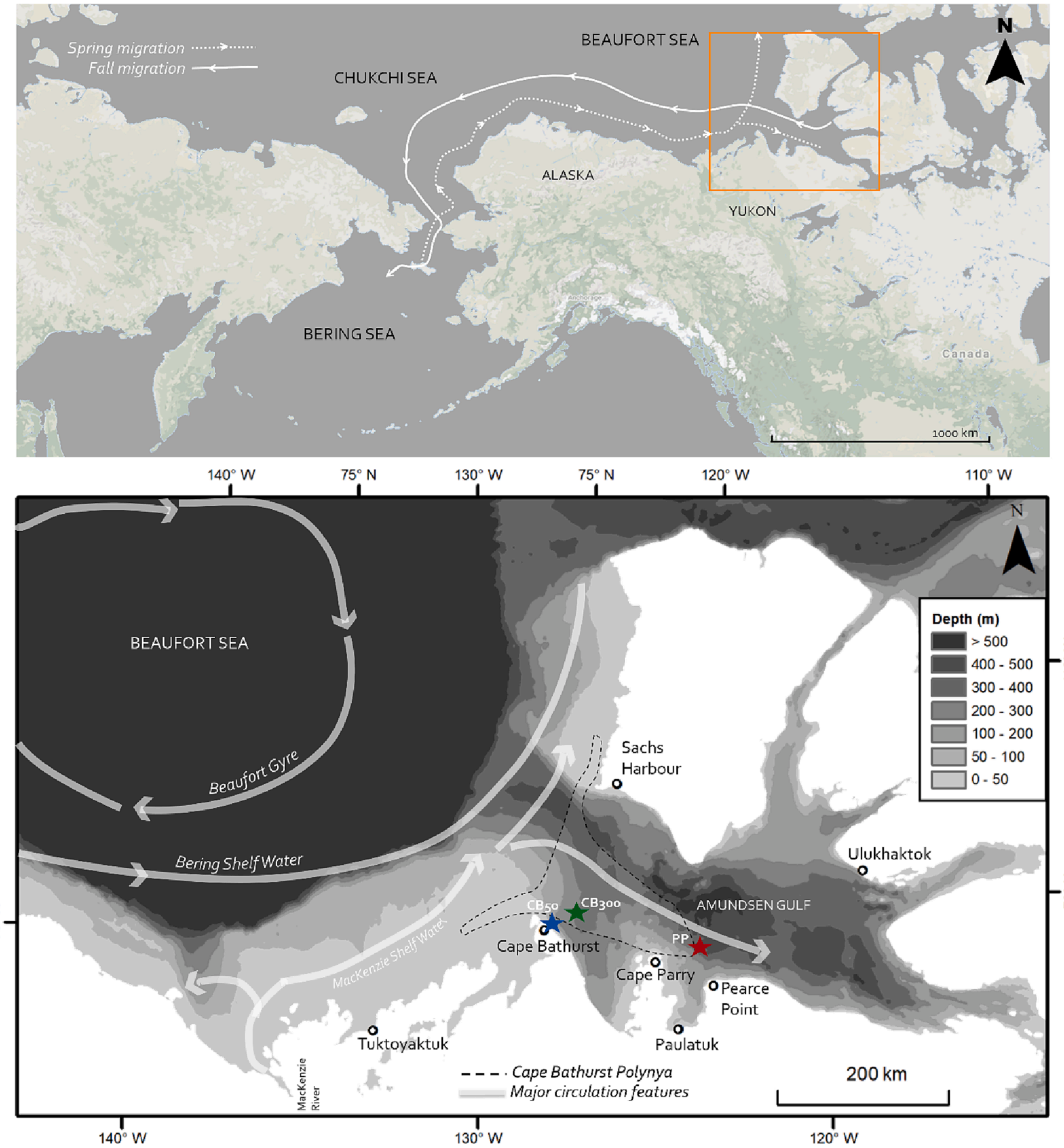

Fig. 1. Top: Map showing typical bowhead migration paths in the western Arctic (solid and dashed white lines). Bottom: Zoomed-in map showing circulation patterns and locations of the study sites (color-coded stars CB50: blue, CB300: green, PP: red) where the acoustic recorders were deployed. Ocean circulation features were adapted and redrawn from a map provided by Tom Weingartner and Seth Danielson, University of Alaska Fairbanks; Corlett & Pickart (2017); and Richerol et al. (2008), and the polynya site from Arrigo & van Dijken (2004).

(Delarue et al., 2009; Wursing and Clark, 1993) and likely serve a function of male acoustic display providing cues of the singer's attributes which are attractive to candidate mates and competitive to rival males (George et al., 1989; Stafford et al., 2018b). The frequency range of bowhead vocalizations directly overlaps with shipping noise (10–1000 Hz) raising conservation concerns for auditory masking from vessel activity (Pine et al., 2018).

The BCB bowhead whales are migratory and are seasonally present in the western Canadian Arctic. BCB whales spend their winters in the Bering Sea, and summers ranging from the Chukchi Sea to the eastern Beaufort Sea and the Amundsen Gulf (Citta et al., 2021) (Fig. 1). They number>16,000 animals (Givens et al., 2016) and the population seems to be healthy and on the increase. Bowheads perform typically a 6,000 km round-trip journey annually (Givens & Heide-Jørgensen, 2021) and use the Canadian Arctic for foraging (Harwood et al., 2017). The migratory phenology of BCB bowheads is largely driven by the seasonality of feeding hotspots throughout their range (Citta et al., 2015). Bowhead whales are filter-feeders, using their large baleen plates to capture zooplankton. Their diet in the southeastern Beaufort Sea consists predominantly of small crustaceans, mostly copepods (76–92%) (e.g., *Limnocalanus macrurus, Calanus hyperboreus* and *C. glacialis*), as well as euphausiids, gammariid and hyperiid, mysids and isopods (Harwood and Borstad, 1985; Sheffield and George, 2021). Zooplankton abundance, density and distribution vary seasonally and correlate with areas of high primary productivity and the timing of phytoplankton blooms (Walkusz et al., 2012). Zooplankton and bowhead occurrence are also associated with areas that are defined by different water masses of distinct temperature and salinity profiles that reflect their origins (Citta et al., 2018; Eisner et al., 2013). Specifically, water from the Pacific Ocean contains the bulk of nutrients and plays an important role supporting the productivity of the Canadian Arctic Ocean (Carmack et al., 1989; Macdonald et al., 1987; Weingartner, 2021), and indirectly affects higher trophic levels via the food web.

The western edge of the Amundsen Gulf (Fig. 1), adjacent to the eastern Beaufort Sea, is recognized as a core area for the summer feeding of bowheads (Citta et al. 2015). The Cape Bathurst polynya, and water-mixing features (upwelling zones) that dominate Cape Bathurst classify this area as a favorable hotspot for feeding bowhead whales in the summer (Citta et al., 2015; Walkusz et al., 2012). Additionally, beluga whales and ringed and bearded seals inhabit the area seasonally. Zooplankton communities here are dominated by copepods, with *Calanus hyperboreus* the most abundant in terms of overall biomass (Darnis et al., 2008; Hop et al., 2011). Even though other parts of the BCB bowhead distribution range (from the Bering Sea to the western Beaufort Sea) have been examined in multiple studies and for multiple years (e.g. Hannay et al., 2013; Tsujii et al., 2021; Ferguson et al., 2021), the southern Amundsen Gulf is understudied in the habitat range of bowhead whales, representing a significant gap in information on their distribution, temporal patterns, and oceanographic drivers. Data on the winter and spring occurrence of bowheads (and other marine mammals) are especially lacking, notably for areas far from shore in the Amundsen Gulf. The earliest information on the distribution of bowheads in the western Canadian Arctic has been derived from the traditional knowledge of subsistence hunters, resulting in a detailed understanding of whale movements and behavior (Huntington et al., 2021a) but constrained to inshore areas close to hunting camps and communities. Methodical monitoring of the temporal and spatial distribution of marine mammals in the Arctic while sea-ice conditions and shipping traffic (routes and intensity) continuously change provides comparative values and should be a priority for conservation managers and policy makers. Marine mammals, positioned at higher trophic levels, make effective bio-indicators of environmental variation at large spatial scales (Moore and Huntington, 2008). Long-term and continuous monitoring allows the detection of shifting patterns in geographic range, seasonality, and migratory behavior that can be interpreted as responses to environmental changes and anthropogenic disruptions.

In this paper, we build on previous passive acoustic monitoring (PAM) studies in the western Canadian Arctic (Halliday et al., 2018, 2019, 2020; Insley et al., 2021) to provide critical information on the ecology of BCB bowheads by investigating their presence at locations and times of year that have been outside the scope of previous surveys. Following the study by Insley et al. (2021) where bowhead whales were detected through the winter of 2019 in the Amundsen Gulf, this work presents results from the analysis of acoustic recordings from that entire year (2018–2019). Specific objectives of this study are to quantify the spatio-temporal patterns in bowhead whale occurrence in the southern Amundsen Gulf and pinpoint the timing of migration into and out of the area by analyzing three one-year-long acoustic datasets from this region. Another major goal is to evaluate how different environmental variables are related to whale presence. This work provides crucial information about the occurrence of a keystone marine species that is a fundamental component of the Arctic trophic system and one of the primary traditional food resources for some Indigenous populations.

2. Materials and methods

2.1. Acoustics

a. Acoustic data collection

Underwater autonomous passive acoustic recorders (SoundTrap ST500, Ocean Instruments) were deployed on bottom-mounted oceanographic moorings at three locations in the southern Amundsen Gulf, including Cape Bathurst at 49 m depth (CB50 site) and 295 m depth (site CB300), and Pearce Point at 351 m depth (site PP) (color-coding throughout figures: CB50 = blue, CB300 = green, and PP = red; Fig. 1, Table 1). Recorders were in place between September 2018 and September 2019 with the goal to detect bowhead whale acoustic signals and to measure underwater sound levels. The recorders sampled at 48 kHz (allowing detection of the entire bowhead vocalization range), with a duty cycle of 5 min of recording every hour and 16-bit depth. The moorings consisted of a heavy anchor, tandem acoustic releases, subsurface floats, and a short vertical line from the releases to the floats where the acoustic recorders were attached, along with other instruments including conductivity-temperature-depth (CTD) loggers and Acoustic Zooplankton Fish Profilers (AZFP) whose measurements are used for subsequent analysis (described below in subsection 4). The water depth at the deployment sites ranged from 49 m (CB50), to 295 m (CB300), and to 351 m (PP), and the recorders were attached to the mooring line 3 to 5.5 m above the bottom (Table 1).

b. Bioacoustic data analysis

Acoustic data were processed using an existing detector/classifier for bowhead calls (Spectro Detector; JASCO Applied Science Ltd, Victoria, British Columbia, Canada) (Moloney et al., 2015; Mouy et al., 2013). The basic acoustic parameters that the detector is programmed to use to classify bowhead calls include: minimum call duration of 0.1 s, frequency band of 40–8000 Hz, minimum call bandwidth of 100 Hz, and minimum intercall interval of 0.2 s. The detector is not set to detect and classify bowhead song, but these are identified manually, as described below. This detector/classifier has been used extensively to detect this species in the Beaufort and Chukchi Seas (e.g., Insley et al., 2021; Halliday et al., 2018, 2019; Hannay et al., 2013), and an evaluation of its performance is presented in the **Appendix**.

All files with automated bowhead detections were analyzed manually by ND through visual and aural inspection of spectrograms in Raven Pro (version 1.6, Cornell Lab of Ornithology) using a fast-Fourier transform size of 3531 points with 90% overlap and a Hann window. Spectrograms (examples in Fig. 2) of each 5-min file were examined over ~ 23 13 s windows at two frequency scales: 0–3 kHz for low-frequency bowhead calls, and 0–24 kHz for the higher-frequency bowhead songs. Time and frequency axes were adjusted by the analysts as needed to include and investigate the signals of interest. During the manual analysis, all bowhead calls identified were annotated, including

Table 1
Information for the three acoustic recorders.

Site ID	Deployment Date	Recovery Date	Latitude	Longitude	Water Depth (m)	Instrument Depth (m)
CB50	07/10/2018	27/09/2019	70.57577	−127.574	49	43.5
CB300	30/09/2018	27/09/2019	70.68122	−126.758	295	289.5
PP	02/10/2018	28/09/2019	70.20092	−123.137	351	348

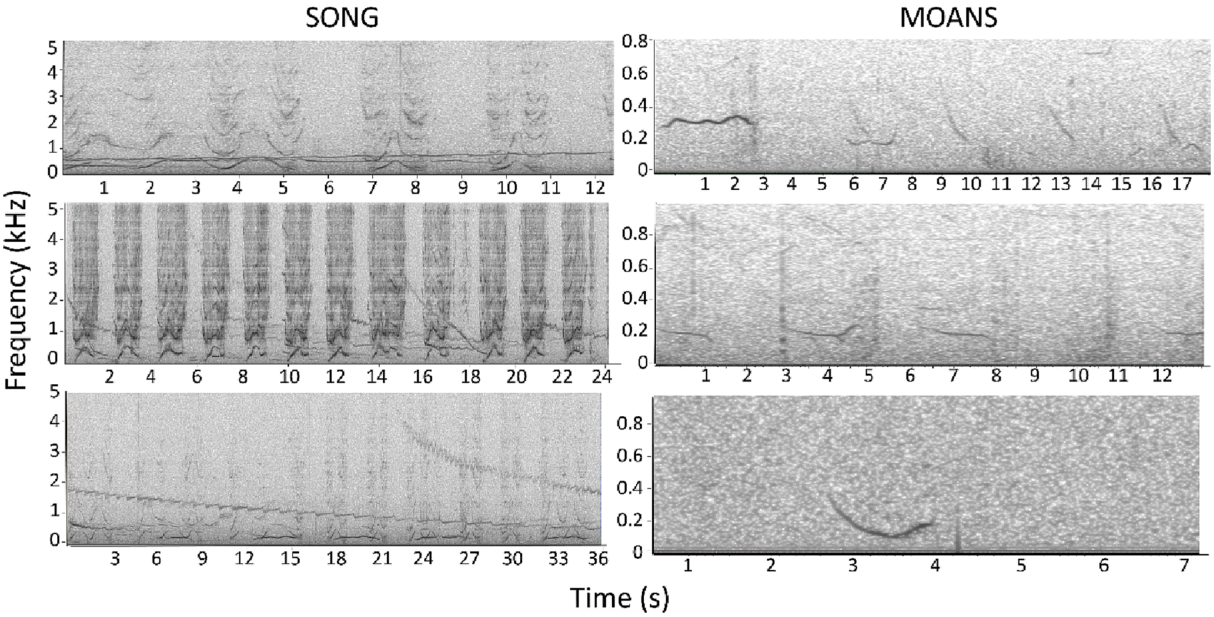

Fig. 2. Spectrogram examples from CB50 of bowhead whale songs on the left, and bowhead whale moans on the right. Note the differences in y and x axis scaling among all spectrograms. Spectrograms on the left include parts of bearded seal calls (trills) interfering with the bowhead songs. Spectrograms on the right also include other ambient sounds that interfere with the bowhead moans.

comments on the type and quality of call, and the confidence of the classification. Bowhead call characteristics were examined to classify the different call types including simple calls (moans) and complex songs. The primary acoustical parameters that were used to determine and classify bowhead calls were the frequency range, and duration of the signal. Specifically, signals considered acceptable for attribution to bowhead whales were of duration between 0.5 and 3 s. Bowhead moans were identified as tonal signals in the 50 to 500 Hz bandwidth (as in Clark and Johnson, 1984). Blackwell et al. (2021) estimated that BCB whale calls have a call repetition rate of 1.3 calls/whale/hour, but this estimate was calculated within their migration corridors, and may not be representative of calling rates in the summer foraging grounds.

Bowhead songs were recognised because they typically have a low-frequency component similar to a moan, but may also include a high-frequency signal between 1 and 3 kHz as part of their biphonated vocalizations (Stafford et al., 2018b; Tervo et al., 2009; Wursing & Clark, 1993). Bowhead songs are easily identified based on their repetitive nature, with series of vocalizations repeated multiple times.

Bowhead moans are of characteristic low frequency and there are no other cetacean species in this region producing similar vocalizations (Clark and Johnson, 1984; Stafford and Clark, 2021), which facilitated the distinction from other whale sound sources. However, bowhead moans can overlap in frequency with ringed seal growls or woofs (Jones et al., 2011; Mizuguchi et al., 2016; Stirling et al., 1987) and their distinction requires careful manual examination of the call characteristics such as inflections and number of pulses. Additionally, ice sounds occasionally overlap in frequency with bowhead calls (especially songs) and can cause misclassifications of the automated detector. During the manual analysis the acoustic context typically allows discrimination of ice signals (which tend to be more continuous) from short bowhead vocalizations and the characteristic song sequences.

The quality of the sound signals and the confidence of the classifications varied from high to medium and low. This was evaluated qualitatively and depended mainly on the relative amplitude of the call and on a visually- and aurally-assessed signal-to-noise ratio (SNR). Using the same methodology, an additional 10% of all files was examined manually and systematically (we selected every tenth file that occurred) to look for any false negatives, test the efficacy of the detector, and examine temporal patterns of all species. To validate the efficiency of the manual analysis (true data), two experienced researchers (ND and WH) reviewed all the recordings that were manually evaluated (including both the files with the automated bowhead detections and the additional 10% of files) and agreed on the reliability of the manual classifications using the criteria and parameters set for call quality and confidence of classification. In total, the manual analysis of the 2018–2019 data included 5,928 5-min sound files between September 2018 and September 2019 from the three recording sites. For CB50, 3,202 sound files were manually analysed (38% of the total number of files recorded); for CB300, 1,564 sound files were analysed (18% of the total); and for PP, 1,162 sound files were analysed (13.5% of the total). At least two to three acoustic samples were manually analyzed per day from each site.

c. Sound levels

Underwater sound levels were quantified with the PAMGuide package in Matlab (Merchant et al., 2015) to evaluate the underwater sound levels to which bowhead whales are exposed. Sound pressure levels (SPL) are calculated in three frequency bandwidths, low: 0.02–1 kHz, medium: 1–10 kHz, and high: 10–24 kHz. SPL was calculated using Hann windows with 50% overlap in 1 s bins, and then averaged across the 5-min file. Daily averages were calculated to produce time series and assess (a) the variability of underwater noise throughout the year at each site, and (b) the relationship between sound levels and environmental conditions (ice concentration and wind speed). Cross-correlation function (CCF) plots between wind speed and underwater SPL were examined for each acoustic site and each of the three frequency bands.

2.2. Temporal patterns

Temporal patterns were examined at two scales: seasonally, where monthly variation was examined; and daily, where hourly variation was examined. These two scales were used to quantify seasonal trends and diel patterns, respectively. These analyses were implemented using the high- and medium-certainty manual detections of bowhead calls at the three sites. We accounted for the different number of sound files analyzed in each day of each deployment by calculating the average number of bowhead calls detected per file per day. All statistical analyses were performed in the R programming language (R Core Team, 2017), and models with the same distribution family were compared using Akaike's information criterion for small samples (AICc) from the MuMIn R package (Barton, 2018).

a. Seasonality

For the assessment of the seasonal pattern in bowhead whale acoustic occurrence, logistic regression models were fit to the binary presence/absence records of bowhead daily detections using a complimentary log-log model (used cloglog R function) and a logit link function. Quasibinomial models were also tested on the binomial data to ensure that the regular binomial model was not over-dispersed. A generalized linear mixed model (GLMM, lme4 R package; Bates et al., 2015) was used for this analysis, with *station*, *month*, and their interaction as fixed effects, and with *week* as a random effect to control for temporal autocorrelation between the daily presence/absence values. Models with different distribution families were tested for goodness-of-fit with a chi-square test based on the residual deviance and degrees of freedom.

b. Dates of arrival and departure

We calculated and plotted the cumulative distribution of days with bowhead calls to determine the arrival and departure dates of BCB bowheads at the three sites in the southern Amundsen Gulf. Three alternative ways were tested for determining these dates to test the effectiveness of each measure. This included indicating the 5% and 10% (for arrival date) and 95% (for departure date) quantiles of the bowhead cumulative distribution for days with whale detections, as shown in Hauser et al. (2017) and Stafford et al. (2021), and also by visually selecting the inflection points of the cumulative distribution plot (**Fig. A1 in the supplementary material**). These points were chosen based on the rate of increase: when it started to constantly increase for the arrival date, and when it stopped increasing for the departure date. Then, the sea-ice concentration at two scales (6 km^2 and 100 km^2) was determined for these dates to examine the ice conditions during these pivotal migration times.

c. Diel patterns

For the evaluation of diel patterns in bowhead vocal activity, we converted the dates into local time (UTC–7), and binned the bowhead call counts into each hour of the day. Gaussian, Poisson, and negative binomial general linear models (GLMs) were compared for the best fit to the data. A GLM with a negative binomial distribution (computed with the function glm.nb from the R package MASS; Venables & Ripley, 2002) was used to examine the count of bowhead calls. Models were fit with *hour*, *month* or *season* (fall: September–November, winter: December–February, spring: March–May, summer: June–August), and *station* as explanatory variables for the quantification of diel trends. The inclusion of an interaction term between *month* and *hour* was also tested in the models to account for the change of daylight throughout the year. We built four types of models: a full model that included data from all three stations, and three separate models, one for each station. Null deviance was used to compare models from different distribution families. Post-hoc pairwise Tukey's test (glht function in the R package multcomp) helped identify significant differences between *hours* and *months*. Autocorrelation function (ACF) and partial autocorrelation function (PACF) plots of the final models' residuals were inspected to determine any temporal correlation structure.

2.3 Habitat modeling

We conducted statistical modeling analyses to investigate the relationship between bowhead whales and their environment. Considering that the bowhead habitat choice is based on the availability and abundance of their prey, especially at their foraging grounds, the variables tested for this relationship are (a) direct measurements of zooplankton biomass, and (b) physical mechanisms and parameters which drive and aggregate zooplankton or primary production that attract bowhead whales and their prey.

The bowhead life cycle depends on sea-ice melting and freeze-up. Lower ice concentration translates to the creation of leads and open water that allow whales to breath. Ecologically, ice strongly affects the penetration of sunlight into the water column as well as the underlying circulation, water mixing and primary production. Wind vectors, similarly have a significant impact on the marine ecosystem by driving currents, drifting ice, producing upwelling that carry nutrients and planktonic prey into bowhead habitat creating efficient foraging opportunities. Temperature and salinity are primary descriptors of the sea water that indicate the origin of water masses (Pacific/Atlantic water, river outflows) and strength of stratification, and also drive and are driven by physical and biological shifts in the ecosystem. Heat accelerates the ice melt and enhances primary productivity in the Arctic, while gradients in temperature and salinity force water circulation (eddies, upwelling, currents) that transfer organisms across the water column. Temperature can catalyze or depress growth in different organisms; thus, both temperature and salinity are closely connected to biological production and bowhead prey aggregation.

Multivariate logistic GLMMs with the bowhead daily presence as response variable and a suite of *in situ* oceanographic variables (recorded by other instruments on the same mooring) and remotely-sensed environmental variables were tested to examine which environmental features may be related to bowhead occurrence during 2018–2019 in the Amundsen Gulf. All variables were collected/extracted for the same period and location as the acoustic sampling and each were averaged per day to match the bowhead occurrence records and to match the different temporal scales of the various datasets.

2.3.1 In situ measurements

The moorings with acoustic recorders also included CTD loggers (Sea-Bird 16plus at CB50, MicroCAT 37SM at CB300 and PP; Sea-Bird Scientific, Bellevue, Washington, USA) deployed on the mooring line above the acoustic recorders (40.5 m at CB50, 287 m at CB300, 345 m at PP). Temperature, salinity and pressure were measured every 15 min at each site. An upward-facing AZFP (ASL Environmental Sciences, Saanichton, BC, Canada) was also deployed at CB50 and PP (AZFP data were not available for CB300 for this analysis). AZFP data (38, 125, 200 and 455 kHz) were acquired at a rate of 1 ping every 5 s (at CB50) and 1 ping every 15 s (PP), and the AZFP data were averaged internally with 25 and 44 cm vertical resolutions, respectively. AZFP measurements allow broad classification of marine mammal prey (zooplankton and fish) and help determine prey presence, vertical distribution, and abundance estimates throughout the year, including the under-ice period. Target abundance estimates were represented by nautical area scattering coefficient (NASC) values, which represent the mean backscattering volume, calculated for each cell and integrated over the entire water column for each 5-min time period. The 455 and 200 kHz data represent small-sized zooplankton, the 125 kHz data represent meso- and micro-zooplankton and small fish, and the 38 kHz data represents pelagic fish which are primarily Arctic cod in the study area (Geoffroy et al., 2011, 2016). During 2018–2019, NASC data from the 125, 200, and 455 kHz transducers were available for CB50, and from the 38, 125, and 455 kHz transducers for PP.

2.3.2 Remotely sensed data

Daily ice concentration data from the Advanced Microwave Scanning Radiometer 2 (AMSR2) sensor onboard the GCOM-W satellite (Spreen et al., 2008) were extracted into two spatial scales: (1) pixel values (6.25 km width) for sea-ice concentration directly over each recorder for each deployment day, which provides the finest resolution daily sea-ice concentrations; and (2) the average of all pixels within a 100 km radius centered over each recorder, which provides a larger scale likely representing the detection range of bowhead calls. All of the process of extracting and averaging the ice concentration data to a daily scale and across all grid cells was performed in ArcMap (version 10.8, Esri, Redlands, California, USA).

Wind data were downloaded from Environment Canada's Historic Climate Database (https://www.canada.ca/en/services/environment/weather/data-research.html) for the Cape Parry climate station, which is the closest station to the mooring sites (~60 km west of PP, and 100 km and 120 km east of CB300 and CB50, respectively). Wind speed and wind direction measurements were downloaded in hourly scale and daily means were calculated and matched with the results of the manual detection analysis. For calculating the daily mean of wind direction, the circular R function (Tsagris et al., 2022) was used. In order to assess how representative the wind measurements were for each acoustic site, we examined CCF plots between wind speed and underwater sound level measurements at each acoustic site and for each of the three frequency bands. Wind direction measurements were transformed into a categorical variable where the numeric value (in degrees) was binned into eight principal wind directions (N, NE, E, SE, S, SW, W, NW). For the assessment of the dominant wind speed and direction, and their variability through the year in relation to the sea-ice state, we used the openair R package (Carslaw, 2022) and the pollutionRose and calendarPlot functions. All names and variables used are described in Table 2.

Table 2
Response and explanatory variables used for the habitat modeling analysis, with their corresponding names used in the text.

Class	Measured	Description of variables	Name
Response		Presence/absence of bowhead acoustic detections in each day	Detection
Explanatory	***In-situ***	Salinity measured with CTD at a fixed depth for each site	Salinity
		Temperature measured with CTD at a fixed depth for each site	Temperature
		NASC values at 125 kHz	z125
		NASC values at 200 kHz	z200
		NASC values at 455 kHz	z455
	Remotely sensed	Mean daily Ice concentration in 100 km radius	Ice100
		Mean daily Ice concentration at the pixel right at the station	Ice6
		Mean daily wind speed measured at Cape Parry weather station	Wind speed
		Mean daily wind direction measured at Cape Parry weather station	Wind direction
		Sea-ice coverage	Ice Season
Model Types		Model that includes CB50, PP data and the AZFP measurements	AZFP STATIONS
		Model that includes CB300, PP data and the CTD measurements	DEEP STATIONS
		Model that includes CB50 data and both CTD and AZFP measurements	SHALLOW STATION
		Model that includes CB300, CB50, PP data and only wind and ice variables	ALL STATIONS

2.4 Data analysis - model selection

The ice concentration at 100 km resolution (Ice100) variable was used to define an additional categorical variable of sea-ice coverage category (Ice Season). We used the dates for each station when there was<20% and>70% ice concentration to define the ice-free and ice-covered seasons (as performed in Woodgate and Peralta-Ferriz, 2021; Andrews et al., 2018), respectively, and the dates between these concentrations were used as the transitional periods (shoulders) between ice-covered and ice-free seasons. Ice season was tested in models as an interaction with each fixed term (for all explanatory variables except ice concentration) in the global model (including all the variables to be tested for relationships) as a way to account for and quantify seasonal effects in the data. The same models were also tested with the ice-free periods defined to be below 15% ice concentration, but no significant differences occurred and 20% was chosen.

Assessing multicollinearity (Zuur et al., 2009) included using the variance inflation factor (VIF). We applied the vif R function (Faraway, 2016) to all the explanatory variables and if the VIF value was>4 the variables were alternately removed in order to reduce multicollinearity and VIF scores (Zuur et al., 2010). Scatterplot matrices and univariate models were also used to identify high collinearity in pairs of predictors and evaluate the level of correlation with the response variable. The predictors that correlated least with bowhead whale occurrence were removed before fitting the models or were not included in the same model with their collinear pair.

ACF and PACF plots of the global model's residuals were used to determine any temporal correlation structure. GLMMs allowed us to account for temporal autocorrelation structure in the data by including *month/week* as a random effect. *Station* was also included as a random effect to account for the variability among the different sites when data from more that one station were included in the models. Models were examined with different random structures, with nested effects (*week, month/week,* or *season/month/week*) and/or crossed effects (*week* + *station, month/week* + *station*, or *season/month/week* + *station*), and compared with the anova function from the stats R package.

The multi-model inference MuMIn R package (Barton, 2018) was used for model selection. As a first step we built a global model, then the dredge function was used to build all possible model combinations based on all the variables included in the global model. Finally, the best model was chosen as the most parsimonious (fewest parameters) among the candidate models. The goodness-of-fit for the estimation of the variance explained by the best and candidate models was assessed with the function r.squaredGLMM (Barton, 2018). The best-ranked models within an AICc difference of 2 (ΔAICc $\leq$ 2) were selected as candidate models, as a means to incorporate model selection uncertainty (Burnham et al., 2011). For diagnostic purposes, the R package car (Fox et al., 2011) was used. Quantile-quantile (Q-Q) plots, residuals versus fitted values, ACF and PACF plots of the final models' residuals were explored for heterogeneity, over-dispersion, and temporal correlation.

The above modeling process was repeated four times, depending on the set of *in-situ* predictors considered and the stations included in each analysis (Table 2): (1) AZFP variables and data from CB50 and PP, producing the *AZFP model* (AZFP STATIONS); (2) CTD data from stations at similar depths including CB300 and PP, producing the *Deep model* (DEEP STATIONS); (3) both AZFP and CTD data from CB50, producing the *Shallow model* (SHALLOW STATION); and (4) data from all three stations with only the remotely-sensed variables (ALL STATIONS). CTD measurements could only be compared between sites of similar depths since the shallow site had conductivity and temperature data with high variability (measured at 40 m) and over a much larger range than data from deep sites (measured at ~ 300 m), thus the model that included CTD variables was based on the CB300 and PP data. AZFP measurements were not available for CB300 and a model that included the NASC values could only be fit for the CB50 and PP data. Consequently, a model that allowed using whale detections from all three stations could only involve remotely-sensed environmental variables. An additional reason for fitting four types of models was to compare the predictive ability of the different data sources and to guide future sampling strategies. For comparison, the same modeling process was repeated using two ice seasons (instead of three), with a threshold set at 50% sea-ice concentration to define the ice-free (<50%) and the ice-covered (≥50%) seasons. The resulting models were compared with their equivalent three-ice-seasons models using AICc and R^2.

SPLs were evaluated as a function of wind speed and station, accounting for changes among the three ice coverage periods (Ice Season: ice free, ice covered, ice shoulder). For that purpose, a GLM with a Gaussian distribution was fit between the daily averages of SPL, pooled from all stations and bandwidths, as response variable, and station with the interaction of wind speed and Ice Season as explanatory variables.

3. Results

3.1. Bioacoustic analysis

Based on the acoustic sampling and analysis described here, quantification of the number of individuals detected was not possible. Any reference to detection rates, call density or call count does not refer to counts of individual whales, but rather to the number of bowhead calls detected.

Manual detections were partly driven by the automated detections in that all automated detections were evaluated manually and used in the analysis. Results from the manual analysis included also the detections from the separate 10% analysis of all files that were considered independently from the automated detections. In the end, the detections used for the analysis are those derived from all manual inspections of acoustic files, which are, however, partly dependent on the initial automated detections (Table 3).

Bowhead whales were detected acoustically at all sites and in all months throughout the one-year sampling period, except for November 2018 at CB50 and CB300 (Table 3, Fig. 3). For the months with bowhead detections in the period from September 2018 until March 2019, the number of days with bowhead calls per month varied from: 1 (December) to 22 (March) at CB50, and 2 (September) to 5 (January) at both CB300 and PP (Fig. 3). Occurrences relative to ice concentration show that at CB50, bowhead whale calls are detected just prior to sea-ice formation (shoulder season noted with grey shading in Fig. 3). Then, in November, no bowhead calls are detected when ice concentration reaches > 70%. Then monthly number of days of bowhead acoustic presence increase each month from December through March. Bowhead whale calls are present during 1/3rd of days in March. At CB300 and PP, bowhead calls are also detected during these ice-covered months.

Most of the bowhead signals were moans; in addition, many complex calls were identified throughout the sampling period. Complex biphonated songs were recorded in early spring and early fall but were recorded most often in April at all sites. Specifically, at CB50, singing was recorded in 100 sound files between 7 March to 7 May 2019 (note that we systematically analyzed 10% (~144 files) of all files during that period) and throughout September (2 to 27 September 2019). Similarly, at CB300, bowhead song occurred in 18 sound files from 11 April to 7 May 2019 and from 7 to 25 September 2019, which is slightly later than at CB50. At PP, song was recorded in 48 sound files from 15 April to 8 June 2019.

Table 3
Summary of the results from the bioacoustic analysis at the three sites for the entire deployment period (all calls were annotated in each file).

	Numbers	**Bowhead whale**		
		CB50	*CB300*	*PP*
Manual analysis	Detections	24,388	11,101	3863
	Files	1919	946	461
	Days	214	173	126
Automated analysis	Detections	5879	1432	436
	Files	2581	762	308
	Days	266	150	98

3.2. Temporal patterns

3.2.1. Seasonality – Daily presence

The seasonality analysis was carried out to quantify any seasonal patterns in the occurrence of bowheads in the Amundsen Gulf. A GLMM binomial model with the presence of bowhead calls per day as response variable and with week and the interaction between the recording *station* and *month* of the year as fixed effects was chosen as the best model. The model (Fig. 4) indicated that at all stations there was higher likelihood to detect bowhead acoustic presence in spring and summer months (April to August), compared to the fall and winter (October to February) ($p < 0.05$ for all comparisons). At both CB sites, significantly higher detections occurred between April and September compared to winter and fall months, with significantly lower likelihood to detect bowheads in October compared to the previous months (April to September). However, at CB50 in February the likelihood of whale presence was higher compared to November and December. At PP, higher bowhead presence occurred between April and August with June and July showing significantly more days with bowhead detections than the rest of the year, including August. At CB50, March showed significantly increased whale presence compared to the previous winter months and compared to the other two stations. Overall, at CB50 there was higher likelihood for bowhead presence throughout the year, compared to CB300 and PP, except November to December at PP when there was higher likelihood of detecting whales. At PP there was lower likelihood for bowhead presence in summer (April to September) compared to both CB sites.

3.2.2 Dates of arrival and departure

The fact that bowheads overwintered at the study site during the deployment period allowed the assessment of arrival date to be more effective using inflection points in the bowhead cumulative distribution plot rather than the use of 5% or 10% quantiles (Table 4, **Fig. A1**). However, the 10% quantile almost coincided with the inflection point for the Cape Bathurst sites. For the departure date from PP the inflection point corresponded to the 95% quantile. Bowheads in 2019 first migrated to CB50 in early spring (March 2), then reached CB300 about a month later (March 31), and PP two weeks after that (April 14) (Table 4, **Fig. A1**). The timing of their departure from the area could only be determined for PP (August 8) since it was the earliest compared to the other sites and our recordings ended before the animals began their fall migration from Cape Bathurst in 2019. All sites were covered with ice (ice concentration > 83%) when the whales migrated to the area, and PP was still ice-free (ice concentration = 0%) when the bowheads started to depart for their fall migration.

3.2.3 Diel patterns – Hourly call count

The variability of bowhead call counts based on the hour of the day for every station and for the months when most bowheads were present (April to September) shows some diel variability between and within the three stations, but no strong consistent patterns are evident.

Full model. A negative binomial GLM with response variable taken to be the counts of bowhead calls per hour per day for the entire year, and explanatory variables *station* and *hour* of the day, was chosen as the best full model. This model indicated that fewer calls were recorded at PP compared to both CB sites ($p < 0.001$). Also, the number of bowhead calls was significantly higher overall from April to September ($p < 0.001$), and in the evening hours, specifically at 17:00 and 21:00 ($p < 0.01$), and 23:00 ($p < 0.05$).

Single station models. Three negative binomial GLMs with the same response and explanatory variables as above (except station) were

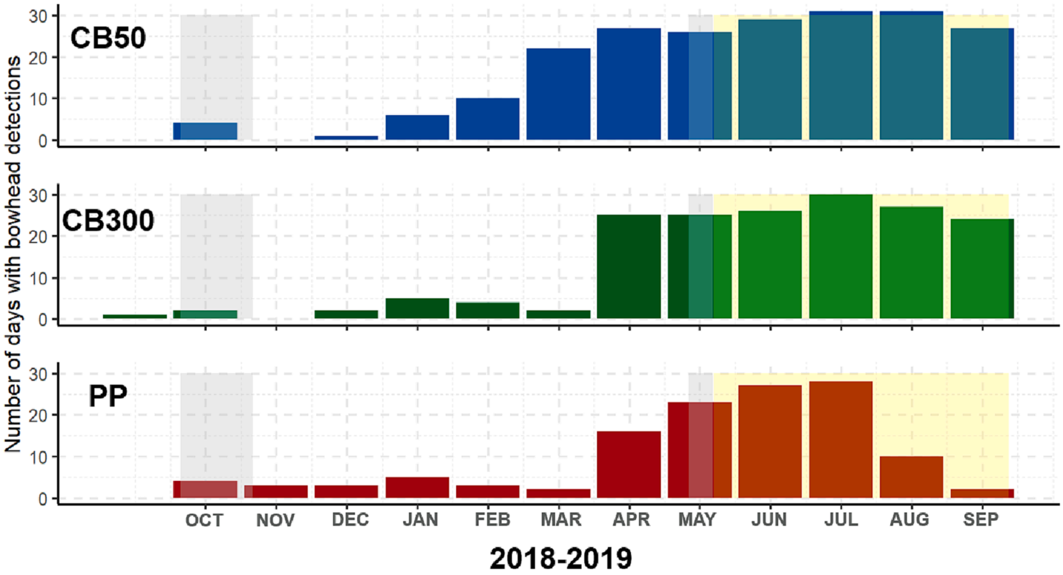

Fig. 3. Number of days with acoustic detections per month for bowhead whales for the CB50 (blue), CB300 (green), and PP (red) sites. The yellow shaded area represents the period at each station when ice concentration is below 20% ("ice-free"), and the grey shaded areas when ice concentration is between 20% and 70% ("ice-shoulder").

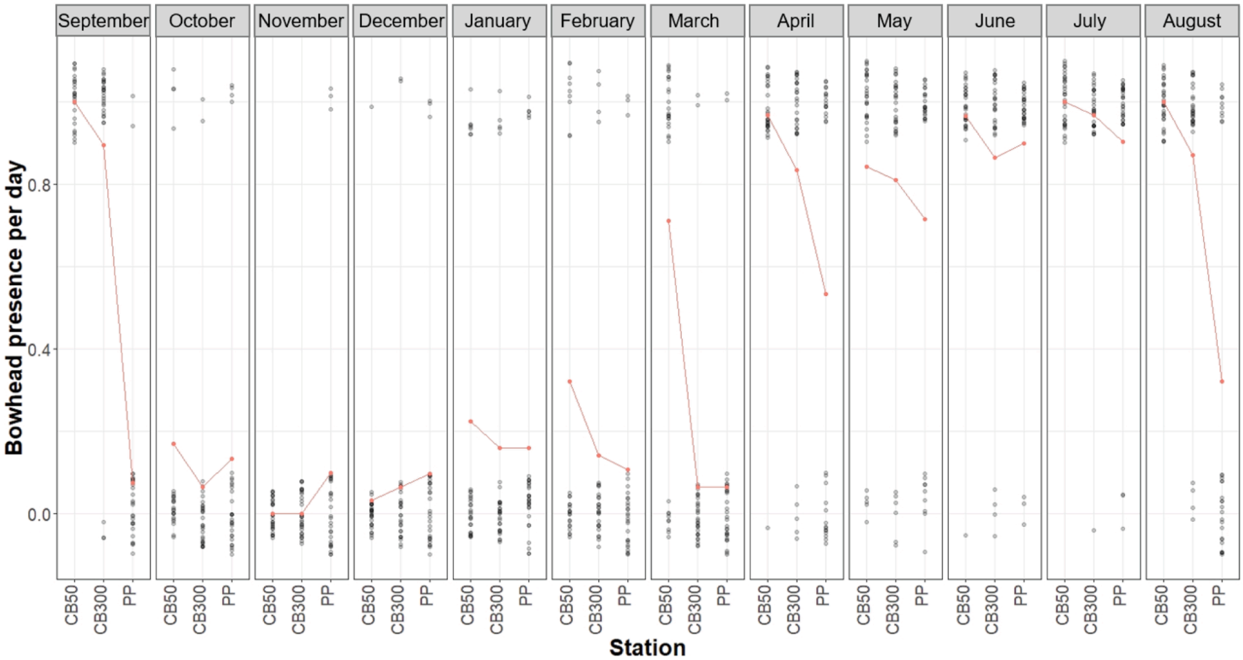

Fig. 4. Seasonal patterns of the year-round bowhead acoustic presence in the Amundsen Gulf. The red line represents the fitted values of the seasonal model of the bowhead whale call detections in a day at three sites (CB50, CB300, PP). Each panel includes values (red line) that represent the GLMER logistic regression model predicted results per month and for each station. Bowheads are present in the area all months of the year. A clear seasonal pattern indicates bowhead presence at all sites from April until September, whereas there are few days with whale detections in fall and winter. The gray points are the raw data with an added jitter (−0.1, 0.1) that allow them to be all seen. The degree of jitter added was 0.1 points both directions for y axis at the highest density.

chosen as the best models for each individual station. ACF plots indicated little evidence for non-zero autocorrelations. At all sites, from April to September there were significantly more bowhead calls compared to the rest of the year ($p < 0.001$), except for PP where more calls were detected in October than September. At CB50, the models showed no significant diel variability observed throughout the year. At CB300, there was significantly higher probability to record more bowhead calls at 17:00 compared to the rest of the day ($p < 0.05$). At PP, there were significantly more bowhead calls detected at 05:00 ($p < 0.05$) and at 17:00 and 21:00 ($p < 0.01$). These diel patterns were not consistent across all months. The pairwise Tukey's tests within each month and station showed significant differences in the numbers of bowhead calls per hour for August at CB300 and for May-August at PP. Heatmaps (Fig. 5) illustrate the number of bowhead detections per hour for these months at these two stations. At CB300, a significantly higher numbers of bowhead calls were found in August at 10:00. At PP, significantly more calls were detected in May at 05:00 and 21:00, in June at 09:00, and in August at 12:00. However, these diel differences

Table 4
Three metrics of migration timing (arrival and departure) of bowhead whales at each recording site during the 2018–2019 study and associated ice concentrations on those dates. The date of migration in the area is calculated three ways: by indicating the 5th and 10th percentile of the bowhead cumulative distribution of days with whale presence, and by visually selecting the inflection points at the cumulative distribution plot (**Fig. A1**). PCTL represents the precise quantile value. The date of departure from the sites is represented by the 95th percentile and the visual determination of the inflection point. Ice concentration is calculated in two scales (6 km pixel and 100 km radius).

	CB50				CB300				PP			
	PCTL	*Date*	*Ice6*	*Ice100*	*PSTL*	*Date*	*Ice6*	*Ice100*	*PCTL*	*Date*	*Ice6*	*Ice100*
Inflection Arrival	0.103	02/03/2019	83	90.5	0.077	31/03/2019	96	91.4	0.185	14/04/2019	83	90.5
5th percentile	0.051	30/01/2019	92	93.4	0.053	19/02/2019	99	90.9	0.056	03/12/2018	91	85.9
10th percentile	0.1	02/03/2019	83	90.5	0.1	05/04/2019	96	94	0.1	02/12/2018	100	99.5
Inflection Departure	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.959	08/08/2019	0	2.3
95th percentile	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0.951	07/08/2019	0	1.3

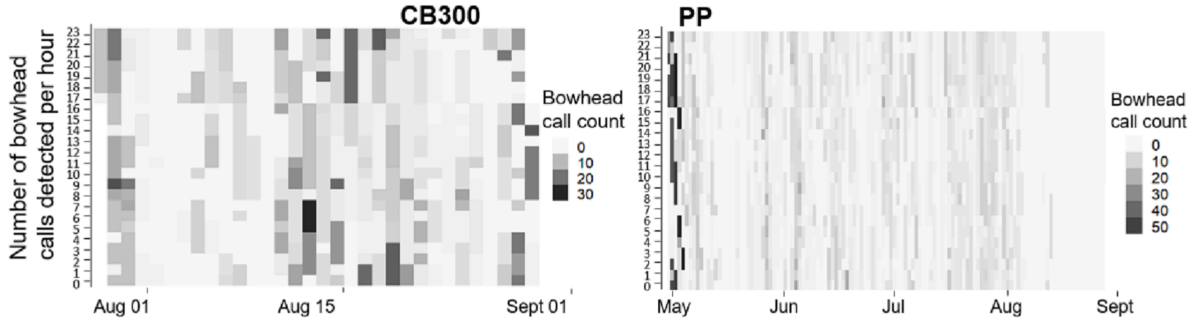

Fig. 5. Heatmaps showing the number of bowhead calls per day for the months and stations that the Tukey's test (see the box plots and the Tukey's test results for all months and stations in the Appendix A) indicate significant differences in diel variability, and indicate that certain days in specific months were driving the diel patterns at PP (and, to a lesser degree, CB300).

show large variation and do not allow us to conclude any consistent diel patterns in bowhead acoustic activity in the wider area, at each site or in each month.

3.3. Habitat modeling

In the study area there was strong variability in wind speed and direction throughout the 2018–2019 study period (**Fig. A4-A6**). However, the easterly winds were prevalent year-round and strengthened during the shoulder seasons (**Fig. A7**) causing ice to break-up at all sites in November, and at CB50 also in April (**Fig. A4-A7**). Northerly and westerly winds intensified during the ice-free season, and southerly winds during the ice covered season (**Fig. A7**). The dominant feature is the presence of sea ice which covers the area in winter (November to April), fractures and opens up in mid-May, and freezes-up in late October. At PP, less sea-ice coverage was observed in October and early November compared to the Cape Bathurst sites.

The statistical modeling was performed to determine the environmental variables associated with the bowhead daily acoustic detections. For all four categories of the habitat models, multicollinearity (VIF > 4) was identified between the two ice variables (Ice100 and Ice6; $r = 0.88$, $p < 0.001$) (**Fig. A3**). Based on the AICc, comparison of the two univariate binomial GLMs that included each of the ice variables and the response, Ice100 was chosen as a more influential variable to bowhead occurrence; thus, Ice6 was omitted from all global models and the analysis. For the SHALLOW model, where all in-situ and remotely sensed variables were considered, salinity with temperature ($|r| = 0.72$, $p < 0.001$), and z200 with z125 ($r = 0.89$, $p < 0.001$), were identified as collinear (VIF > 4). Each of the variables in the collinear pairs was examined in separate models to avoid multicollinearity.

AZFP model. From the four top candidate models (**Table A1**) that included data from CB50 and PP, the most parsimonious contained five explanatory variables and one interaction (Table 5). The variables that showed a significant relationship with bowhead year-round occurrence at the two sites were Ice Season, z125, and the interaction between Wind speed and Ice season. The modeling results showed that the acoustic occurrence of bowheads at CB50 and PP increased during the ice-free period (odds ratio, OR $= 32.87$, $p < 0.01$), and with increasing z125 (OR $= 1.02$, $p < 0.001$). The interaction between Wind speed and Ice season (OR $= 0.93$, $p < 0.01$) indicated a negative relationship with bowhead daily detections during the ice free period in all candidate models (OR $= 0.93$–0.94, $p < 0.05$) (**Table A1**), while the relationship was positive during the ice covered and shoulder seasons. Wind speed alone was not significant (OR $= 0.98$–0.99, $p > 0.05$) in any of the candidate models but indicated a negative effect on whale daily detections. No effect or significant relationship was shown with the z455 (OR $= 1$, $p > 0.05$). All five competing models agreed on the significant predictors and their relationship to bowhead occurrence.

DEEP model. The significant variables in all four competing top models that included data from the deep stations (CB300 and PP) maintained their effect and significance in all models that included them (**Table A2**). The most parsimonious model included two explanatory variables (ice season, temperature) and two interactions with ice season (with wind speed, and temperature). According to this model, at CB300 and PP, the probability of bowheads being acoustically present in a day was higher when temperature (measured at ~ 300 m depth) was higher, during the ice free period (OR $= 8.3 \times 10^8$, $p < 0.001$). This correlation was the strongest among the chosen models, and showed that in the absence of ice, temperature has a strong positive effect on bowhead presence. Conversely, during the ice covered and shoulder seasons the effect of temperature on whale occurrence was negative. Temperature alone had a significant negative relationship with the bowhead daily detections (OR $= 0.01$, $p < 0.05$). Additionally, the probability of detecting whales in a day was lower when wind speed increased during the ice free period (OR $= 0.93$, $p < 0.001$) with the effect remaining negative during the ice covered and shoulder season, even though it was of lower magnitude (Fig. 6). Wind speed alone did not have a statistically significant relationship with bowhead presence (OR $= 0.99$, $p < 0.05$).

SHALLOW model. The most parsimonious model of the six top

Table 5
Top parsimonious models within 2 AICc values from their competing models in each of the four model categories (all competing models are shown in Tables 1-4 in the Appendix A). Effect size of the fixed effects are displayed as odds ratios. Ice Season is a categorical term: ice free = ice free, ice cov = ice covered, ice sh =ice shoulder. The significant variables are in bold and the significance, as dictated by the p-value levels, is represented by these codes: *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

YEAR-ROUND MODELS	AZFP	DEEP	SHALLOW	ALL
(Intercept)	0.31	2.51	0.13	0.89
Ice season [ice free]	**32.87****	**0.02***	**1.77E+91****	**8.93***
Ice season [ice sh]	1.67	0.92	0	1.62
Salinity			1.06	
Temperature		**0.01***		
Wind speed	0.99	0.99		0.98
z125	**1.02*****			
z455			0.99	
Salinity * Ice Season [ice free]			**0****	
Salinity * Ice season [ice sh]			24.35	
Ice season [ice free] * Temperature		**8.3 × 10^8*****		
Ice season [ice sh] * Temperature		5.62		
Ice season [ice free] * Wind speed	**0.93****	**0.93*****		**0.94*****
Ice season [ice sh] * Wind speed	1.05	1.01		1.02
Random Effects				
σ^2	3.29	3.29	3.29	3.29
τ_{00} week:month	0.4	0.26	0.1	0.16
τ_{00} month	4.83	2.54	6.14	5.01
τ_{00} station	1.94	0.1		1.1
ICC	0.69	0.47	0.65	0.66
N station	2	2		3
N week	53	53	52	53
N month	12	12	12	12
Observations	701	706	348	1054
Marginal R^2 / Conditional R^2	*0.101 / 0.717*	*0.214 / 0.582*	*0.784 / 0.925*	*0.053 / 0.674*
AICc	578.175	578.535	219.419	828.875

competing models (**Table A3**) that examined all environmental variables and bowhead data from CB50 included four explanatory variables (Table 5). This model suggests that the ice season is most important for explaining the presence of bowhead vocalizations at CB50 throughout the year (OR = 1.77E + 91, $p < 0.01$), such that whale occurrence increased during the ice free period (Fig. 6). At five out of the six competing models, bowhead presence was significantly more likely during the ice free period, indicating a strong relationship between whales and sea-ice state. Z455 and salinity during the ice free period were negatively correlated with bowhead acoustic occurrence at CB50, and these variables were significant in most of the competing models (**Table A3**). Salinity during the ice free period (OR = 0, $p < 0.01$) had the largest negative effect on the variability of whale occurrence at CB50. Conversely, salinity during the ice shoulder had a positive effect on the bowhead occurrence (Fig. 6).

ALL STATIONS model. Out of five top competing models, the most parsimonious that included data from all three sites contained three predictor variables (**Table A4**). The chosen model included two significant relationships indicating that: (1) as wind speed increased during the ice free period, bowhead daily presence decreased (OR = 0.94, $p < 0.001$), and (2) bowhead presence was significantly more likely during the ice free period (OR = 8.93, $p < 0.01$) (Table 5, Fig. 6). The rest of the competing models also contained a significantly negative correlation with wind speed alone (OR = 0.97$p < 0.05$). Even though wind direction was present in two of the competing models, any relationships with the bowhead daily detections were not significant (**Table A4**).

The AZFP, DEEP, and ALL STATIONS models showed low marginal R^2 values (0.10, 0.21, 0.05, respectively), indicating that the models' fixed effects explained little variation. These models had much larger conditional R^2 values (0.72, 0.58, 0.68 respectively) (Table 5), suggesting that other factors captured in the random effects explained a greater proportion of the variation. A conditional R^2 that approaches one is an indication that most of that unexplained variation is between stations rather than between observations within stations. The SHALLOW model that considered all environmental variables and included data from only one station had $R^2 = 0.78$ (conditional $R^2 = 0.92$), explaining a very large amount of variability in the data. Overall, the use of a categorical Ice season variable with three levels (accounting for the ice shoulder period) instead of two (ice covered and ice free) improved to a great extend the performance of all four types of models and increased their variance explained (marginal R^2: AZFP – 0.083, DEEP – 0.076, ALL – 0.034, SHALLOW – 0.35; conditional R^2: AZFP – 0.69, DEEP – 0.65, ALL – 0.68, SHALLOW – 0.78).

Models that included only the spring-summer data were also examined but gave very similar results to the year-round models when considering the ice-free period results.

3.4. *Sound levels*

The measurement of underwater sound levels was implemented to consider any interferences of noise on the detectability of the whales. Seasonal variability of sound levels was observed at all sites (Fig. 7, Table 6). A GLM showed that about 30% of the sound level variability at all stations and frequencies was driven by wind speed with the two variables showing a linear positive relationship (Table 6). The significant increase of sound levels in all cases in the summer coincided with the absence of ice that exposes the underwater soundscape to the influence of processes at the air-ocean interface (e.g. waves). Thus, the effect of wind speed to the increase of underwater sound levels is more prominent during the ice free period (Table 6). Sound levels at CB50 were substantially higher compared to CB300 and PP, mainly due to strumming noise produced by the mooring but also linked to the shallow depth of the site. No files that were polluted by strumming noise were removed from the sound levels analysis, since strumming sound can be a legitimate concern when trying to detect bowhead vocalizations, and the point of the analysis was to assess the influence of sound levels on the detection of bowhead vocalizations.

The CCF plots of wind speed measurements from the Cape Parry weather station and the SPLs measured at each site revealed a strong correlation, especially at higher frequencies (Fig. 7). Specifically, at CB50 and CB300, the highest correlation was 53% at the 10–24 kHz bandwidth (–1 and –3 h lag, respectively). SPLs at PP were 58% correlated (1 h lag) at the 1–10 kHz frequency band with the wind speed measurements. The positive or negative lags are most likely related to the position of each acoustic site compared to the Cape Parry climate station. The use of the smoothed variables for the visual examination of the seasonal variability and the relationship between wind speed, sea-ice coverage and SPLs indicate that as sea ice disappears in May, the SPLs at all three frequency bands respond with an abrupt increase (Fig. 7). This effect appeared to be stronger at the medium frequency band (1–10 kHz).

4. Discussion

The analysis of three year-long acoustic datasets from the southern Amundsen Gulf provides important insights into the spatial and temporal variability of the bowhead occurrence in the western Canadian Arctic. The endemic bowhead whales were detected at all three stations for most months of the year, confirming the ecological importance of the southern Amundsen Gulf. Most importantly, all three study sites represent prime habitat for bowheads during the summer, and were chosen by some individuals during the entire year. Systematic manual bioacoustic analysis of a sample of the recordings (13.5% to 38% of the acoustic

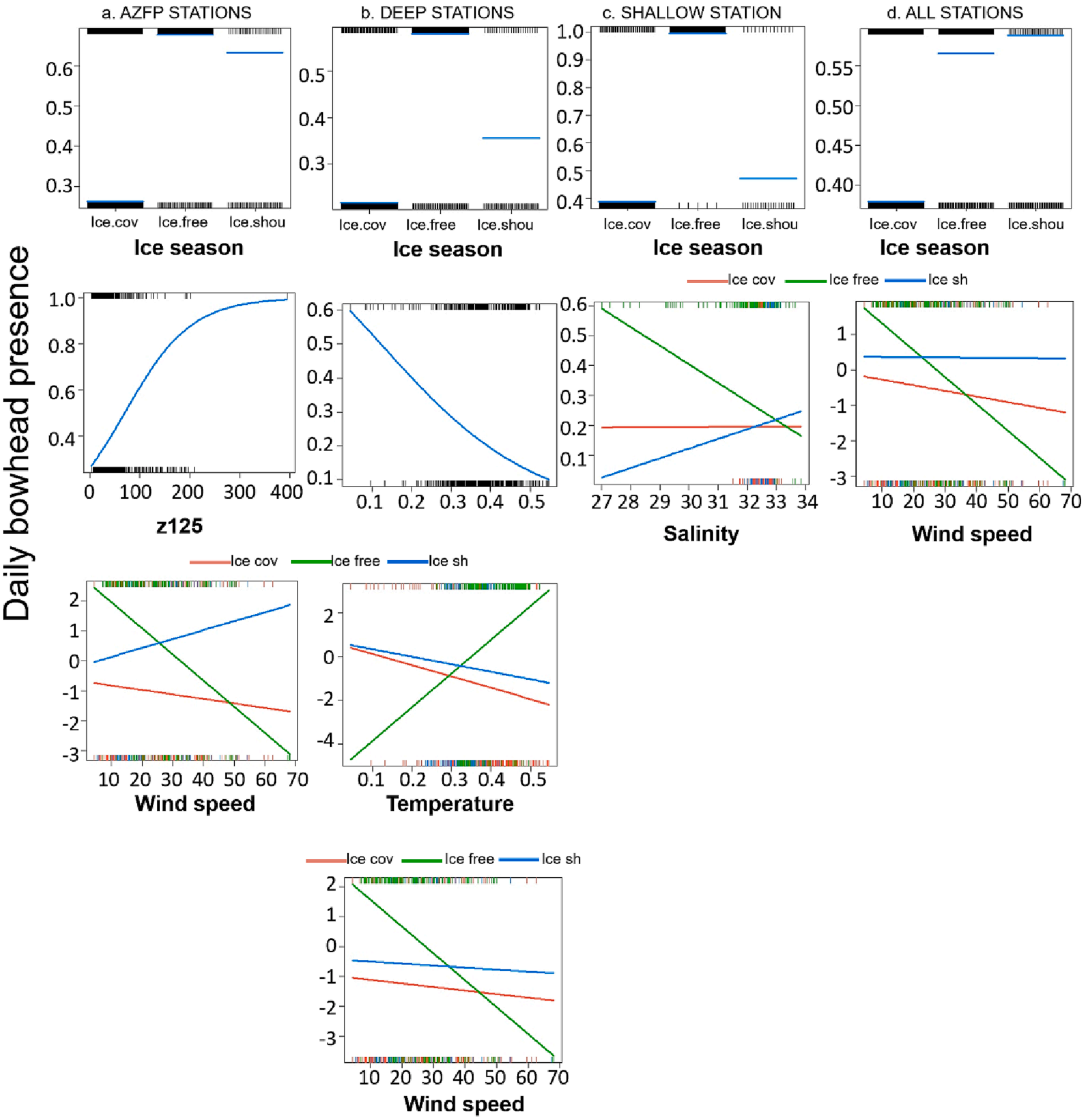

Fig. 6. GLMER effect plots for variables with significant relationships with bowhead whale acoustic detections. Plots are presented in four panels, one for each category of models (see Table 2 for the definition of each model type). In each panel separate rugs are drawn on the top for observations with positive residuals and on the bottom for observations with negative residuals (Y = 1 and Y = 0, respectively). Cross-sectional plots (with the red and green lines) represent the interaction between wind speed, salinity and temperature (continuous terms) with sea-ice coverage (a categorical term: ice free = ice free, ice cov = ice covered, ice sh = ice shoulder), and their relationship to whale detections. The regression lines for each category are overlaid. Note the differences in the axes scales.

files) allowed us to quantify temporal patterns, and measurements of environmental variables and estimates of bowhead prey assisted the assessment of drivers of habitat use for bowhead whales through an entire year (September 2018 – October 2019) off Cape Bathurst and Pearce Point.

4.1. *Temporal patterns in bowhead detections*

Our results showing the peak of bowhead occurrence in this part of the Amundsen Gulf during the spring and summer months at all acoustic stations agree with results from previous studies (Citta et al., 2015; Clarke et al., 2018; Halliday et al., 2018; Harwood et al., 2017) and Indigenous knowledge (Huntington et al., 2021a). This summer residency reflects part of the general migration pattern of bowheads, who typically spend their summers feeding in the western Canadian Arctic. The almost continuous acoustic records of bowhead calls from April until August verifies that the southwest Amundsen Gulf is an important site for bowhead whales in the summer. Cape Bathurst is of special ecological importance and makes a good habitat for bowheads, especially near the shallow site that was occupied continuously by whales from March until September, longer than tagged bowheads in 2006–2012 who left the area by mid-August (Citta et al., 2015). Recurring upwelling events make Cape Bathurst an ecological hotspot, at times occupied by a large abundance of foraging bowheads, about ten times greater than bowhead densities on the Beaufort Shelf (Citta et al., 2015; Harwood et al., 2010; Walkusz et al., 2012). Surprisingly,

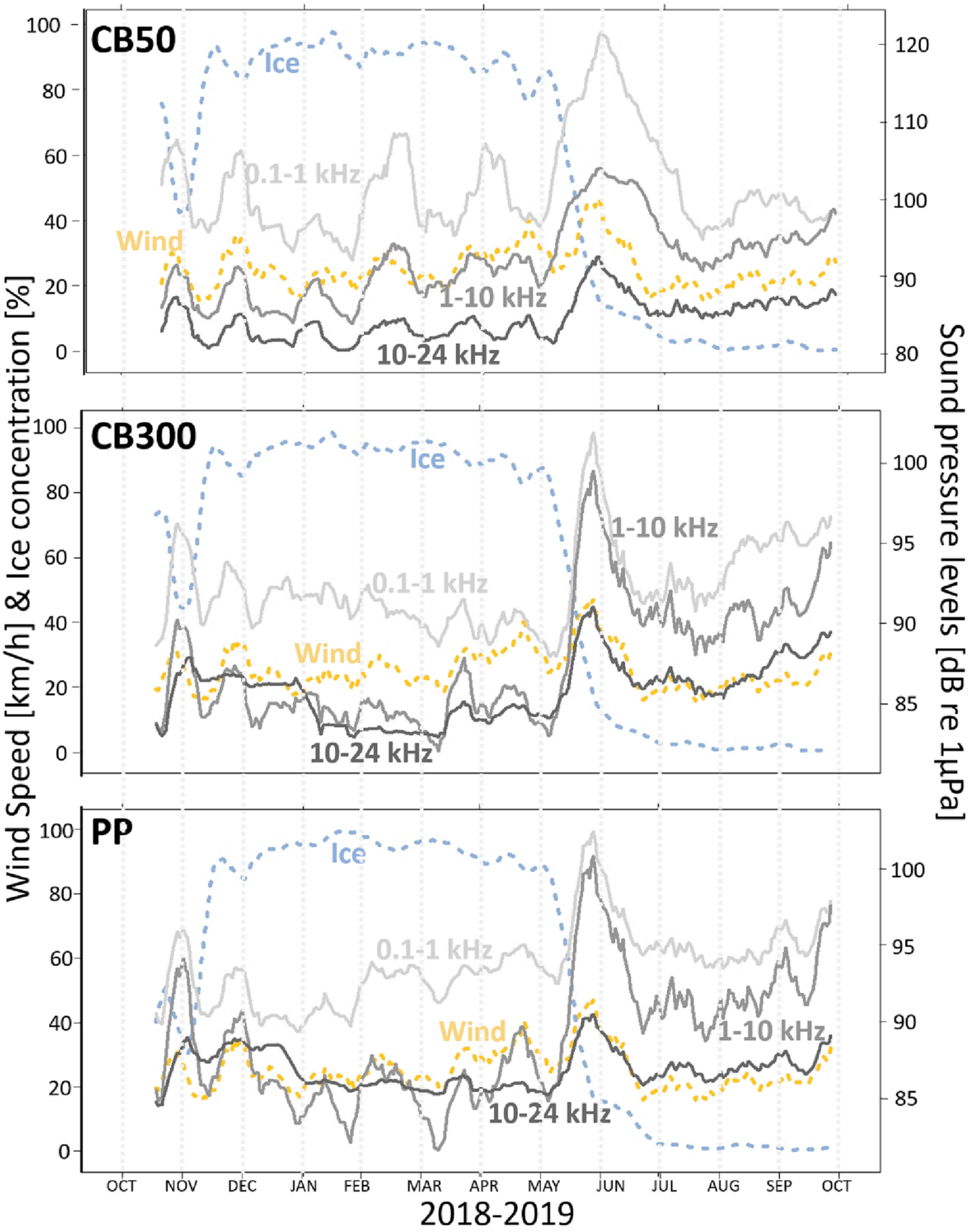

Fig. 7. Seasonal patterns of the daily mean underwater sound levels (dB re 1 μPa) at three frequency bands, wind speed and ice concentration (represented by the five colors) in all three sites. All lines are smoothed with a 13-day moving average, which is sufficient to reveal the trend while removing noise and short-term fluctuations.

bowhead calls were also detected during winter, although at low detection rates (1–5 days per month), when the animals were expected to have migrated from the Canadian Beaufort Sea/Amundsen Gulf to their winter breeding grounds in the northern Bering Sea. This observation is discussed by Insley et al. (2021).

Seasonal analyses demonstrated some variations in bowhead presence between stations, with a generally higher probability to detect bowheads near Cape Bathurst (CB50) throughout the year compared to the other two sites. CB50 is preferred by the animals compared to the adjacent deeper site (CB300) even though they are only 32 km apart (CB50 is 170 km from PP). Located in relatively shallow water (43 m) about 12 km from the shore (PP is ~ 40 km from the shore), the CB50 site is part of the Cape Bathurst flaw lead polynya complex where the absence of solid ice could facilitate the presence of whales (Arrigo and van Dijken, 2004; Citta et al., 2015) in the winter and year-round.

The shallower habitat of the CB50 recorder is likely what increased the probability of bowhead occurrence compared to the deeper stations (CB300 and PP at 290 and 348 m, respectively). Bowheads from the Eastern Canada-West Greenland stock are found to feed at shallower depths in spring and summer (at 70 and 120 m, respectively) compared to the rest of the year (250 m) (Fortune et al., 2020). Also, bowheads from the BCB stock while in the Amundsen Gulf, spend most time feeding at about 75 m (Citta et al., 2015). At a shallow site of the Alaskan Beaufort Sea, Thode et al. (2016) estimated that bowheads were calling at depths between 25 and 30 m. However, there is not enough known about the actual calling behavior of bowheads at different depths, seasons, sites, or in the context of specific activities. In our research we did not account for animals that were not vocalizing, but expect that our acoustic monitoring fully captures the daily presence of calling and foraging individuals representing meaningful temporal patterns at each site. Additionally, bowhead calls have a source level around 150 dB re 1 μPa at 1 m (Cummings & Holliday, 1987; Thode et al., 2020), such that a

Table 6
GLM results showing the relationship between SPLs and wind speed when all three frequency bandwidths (low, medium, high) are pooled. Ice Season is a categorical term: ice free = ice free, ice cov = ice covered, ice sh = ice shoulder. The significance of the variables, as dictated by the p-value levels, is represented by these codes: *, $p \leq 0.05$; **, $p \leq 0.01$; ***, $p \leq 0.001$.

Predictors	Estimates
(Intercept)	86.72***
Station [CB300]	−4.15***
Station [PP]	−2.91***
Ice season [ice free]	1.54**
Ice season [ice sh]	−1.8*
Wind speed	0.16***
Ice season [ice free] * Wind speed	0.13***
Ice season [ice sh] *Wind speed	0.17***
Observations	3162
R^2	0.304
AICc	20498.902

bowhead vocalizing near the surface would easily be detected by the recorders at 43 m and near 300 m depth, and over distances > 10 km. Shallow water acts as a high (and low) pass filter on low frequency sounds so the detection range is likely less on the shelf than it is in deeper water. Therefore, bowhead signals should propagate effectively and be detectable over greater distances at the deeper sites (CB300 and PP). That, combined with the higher detection rates at CB50, reinforces the indication of bowheads selecting for the Cape Bathurst shallow habitat, particularly during the spring and summer.

Even though our ability to detect bowhead calls and the maximum distance for detections change with underwater sound, depth, and temperature, we do not expect systematic biases at our determination of spatio-temporal patterns. Specifically, the much higher sound levels at the shallow site (CB50), and especially in the summer (Fig. 7), might cause lower bowhead detections at this site which do not appear to affect the patterns presented here. Instead, more bowhead detections occurred at CB50 in the summer and also compared to the deeper sites, emphasizing the robust assessments of the spatial patterns.

The higher sound levels recorded in summer at all sites (Fig. 7), when the number of bowhead whale calls was significantly higher, suggest that the seasonal pattern quantified for bowhead occurrence was also not an artefact of the seasonal variability of wind speed and underwater noise levels. Even though the sound models and the habitat models suggest that wind likely had a masking effect on the detectability of bowhead signals, the shape of the seasonal patterns presented here should be unaffected. Nevertheless, the detection rates of the whales are likely to be underestimated, particularly at the deep sites (as shown by the DEEP model). The SHALLOW model does not imply an effect of wind speed on the bowhead daily presence at CB50, which is likely related to higher received levels of bowhead calls at CB50 due to their proximity to the recorder. On the other hand, CB50 had higher flow-noise than the other sites, increasing the sound levels at low frequencies (<100 or 200 Hz) (Bassett et al., 2014; Simard et al., 2014). With the majority of bowhead signals ranging in frequency between 100 and 500 Hz, we expect some effect of strumming noise on the detectability of the bowhead calls produced at the lower end of the frequency range, likely resulting in an underestimation of the number of calls detected at CB50. Despite this potential masking from flow noise, CB50 still had a strong seasonal pattern and higher bowhead residency compared to the deeper sites.

Considering any other potential biases to bowhead whale presence, whether the high-frequency AZFP signals (at 38, 125, 200, and 455 kHz) are perceived by the animals and disturb them in any way, is unknown. However, the AZFP emissions are highly directional and are likely to be, at most, detectable only by bowheads almost directly above the mooring. Further, since AZFPs were deployed at all sites and functioned throughout the deployments, we expect any possible effects to be similar at all sites, and hence do not expect any interference or bias on the seasonal patterns presented here. During periods with increased underwater sound levels (e.g., storms, noisy ice processes), the detectability (manual or automated) of bowhead calls decrease due to masking. However, manual analysis allowed calls of much lower amplitude to be identified with sufficient confidence compared to the automated detector. Overall, any masking effect due to the variability of sound was not taken into account for the quantification of seasonal patterns of the whale occurrence; as a result, our figures can be considered conservative.

Additional false negatives from the automated detector occurred due to similarities with other marine mammal sounds. For example, bowhead song was often misclassified by the detector as beluga calls due to its high-frequency components. Also, a type of bearded seal call of lower frequency and shorter duration and two types of ringed seal call (growls and woofs) were often misclassified by the detector as bowhead moans due to overlap in their acoustic characteristics. By manually analyzing all automated detections, all misclassifications by the detector were excluded from the results presented here. During the period of ice cover, the detected bowhead calls were largely of lower amplitude and were more likely to be confused for ringed seal sounds. Nonetheless, our winter results include several examples of acoustic signals with no wavering or pulsed component so that we are confident they belong to bowheads and are not confused with other species, including ringed seals. Additional efforts, including careful manual analysis, are generally required to discriminate species with confidence when ranges overlap temporally and spatially.

The seasonal pattern was characterized by west-east-west movements. Acoustic detections progress across the three sites, eastward in the spring and westward in fall, following the typical migratory route of bowheads, similar to Clark et al. (2015) but on a smaller spatial scale. In 2018–2019, migrating bowheads arrived first at CB50 (most western site) in early March, but did not arrive at CB300 or PP until early and mid-April, respectively. At the end of the season, evidence of the fall whale migration started at PP (most eastern site) in August, while bowheads migrated away from the two CB stations in October. During this study, abundance estimates of mesozooplankton increased at CB50 in the fall (Fig. 8, **Fig. A3**) suggesting a food-web or aggregation response of potential forage zooplankton that could have influenced fall bowhead occupation of CB50. Also, dominant easterly winds influenced ice motion that may have supported the localized east to west movements of the whales near Cape Bathurst.

The steep increase in bowhead detection across sites in April resulted partly from singing activity, mentioned above, which occurred during the arrival of whales at their foraging grounds. Songs were detected as early as 7 March 2019 at CB50, and as late in the season as 27 September 2019 at CB50. The peak of singing takes place predominantly from December to February at the Bering Sea breeding grounds, typically lasting from October to April annually (Delarue et al., 2009). Therefore, our song detections in the Amundsen Gulf are likely part of the ending (in spring) and beginning (in early fall) of their stereotypical winter singing behavior, which might serve communication and coordination functions during migration. Songs are presumed to be produced by males as a reproductive display or during agonistic behaviour (Stafford and Clark, 2021), indicating that all three sites are occupied by male bowheads. Although more larger animals were also found in the Amundsen Gulf during aerial surveys in the 1980s (Koski et al., 1989), with our acoustic recordings we are unable to conclude whether there were strong sex or age segregations at our sites. Bowhead song was reported here for the first time on the BCB summer grounds, even though PAM has been implemented elsewhere in the Amundsen Gulf since 2014 (e.g., Halliday et al., 2018, 2019, 2020). Further details of the call types detected and their acoustic parameters or their temporal occurrence is not common practice to be presented in studies of cetacean temporal patterns or habitat preferences (Diogou et al., 2019c, 2019b, 2019a; Halliday et al., 2018) and falls out of the scope of this work.

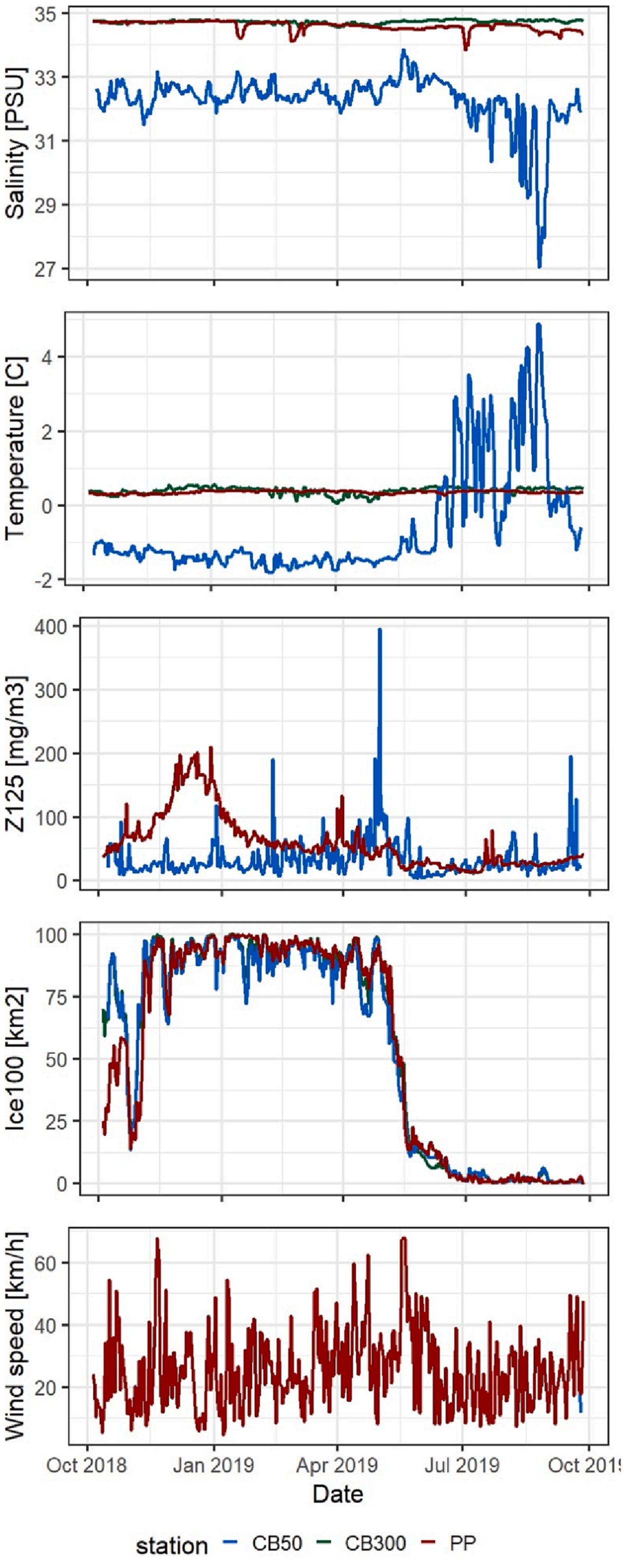

Fig. 8. Daily averages time series of the significant *in situ* and remotely sensed oceanographic variables used to explain the year-round variability of bowhead whale occurrence at the three study sites. The same wind speed data were used for all stations, which is why only one line is present on the wind speed plot. These variables appear in the four model categories and are presented for each station (different colors). Abbreviations are defined in Table 2.

The absence of consistent diel patterns throughout the year or across all sites agree with Halliday et al. (2018) at the northern Amundsen Gulf, and Blackwell et al. (2007) at the western Beaufort Sea, who also did not observe strong diel patterns. However, like Blackwell et al. (2007) who recorded significantly higher detection rates at night than in daytime during their fall recordings, we recorded higher detection rates in the late hours of the day. Diel differences were more prominent at the deep sites in summer and may represent a synchronization to the movements of copepods and euphausiids, key prey species for bowheads that undergo diel vertical migration and feed at the surface at night in the eastern Beaufort Sea in the summer (Dmitrenko et al., 2020).The increased whale detection rates during the later hours of the day could be related to increased vocal activity due to foraging in deeper waters (i.e., Pearce Point) where zooplankton DMV was evident. However, synchronized diel movements of zooplankton at CB50 was not evident given the highly-dynamic shallow water column (AZFP unpublished data, A. Niemi), such that call numbers did not significantly vary over the diel cycle.

4.2. Habitat associations with bowhead detections

Year-round variability in ice concentration, wind speed, zooplankton, bottom salinity, and bottom temperature were significantly associated with the bowhead acoustic occurrence in the Amundsen Gulf in 2018–2019, as shown in the four types of the most parsimonious models. Even though habitat variables only explain a part of the variation (5 to 78%) in the acoustic presence of bowhead whales, these relationships allow us to generate hypotheses about the potential mechanisms that determine bowhead whale distribution at their feeding grounds. The low marginal R^2 values for most models indicated that there are likely one or more factors that we failed to capture in our models. However, it is common in ecological studies to only explain$<$10% on average (2.5 to 5.4%) of the variance observed in the data (Møller and Jennions, 2002), and, in particular, whale habitat models tend to show low predictive power. The higher R^2 value for the SHALLOW model is likely due to the fact that it includes data from only one station when should be easier to capture the habitat preferences compared to attempting that for different sites where variability is much higher. Here, we discuss the bowhead distribution by seeking clues that reveal the physical mechanisms that may aggregate prey and optimize foraging for the whales.

Ice concentration provides a dominant control for Arctic organisms and their distributions (Bluhm et al., 2017). Ice is a fundamental feature of bowhead habitat selection (Ferguson et al., 2010; Steiner et al., 2021) affecting them by influencing access to habitat and via food-web processes. All four models point to ice being the most important predictor of bowhead whale acoustic presence. Bowheads navigate a highly dynamic ice-covered environment, travelling from thick pack ice fields to young, thin ice areas and open water in the summer. Similarly to Clark et al. (2015), who detected bowheads in fully ice-covered areas in the western Beaufort Sea during winter and fall, our detections reveal that bowheads arrived when ice concentration was still high (80–100%) at their spring feeding sites in the southern Amundsen Gulf. However, our models indicate that their daily occurrence was less probable when the sea was ice covered (i.e. $>$ 70%), agreeing with previous work at the northern Amundsen Gulf (Halliday et al., 2018).

At the shallow CB50 site, the chance to detect bowhead calls increased significantly during the ice-free season. However, at the deep sites that relationship reverses, with a higher presence of bowheads at CB300 and PP in November-December. The formation of land-fast ice (immobile, attached to the coastline) by November/December at the CB50 site may have caused the pack ice (mobile, wind-driven) around CB300 and PP to be more preferable habitat for whales during that period. Thus, in late fall, bowhead whales appear to be detected more at deeper sites and further from the shore, exhibiting a preference for mobile first-year ice (i.e. in **Fig. A6** compared to ice concentration in

Fig. A4 during November). Additionally, sound propagation is more efficient at the deeper sites, so distant bowheads during November-December are more easily detected at CB300 and PP compared to CB50.

The control of sea ice on upwelling (Pickart et al., 2013, 2009), stratification and circulation (Meneghello et al., 2021), and primary producers that fuel Arctic food webs (Niemi et al., 2019) can influence foraging opportunities for whales. This control exerted by sea ice on food resources likely contributed to the positive relationship we observed of the bowhead detections with zooplankton density and the ice-free season (AZFP model).

Temperature is an important driver for the marine ecosystem and crucial for bowhead whales that thrive in low water temperatures (<2°C) and ice dominated environments. In our models, bottom temperature at the deep sites is among the most influential oceanographic variables showing a negative relationship with bowhead occurrence during the ice covered period and a positive one during summer (ice free period). The linkage between temperature at depth and bowhead detections is unclear, and it could be (a) related to the presence of prey that respond directly to temperature or undergo seasonal migrations to the Atlantic layer in Amundsen Gulf (Darnis and Fortier, 2014) or (b) a reflection of overall seasonal changes in the system. Since the temperature at CB300 and PP is measured at about 300 m, the corresponding water mass represents waters of Atlantic Ocean origin, which occur below waters of Pacific Ocean origin (Scheifele et al., 2021). Temperature fluctuations at that depth could be linked to eddies (Kubryakov et al., 2021) or downwelling and relaxation events which have also been associated with higher copepod nauplii abundances compared to intense upwelling that lasted 1–5 days (Jones and Halpern, 1981; Papastephanou et al., 2006; Smith et al., 1986). Additionally, in the Barents Sea, bowheads' main prey*,* *C. hyperboreus* and *C. glacialis,* showed a negative relationship with temperature and higher biomass in deep vs. shallow water (Aarflot et al., 2018), while faster hatching and development times have been shown in *C. glacialis* at lower temperatures (0 °C) (Cornelius et al., 2013; Weydmann et al., 2015). Finally, the strong positive relationship with temperature in the summer likely masks a seasonal trend in both temperature and whale presence.

The negative correlation between salinity and bowhead presence during summer at CB50 likely corresponds with seasonal ice melt that lowers water salinity at the time of bowhead migration into Amundsen Gulf. The plume of the Mackenzie River would also decrease salinity at CB50 as it moves at the surface and turns eastward into Amundsen Gulf. The Mackenzie River source of freshwater peaks in May and continues throughout the summer (Carmack and Macdonald, 2001; Lansard et al., 2012). Discharge from the Husky and/or Horton Rivers into Franklin Bay could also decrease the water salinity at CB50 (Lansard et al., 2012), contributing to the observed relationship between salinity and bowhead presence at this hotspot location. The abundance of bowheads' prey, *C. glacialis,* also declined with salinity and temperature in samples from shallow areas in the eastern Arctic (Daase and Ola, 2007).

Previous studies have shown a strong response of bowheads to concentrated calanoid copepod prey at Cape Bathurst (Walkusz et al., 2012). Estimates of copepod abundance (z455) were indeed highest at CB50 and analyses over a diel cycle indicated that z455 was low in the presence of bowheads suggesting efficient foraging. Bowhead detections were only positively associated with z125, not z455, throughout the year. These results suggest that at both CB50 and PP, the less abundant, yet highly nutritious, prey such as euphausiids and amphipods, could be especially important to support bowhead presence during the ice-covered period when key copepod species (e.g. *C. hyperboreus*) have undergone their seasonal migration to deeper water (Darnis et al., 2017). Highest z125 values at PP occurred in December (Fig. 8), coinciding with the highest chance to detect bowheads that month at PP compared to the CB sites (Fig. 4). The z125 increase at PP may represent an offshore movement of prey to which the bowheads may respond if present during winter. The z125 peak in May and overall higher values through June at CB50 (Fig. 8), coincide with the higher probability to detect bowheads there in April-June (Fig. 4). At other Arctic sites, such as the Chukchi Sea and the western Beaufort Sea that bowheads use as corridors during their migration routes, no relationship was established between whales and their abundance of prey (Stafford et al., 2021; Tsujii et al., 2021).

Wind speed appeared as a significant variable for all model types, emphasizing the consistent negative effect that wind can have on bowhead daily detections. High wind speeds can increase underwater sound levels significantly (Fig. 7, **Table A5**), thus decreasing the detection of acoustic signals of interest. Hence, wind noise can mask low-amplitude bowhead calls, and produce the negative relationship between wind speed and bowhead daily occurrence across sites. However, the fact that wind speed does not appear to negatively affect the bowhead daily presence at the shallow station (CB50), where sound levels are higher, indicates that the wind-induced underwater noise is likely less significant for the detectability of bowhead signals at a site with a high number of whales. The opposite seems to be true for the deeper sites where the occurrence of bowheads is lower (the probability of detecting bowhead calls increases with the number of whales present). The interaction between wind speed and Ice season indicates that the negative effect of wind speed becomes stronger during the ice-free period, likely because ice has a dampening effect on underwater noise production by winds. The same relationships were observed at the northern Amundsen sites in 2015–2016 (Halliday et al., 2021; Insley et al., 2017), and at the western Beaufort Sea when bowhead detection rates would decrease on windy days (Blackwell et al., 2007). However, wind magnitude can also have an ecological impact on the ecosystem. For instance, in a highly productive system in oceanic waters around southwest Africa, primary productivity remained low during strong upwelling winds but increased as soon as winds weakened (Jones and Halpern, 1981). However, the positive effect of wind speed during the ice shoulder season in the AZFP model is likely an indication of increased easterly winds in mid-May (**Figure A7**) that advect ice offshore and cause upwelling of nutrients and the formation of phytoplankton blooms that fuel the entire food web (Arrigo and van Dijken, 2004; Carmack and Macdonald, 2001; Pickart et al., 2013). Even though wind direction plays a significant role in the functioning of the ecosystem, it remained an insignificant variable in all our models. The relationship between whale occurrence and wind direction might be lagged, or perhaps a finer scale wind measurement (closer to the site locations) is required to capture potential effects on the ocean biological productivity.

5. Conclusions

Passive acoustics is a highly efficient tool for the assessment of bowhead whale distribution and the only method to measure comparative values and monitor changes in the underwater soundscape. With a complete year of acoustic recordings from multiple locations in the western Canadian Arctic, this work emphasizes the importance of the southern Amundsen Gulf for foraging bowhead whales that are constantly present in summer but also more sparsely in winter. The Cape Bathurst area has been described as an ecological hotspot and important habitat for bowhead whales. This study confirms the continued use of the area by bowheads, identifying smaller-scale variability in habitat use at Cape Bathurst such that locations < 50 km apart can have drastically different bowhead presence. Bowheads first reach the shallower Cape Bathurst in early spring when a combination of strong easterly winds, the polynya and lower ice coverage allow access to the area, and an earlier start of pelagic primary production. The presence/absence of sea ice plays a key role in the habitat use of whales that dominate all sites during the ice free period. Some bowhead whales were found to overwinter at all sites in the southern Amundsen Gulf in 2019, suggesting that the decrease in the seasonal cycle of sea ice and the presence of euphausiids and amphipods could support them physically and nutritionally, and, at a larger scale, is triggering unprecedented shifts in the marine ecosystem (as explained in Insley et al., 2021).

With this work, we have sought to improve our understanding of how changes in factors such as sea-ice coverage, wind speed, water temperature, salinity, and zooplankton density effect bowheads in the Amundsen Gulf. Decreasing bottom water temperature and wind speed are considered here as indications of relaxation or downwelling events and perhaps eddies, that help aggregate bowhead prey and make it available for the whales at deep sites. Considering the complexity of physical and biological processes taking place in the water column and within the trophic web, these variables do not fully explain bowhead whale ecology. Further investigation of additional oceanographic variables, *in situ* and sensed remotely, both along the water column and on the sea surface (such as water column stratification, sea surface height anomalies and upwelling indices, sea surface temperature, and currents), should improve future models.

Expanding the network of acoustic stations and the temporal scale of acoustic observations is imperative to allow interannual comparisons of bowhead habitat use and clarify their responses to underlying ecological processes. Further investigation of the AZFP data over the water column and through time could provide additional information on the prey-predator dynamics. These recommendations are the basis of our plans for our next research efforts. The Arctic, one of the last relatively pristine acoustic habitats in the world, is undergoing rapid changes. Due to its intrinsic harsh conditions and remoteness, the use of passive acoustic methods is paramount to long-term Arctic underwater monitoring, and is crucial for the conservation of the entire Arctic ecosystem and its native anthropo-communities.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

We are grateful to the captain and crew of the CCGS Sir Wilfrid Laurier, the crew from DFO, and specifically the Chief Science Officer, H. Melling, for deploying and recovering our oceanographic moorings. Many thanks also to the three anonymous reviewers that helped with insightful comments to improve this manuscript. Acoustic monitoring work by WCS Canada is licenced under Aurora Research Institute permit 16330, and research was approved and support by the Inuvialuit Game Council (IGC) and Fisheries Joint Management Committee (FJMC). We are extremely grateful to both IGC and FJMC for continuing to support our research and providing valuable insights into the amazing and changing ecosystem in the Inuvialuit Settlement Region. Funding for this project was provided by the Canada Nature Fund for Aquatic Species at Risk (DFO), Ecosystem Stressors program (DFO), and the Weston Family Foundation, Canada. Funding was also provided by a Mitacs Accelerate PDF to N.D.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2023.103004.

References

Aarflot, J.M., Skjoldal, H.R., Dalpadado, P., Skern-mauritzen, M., 2018. Original Article Contribution of Calanus species to the mesozooplankton biomass in the Barents Sea 75, 2342–2354. https://doi.org/10.1093/icesjms/fsx221.

Andrews, J., Babb, D., Barber, D.G., 2018. Climate change and sea ice: Shipping in Hudson Bay, Hudson Strait, and Foxe Basin (1980–2016). Elementa 6, 1–23. https://doi.org/10.1525/elementa.281.

Arrigo, K.R., van Dijken, G.L., 2004. Annual cycles of sea ice and phytoplankton in Cape Bathurst polynya, southeastern Beaufort Sea, Canadian Arctic. Geophys. Res. Lett. 31, 2–5. https://doi.org/10.1029/2003GL018978.

Barton, K., 2018. R Package 'MuMIn.'.

Bassett, C., Thomson, J., Dahl, P.H., Polagye, B., 2014. Flow-noise and turbulence in two tidal channels. J. Acoust. Soc. Am. 135, 1764–1774. https://doi.org/10.1121/1.4867360.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 48.

Blackwell, S.B., Richardson, W.J., Greene, C.R., Streever, B., 2007. Bowhead whale (Balaena mysticetus) migration and calling behaviour in the Alaskan Beaufort Sea, autumn 2001 -04: An acoustic localization study. Arctic 60, 255-270. Doi: 10.14430/arctic218.

Blackwell, S.B., Thode, A.M., Conrad, A.S., Ferguson, M.C., Berchok, C.L., Stafford, K.M., Marques, T.A., Kim, K.H., 2021. Estimating acoustic cue rates in bowhead whales. Balaena mysticetus, during their fall migration through the Alaskan Beaufort Sea 3611, 3611–3625. https://doi.org/10.1121/10.0005043.

Bluhm, B.A., Hop, H., Melnikov, I.A., Poulin, M., Vihtakari, M., Collins, E.R., Gradinger, R., Juul-Pedersen, T., von Quillfeldt, C., 2017. Circumpolar biodiversity monitoring program. Government Printing Office, State of the Arctic marine biodiversity report.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6.

Carmack, E.C., Macdonald, R.W., 2001. Oceanography of the Canadian shelf of the Beaufort Sea: A setting for marine life. Arctic 55, 29–45. https://doi.org/10.14430/arctic733.

Carmack, E.C., Macdonald, R.W., Papadakis, J.E., 1989. Water mass structure and boundaries in the Mackenzie shelf estuary. J. Geophys. Res. 94, 18043. https://doi.org/10.1029/jc094ic12p18043.

Carslaw, D., 2022. Package ' openair .'.

Citta, J.J., Okkonen, S.R., Quakenbush, L.T., Maslowski, W., Osinski, R., George, J.C., Small, R.J., Brower, H., Heide-Jørgensen, M.P., Harwood, L.A., 2018. Oceanographic characteristics associated with autumn movements of bowhead whales in the Chukchi Sea. Deep. Res. Part II Top. Stud. Oceanogr. 152, 121-131. Doi: 10.1016/j.dsr2.2017.03.009.

Citta, J.J., Quakenbush, L., George, J.C., 2021. Chapter 4. Distribution and behavior of Bering Chukchi Beaufort. In: The Bowhead Whale. INC, pp. 31-56. Doi: 10.1016/B978-0-12-818969-6.00004-2.

Citta, J.J., Quakenbush, L.T., Okkonen, S.R., Druckenmiller, M.L., Maslowski, W., Clement-Kinney, J., George, J.C., Brower, H., Small, R.J., Ashjian, C.J., Harwood, L.A., Heide-Jørgensen, M.P., 2015. Ecological characteristics of core-use areas used by Bering-Chukchi-Beaufort (BCB) bowhead whales, 2006–2012. Prog. Oceanogr. 136, 201–222. https://doi.org/10.1016/j.pocean.2014.08.012.

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. Prog. Oceanogr. 136, 223–240. https://doi.org/10.1016/j.pocean.2015.05.007.

Clark, C.W., Johnson, J.H., 1984. The sounds of the bowhead whale, Balaena mysticetus, during the spring migrations of 1979 and 1980. J. Zool. 62, 1436–1441.

Clarke, J.T., Ferguson, M.C., Willoughby, A.L., Brower, A.A., 2018. Bowhead and beluga whale distributions, sighting rates, and habitat associations in the western beaufort sea in summer and fall 2009–16, with comparison to 1982–91. Arctic 71, 115–138. https://doi.org/10.14430/arctic4713.

Cooper, L.W., Grebmeier, J.M., 2022. A chlorophyll biomass time-series for the distributed biological observatory in the context of seasonal sea ice declines in the Pacific Arctic region. Geosciences 12, 307. https://doi.org/10.3390/geosciences12080307.

Corlett, W.B., Pickart, R.S., 2017. The Chukchi slope current. Prog. Oceanogr. 153, 50–65. https://doi.org/10.1016/j.pocean.2017.04.005.

Cornelius, J., Torkel, G., Nielsen, G., Hjorth, M., 2013. Effects of pyrene exposure and temperature on early development of two co-existing Arctic copepods 184-198. Doi: 10.1007/s10646-012-1016-y.

COSEWIC, 2009. COSEWIC Assessment and Update Status Report on the Bowhead Whale Balaena mysticetus, Bering-Chukchi-Beaufort Population and Eastern Canada-West Greenland.

Cummings, W.C., Holliday, D., 1987. Sounds and source levels from bowhead whales off Pt. Barrow, Alaska. J. Acoust. Soc. Am. 82, 814–821.

Daase, M., Ola, J.O.N., 2007. The influence of advection on Calanus near Svalbard : statistical relations between salinity, temperature and copepod abundance. J. Plankton Res. 29, 903–911. https://doi.org/10.1093/plankt/fbm068.

Darnis, G., Barber, D.G., Fortier, L., 2008. Sea ice and the onshore-offshore gradient in pre-winter zooplankton assemblages in southeastern Beaufort Sea. J. Mar. Syst. 74, 994–1011. https://doi.org/10.1016/j.jmarsys.2007.09.003.

Darnis, G., Fortier, L., 2014. Temperature, food and the seasonal vertical migration of key arctic copepods in the thermally stratified Amundsen Gulf (Beaufort Sea, Arctic Ocean) GE. J. Plankton Res. 36, 1092–1108. https://doi.org/10.1093/plankt/fbu035.

Darnis, G., Hobbs, L., Geoffroy, M., Grenvald, J.C., Renaud, P.E., Berge, J., Cottier, F., Kristiansen, S., Daase, M., Søreide, E.J., Wold, A., Morata, N., Gabrielsen, T., 2017. From polar night to midnight sun: Diel vertical migration, metabolism and biogeochemical role of zooplankton in a high Arctic fjord (Kongsfjorden, Svalbard). Limnol. Oceanogr. 62, 1586–1605. https://doi.org/10.1002/lno.10519.

Dawson, J., Pizzolato, L., Howell, S.E.L., Copland, L., Johnston, M.E., 2018. Temporal and Spatial Patterns of Ship Traffic in the Canadian Arctic from 1990 to 2015 71, 15-26.

Delarue, J., Laurinolli, M., Martin, B., 2009. Bowhead whale (Balaena mysticetus) songs in the Chukchi Sea between October 2007 and May 2008. J. Acoust. Soc. Am. 126, 3319–3328. https://doi.org/10.1121/1.3257201.

Diogou, N., Klinck, H., Frantzis, A., Nystuen, J., Papathanassiou, E., Katsanevakis, S., 2019a. Year-round acoustic presence of sperm whales (Physeter macrocephalus) and baseline ambient ocean sound levels in the Greek Seas 20, 208–221.

Diogou, N., Palacios, D.M., Nieukirk, S.L., Nystuen, J.A., Papathanassiou, E., Katsanevakis, S., Klinck, H., 2019b. Sperm whale (Physeter macrocephalus) acoustic ecology at Ocean Station PAPA (Gulf of Alaska) - Part 1: Detectability and seasonality. Deep. Res. Part I Oceanogr. Res. Pap. 150, 103047 https://doi.org/10.1016/j.dsr.2019.05.007.

Diogou, N., Palacios, D.M., Nystuen, J.A., Papathanassiou, E., Katsanevakis, S., Klinck, H., 2019c. Sperm whale (Physeter macrocephalus) acoustic ecology at Ocean Station PAPA in the Gulf of Alaska - Part 2: Oceanographic drivers of interannual variability. Deep. Res. Part I Oceanogr. Res. Pap. 150, 103044 https://doi.org/10.1016/j.dsr.2019.05.004.

Dmitrenko, I.A., Petrusevich, V., Darnis, G., Kirillov, S.A., Komarov, A.S., Ehn, J.K., Forest, A., Fortier, L., Rysgaard, S., Barber, D.G., 2020. Sea-ice and water dynamics and moonlight impact the acoustic backscatter diurnal signal over the eastern Beaufort Sea continental slope. Ocean Sci. 16, 1261–1283. https://doi.org/10.5194/os-16-1261-2020.

Eisner, L., Hillgruber, N., Martinson, E., Maselko, J., 2013. Pelagic fish and zooplankton species assemblages in relation to water mass characteristics in the northern Bering and southeast Chukchi seas. Polar Biol. 36, 87–113. https://doi.org/10.1007/s00300-012-1241-0.

Faraway, J.J., 2016. faraway: Functions and Datasets for Books by Julian Faraway. R package.

Ferguson, S.H., Dueck, L., Loseto, L.L., Luque, S.Á.P., 2010. Bowhead whale Balaena mysticetus seasonal selection of sea ice. Mar. Ecol. Prog. Ser. 411, 285–297. https://doi.org/10.3354/meps08652.

Ferguson, M.C., Clarke, J.T., Brower, A.A., Willoughby, A.L., Okkonen, S.R., 2021. Chapter 24. Ecological variation in the western Beaufort, in: The Bowhead Whale. INC, pp. 365-380. Doi: 10.1016/B978-0-12-818969-6.00024-8.

Fortune, S., Ferguson, S.H., Trites, A., LeBlanc, B., LeMay, V., Hudson, J., Baumgartner, M., 2020. Seasonal diving and foraging behaviour of Eastern Canada-West Greenland bowhead whales. Mar. Ecol. Prog. Ser. 643, 197–217. https://doi.org/10.3354/meps13356.

Fox, J., Weisberg, S., Fox, J., 2011. An R companion to applied regression. Third Edition.

Frey, K.E., Comiso, J.C., Cooper, L.W., Grebmeier, J.M., Stock, L.V., 2021. Arctic Ocean primary productivity: The response of marine algae to climate warming and sea ice decline. Arct. Rep. Card 2021 (21), 1–12.

Geoffroy, M., Majewski, A., LeBlanc, M., Gauthier, S., Walkusz, W., Reist, J.D., Fortier, L., 2016. Vertical segregation of age-0 and age-1 + polar cod (Boreogadus saida) over the annual cycle in the Canadian Beaufort Sea. Polar Biol 1023–1037. https://doi.org/10.1007/s00300-015-1811-z.

Geoffroy, M., Robert, D., Mesozooplankton, Á.P.Á., 2011. The aggregation of polar cod (Boreogadus saida) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. Polar Biol 1959–1971. https://doi.org/10.1007/s00300-011-1019-9.

George, J.C., Clark, C., Carroll, G.M., Ellison, W.T., 1989. Observations on the ice-breaking and ice navigation behavior of migrating bowhead whales (Balaena mysticetus) near Point Barrow, Alaska, Spring 1985. Arctic 42, 24–30. https://doi.org/10.14430/arctic1636.

George, J.C., Lubetkin, S.C., Zeh, J.E., Thewissen, J.G.M., Wetzel, D., Givens, G.H., 2021. Chapter 21. Age estimation. In: The Bowhead Whale. INC, pp. 309-322. Doi: 10.1016/B978-0-12-818969-6.00021-2.

Givens, G.H., Heide-jørgensen, M.P., 2021. Chapter 6. Abundance. In: The Bowhead Whale. INC, pp. 77-86. Doi: 10.1016/B978-0-12-818969-6.00006-6.

Givens, G.H., Edmondson, S.L., George, J.C., Suydam, R., Charif, R.A., Rahaman, A., Hawthorne, D., Tudor, B., Delong, R.A., Clark, C.W., 2016. Horvitz-Thompson whale abundance estimation adjusting for uncertain recapture, temporal availability variation, and intermittent effort. Environmetrics 27, 134–146. https://doi.org/10.1002/env.2379.

Guarino, M.V., Sime, L.C., Schröeder, D., Malmierca-Vallet, I., Rosenblum, E., Ringer, M., Ridley, J., Feltham, D., Bitz, C., Steig, E.J., Wolff, E., Stroeve, J., Sellar, A., 2020. Sea-ice-free Arctic during the Last Interglacial supports fast future loss. Nat. Clim. Chang. 10, 928–932. https://doi.org/10.1038/s41558-020-0865-2.

Gulland, F.M.D., Baker, J.D., Howe, M., LaBrecque, E., Leach, L., Moore, S.E., Reeves, R. R., Thomas, P.O., 2022. A review of climate change effects on marine mammals in United States waters: Past predictions, observed impacts, current research and conservation imperatives. Clim. Chang. Ecol. 3, 100054 https://doi.org/10.1016/j.ecochg.2022.100054.

Halliday, W.D., Insley, S.J., de Jong, T., Mouy, X., 2018. Seasonal patterns in acoustic detections of marine mammals near Sachs Harbour, Northwest Territories. Arct. Sci. 278, 259–278. https://doi.org/10.1139/as-2017-0021.

Halliday, W.D., Pine, M.K., Insley, S.J., Soares, R.N., Kortsalo, P., Mouy, X., 2019. Acoustic detections of arctic marine mammals near ulukhaktok, northwest territories, Canada. Can. J. Zool. 97, 72–80. https://doi.org/10.1139/cjz-2018-0077.

Halliday, W.D., Pine, M.K., Insley, S.J., 2020. Underwater noise and arctic marine mammals: Review and policy recommendations. Environ. Rev. 28, 438–448. https://doi.org/10.1139/er-2019-0033.

Halliday, W.D., Barclay, D., Barkley, A.N., Cook, E., Dawson, J., Hilliard, R.C., Hussey, N. E., Jones, J.M., Juanes, F., Marcoux, M., Niemi, A., Nudds, S., Pine, M.K., Richards, C., Scharffenberg, K., Westdal, K., Insley, S.J., 2021. Underwater sound levels in the Canadian Arctic, 2014–2019. Mar. Pollut. Bull. 168, 112437 https://doi.org/10.1016/j.marpolbul.2021.112437.

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. Cont. Shelf Res. 67, 127–146. https://doi.org/10.1016/j.csr.2013.07.009.

Harwood, L.A., Borstad, G., 1985. Bowhead Whale Monitoring Study in the SouthEast Beaufort Sea, July-September 1984. Ottawa.

Harwood, L.A., Auld, J., Joynt, A., Moore, S.E., 2010. Distribution of bowhead whales in the SE Beaufort Sea during late summer, 2007–2009. DFO Can. Sci. Advis. Sec. Res, Doc.

Harwood, L.A., Quakenbush, L.T., Small, R.J., George, J.C., Pokiak, J., Pokiak, C., Heide-Jørgensen, M.P., Lea, E.V., Brower, H., 2017. Movements and inferred foraging by bowhead whales in the Canadian Beaufort sea during August and September, 2006–12. Arctic 70, 161–176. https://doi.org/10.14430/arctic4648.

Hauser, D., 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. Glob. Chang. Biol. 23, 2206–2217. https://doi.org/10.1111/gcb.13564.

Haver, S.M., Gedamke, J., Hatch, L.T., Dziak, R.P., Van Parijs, S., McKenna, M.F., Barlow, J., Berchok, C., DiDonato, E., Hanson, B., Haxel, J., Holt, M., Lipski, D., Matsumoto, H., Meinig, C., Mellinger, D.K., Moore, S.E., Oleson, E.M., Soldevilla, M. S., Klinck, H., 2018. Monitoring long-term soundscape trends in U.S. Waters: The NOAA/NPS Ocean Noise Reference Station Network. Mar. Policy 90, 6–13. https://doi.org/10.1016/J.MARPOL.2018.01.023.

Hop, H., Mundy, C.J., Gosselin, M., Rossnagel, A.L., Barber, D.G., 2011. Zooplankton boom and ice amphipod bust below melting sea ice in the Amundsen Gulf. Arctic Canada. Polar Biol. 34, 1947–1958. https://doi.org/10.1007/s00300-011-0991-4.

Huntington, H.P., Daniel, R., Hartsig, A., Harun, K., Heiman, M., Meehan, R., Noongwook, G., Pearson, L., Prior-parks, M., Robards, M., Stetson, G., 2015. Vessels, risks, and rules : Planning for safe shipping in Bering Strait. Mar. Policy 51, 119–127. https://doi.org/10.1016/j.marpol.2014.07.027.

Huntington, H.P., Ferguson, S.H., George, J.C., Noongwook, G., Quakenbush, L., Thewissen, J.G.M., 2021a. Chapter 34. Indigenous knowledge in research and management, in: The Bowhead Whale. INC, pp. 549-564. Doi: 10.1016/B978-0-12-818969-6.00034-0.

Huntington, H.P., Sakakibara, C., Noongwook, G., Kanayurak, N., Skhauge, V., Zdor, E., Inutiq, S., Lyberth, B., 2021b. Chapter 31. Whale hunting in Indigenous Arctic cultures, in: The Bowhead Whale. INC, pp. 499-518. Doi: 10.1016/B978-0-12-818969-6.00031-5.

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. https://doi.org/10.14430/arctic4662.

Insley, S.J., Halliday, W.D., Mouy, X., Diogou, N., Sea, B., Sci, R.S.O., 2021. Bowhead whales overwinter in the Amundsen Gulf and Eastern Beaufort Sea 8, 202268.

Jones, B.H., Halpern, D., 1981. Biological and physical aspects of a coastal upwelling event observed during March-April 1974 off northwest Africa. Deep-Sea. Deep. Res. Part I 28, 71–81.

Jones, J.M., Roth, E., Thayre, B.J., Sia, I., Mahoney, M., Zeller, C., Johnson, M., Jackson, C., Kitka, K., Pickett, D., Small, R., Gentes, Z., Wiggins, S., Hildebrand, J., 2011. Seasonal presence of ringed, ribbon, and bearded seal vocalizations in the Chukchi Sea north of Barrow. Alaska. J. Acoust. Soc. Am. 130, 2321. https://doi.org/10.1121/1.3654276.

Koski, W.R., Miller, G.W., Davis, R.A., 1989. The potential effects of tanker traffic on the Bowhead Whale in the Beaufort Sea.

Kubryakov, A.A., Kozlov, I.E., Manucharyan, G.E., 2021. Large mesoscale eddies in the Western Arctic Ocean from satellite altimetry measurements. J. Geophys. Res. Ocean. 126, 1–26. https://doi.org/10.1029/2020JC016670.

Lansard, B., Mucci, A., Miller, L.A., MacDonald, R.W., Gratton, Y., 2012. Seasonal variability of water mass distribution in the southeastern Beaufort Sea determined by total alkalinity and δ18O. J. Geophys. Res. Ocean. 117, 1–19. https://doi.org/10.1029/2011JC007299.

Lefebvre, K.A., Fachon, E., Bowers, E.K., Kimmel, D.G., Snyder, J.A., Stimmelmayr, R., Grebmeier, J.M., Kibler, S., Ransom Hardison, D., Anderson, D.M., Kulis, D., Murphy, J., Gann, J.C., Cooper, D., Eisner, L.B., Duffy-Anderson, J.T., Sheffield, G., Pickart, R.S., Mounsey, A., Willis, M.L., Stabeno, P., Siddon, E., 2022. Paralytic shellfish toxins in Alaskan Arctic food webs during the anomalously warm ocean conditions of 2019 and estimated toxin doses to Pacific walruses and bowhead whales. Harmful Algae 114, 102205. https://doi.org/10.1016/j.hal.2022.102205.

Ljungblad, D.K., Leatherwood, S., Dahlheim, M.E., 1980. Sounds recorded in the presence of adult and calf bowhead whales, Balaena mysticetus. Mar. Fish. Rev. 42, 86–87.

Ljungblad, D.K., Thompson, P.O., Moore, S.E., 1982. Underwater sounds recorded from migrating bowhead whales, Balaena mysticetus, in 1979. J. Acoust. Soc. Am. 71, 477–482. https://doi.org/10.1121/1.387419.

Macdonald, R.W., Wong, C.S., Erickson, P.E., 1987. The distribution of nutrients in the Southeastern Beaufort Sea: implications for water circulation and primary production 92, 2939–2952.

Meneghello, G., Marshall, J., Lique, C., Isachsen, P.E., Doddridge, E., Campin, J., Regan, H., Talandier, C., 2021. Genesis and decay of mesoscale baroclinic eddies in the seasonally ice-covered interior Arctic Ocean. J. Phys. Oceanogr. 51, 115–129. https://doi.org/10.1175/JPO-D-20-0054.1.

Merchant, N.D., Fristrup, K.M., Johnson, M.P., Tyack, P.L., Witt, M.J., Blondel, P., Parks, S.E., 2015. Measuring acoustic habitats. Methods Ecol. Evol. 6, 257–265. https://doi.org/10.1111/2041-210X.12330.

Mizuguchi, D., Tsunokawa, M., Kawamoto, M., Kohshima, S., 2016. Underwater vocalizations and associated behavior in captive ringed seals (Pusa hispida). Polar Biol. 39, 659–669. https://doi.org/10.1007/s00300-015-1821-x.

Moloney, J., Hillis, C., Mouy, X., Urazghildiiev, I., Dakin, T., 2015. Autonomous multichannel acoustic recorders on the VENUS ocean observatory. 2014 Oceans - St John's, OCEANS 2014. https://doi.org/10.1109/OCEANS.2014.7003201.

Moore, S.E., Clarke, J.T., Okkonen, S.R., Grebmeier, J.M., Berchok, C.L., Stafford, K.M., 2022. Changes in gray whale phenology and distribution related to prey variability and ocean biophysics in the northern Bering and eastern Chukchi seas. PLoS One 17, 1–26. https://doi.org/10.1371/journal.pone.0265934.

Moore, S.E., Huntington, H.P., 2008. Arctic marine mammals and climate change: Impacts and resilience. Ecol. Appl. 18, 157–165. https://doi.org/10.1890/06-0571.1.

Moore, S.E., Stafford, K.M., Melling, H., Berchok, C., Wiig, O., Kovacs, K.M., Lydersen, C., 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 Biol. 35, 475–480. https://doi.org/10.1007/s00300-011-1086-y.

Mouy, X., Oswald, J., Leary, D., Delarue, J., Vallarta, J., Rideout, B., Mellinger, D., Erbe, C., Hannay, D.E., Martin, B.S., 2013. Passive acoustic monitoring of marine mammals in the Arctic. In: NGO, D. (Ed.), Detection Classification Localization of Marine Mammals Using Passive Acoustics. 2003-2013: 10 Years of International Reserarch. Paris, p. 297.

Niemi, A., Ferguson, S.H., Hedges, K., Melling, H., Michel, C., Ayles, B., Azetsu-scott, K., Coupel, P., Deslauriers, D., Devred, E., Doniol-valcroze, T., Dunmall, K., Eert, J., Galbraith, P., Geoffroy, M., Gilchrist, G., Hennin, H., Howland, K., Kendall, M., Kohlbach, D., Lea, E., Loseto, L., Majewski, A., Marcoux, M., Matthews, C., Mcnicholl, D., Mosnier, A., Mundy, C.J., Ogloff, W., Perrie, W., Richards, C., Richardson, E., Reist, J., Roy, V., Sawatzky, C., Scharffenberg, K., Tallman, R., Tremblay, J.-éric, Tufts, T., Watt, C., Williams, W., Worden, E., Yurkowski, D., Zimmerman, S., 2019. State of Canada ' s Arctic Seas Canadian Technical Report of Fisheries and Aquatic Sciences 3344, Canadian Technical Report of Fisheries and Aquatic Sciences.

PAME, 2019. Underwater Noise in the Arctic: A State of Knowledge Report. Rovaniemi.

Papastephanou, K.M., Bollens, S.M., Slaughter, A.M., 2006. Cross-shelf distribution of copepods and the role of event-scale winds in a northern California upwelling zone 53, 3078-3098. Doi: 10.1016/j.dsr2.2006.07.014.

Pickart, R.S., Moore, G.W.K., Torres, D.J., Fratantoni, P.S., Goldsmith, R.A., Yang, J., 2009. Upwelling on the continental slope of the alaskan beaufort sea: Storms, ice, and oceanographic response. J. Geophys. Res. Ocean. 114, 1–17. https://doi.org/10.1029/2008JC005009.

Pickart, R.S., Schulze, L.M., Moore, G.W.K., Charette, M.A., Arrigo, K.R., Dijken, G.V., Danielson, S.L., 2013. Long-term trends of upwelling and impacts on primary productivity in the Alaskan Beaufort Sea. Deep. Res. Part I 79, 106–121. https://doi.org/10.1016/j.dsr.2013.05.003.

Pine, M.K., Hannay, D.E., Insley, S.J., Halliday, W.D., Juanes, F., 2018. Assessing vessel slowdown for reducing auditory masking for marine mammals and fish of the western Canadian Arctic. Mar. Pollut. Bull. 135, 290–302. https://doi.org/10.1016/j.marpolbul.2018.07.031.

Pizzolato, L., Howell, S.E.L., Dawson, J., Laliberté, F., Copland, L., 2016. The influence of declining sea ice on shipping activity in the Canadian Arctic. Geophys. Res. Lett. 43, 12146–12154. https://doi.org/10.1002/2016GL071489.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Rantanen, M., Karpechko, A.Y., Lipponen, A., Ruosteenoja, K., Vihma, T., Laaksonen, A., Nordling, K., Hyvärinen, O., 2021. The Arctic has warmed nearly four times faster than the globe since 1979. Commun. Earth Environ. 3, 168. https://doi.org/10.1038/s43247-022-00498-3.

Richerol, T., Rochon, A., Blasco, S., Scott, D.B., Schell, T.M., Bennett, R.J., 2008. Evolution of paleo sea-surface conditions over the last 600 years in the Mackenzie Trough, Beaufort Sea (Canada). Mar. Micropaleontol. 68, 6–20. https://doi.org/10.1016/j.marmicro.2008.03.003.

Scheifele, B., Waterman, S., Carpenter, J.R., 2021. Turbulence and mixing in the arctic ocean's amundsen gulf. J. Phys. Oceanogr. 51, 169–186. https://doi.org/10.1175/JPO-D-20-0057.1.

Sheffield, G., George, J.C., 2021. Chapter 28. Diet and prey, The Bowhead Whale. INC. Doi: 10.1016/B978-0-12-818969-6.00028-5.

Simard, Y., Loseto, L., Gautier, S., Roy, N., 2014. Monitoring beluga habitat use and underwater noise levels in the Mackenzie Estuary: Application of passive acoustics in summers 2011 and 2012, Canadian Technical Report of Fisheries and Aquatic Sciences.

Smith, S.L., Jones, B.H., Atkinson, L.P., Brink, K.H., 1986. Zooplankton in the upwelling fronts off Pt. Conception, California. Mar. Interfaces Ecohydrodynam. 42, 195–213.

Spreen, G., Kaleschke, L., Heygster, G., 2008. Sea ice remote sensing using AMSR-E 89-GHz channels. J. Geophys. Res. 113 https://doi.org/10.1029/2005J C0033 84.

Stafford, K.M., Clark, C.W., 2021. Chapter 22. Acoustic behavior, in: The Bowhead Whale. pp. 323-338. Doi: 10.1016/B978-0-12-818969-6.00022-4.

Stafford, K.M., Lydersen, C., Wiig K.m., K., 2018b. Extreme diversity in the songs of Spitsbergen's bowhead whales. Biol. Lett. 14 https://doi.org/10.1098/rsbl.2018.0056.

Stafford, K.M., Citta, J.J., Okkonen, S.R., Zhang, J., 2021. Bowhead and beluga whale acoustic detections at DBO 6 in the western Beaufort Sea. PLoS One 16, 0253929.

Stafford, K.M., Farley, E. V., Ferguson, M., Kuletz, K.J., Levine, R., 2022. Northward range expansion of subarctic upper trophic level animals into the Pacific Arctic region. Oceanography 35, 158-166. Doi: 10.5670/oceanog.2022.101.

Steiner, N.S., Bowman, J., Campbell, K., Chierici, M., Fransson, A., Herr, H., Insley, S.J., Kauko, H.M., Lannuzel, D., Loseto, L., Lynnes, A., Majewski, A., Meiners, K.M., Miller, L.A., Michel, N., Moreau, S., 2021. Climate change impacts on sea-ice ecosystems and associated ecosystem services. Elem. Sci. Anthr. 9, 1–55.

Stirling, I., Calvert, W., Spencer, C., 1987. Evidence of stereotyped underwater vocalizations of male Atlantic walruses (Odobenus rosmarus rosmarus). Can. J. Zool. 65, 2311–2321. https://doi.org/10.1139/z87-348.

Tervo, O.M., Parks, S.E., Miller, L.A., 2009. Seasonal changes in the vocal behavior of bowhead whales (Balaena mysticetus) in Disko Bay. Western-Greenland. J. Acoust. Soc. Am. 126, 1570–1580. https://doi.org/10.1121/1.3158941.

Tervo, O.M., Christoffersen, M.F., Simon, M., Miller, L.A., Jensen, F.H., Parks, S.E., Madsen, P.T., 2012. High source levels and small active space of high-pitched song in bowhead whales (Balaena mysticetus). PLoS One 7, 52072. https://doi.org/10.1371/journal.pone.0052072.

Thode, A.M., Blackwell, S.B., Seger, K.D., Conrad, A.S., Kim, K.H., Michael Macrander, A., 2016. Source level and calling depth distributions of migrating bowhead whale calls in the shallow Beaufort Sea. J. Acoust. Soc. Am. 140, 4288–4297. https://doi.org/10.1121/1.4968853.

Thode, A.M., Blackwell, S.B., Conrad, A.S., Kim, K.H., Marques, T., Thomas, L., Oedekoven, C.S., Harris, D., Bröker, K., 2020. Roaring and repetition: How bowhead whales adjust their call density and source level (Lombard effect) in the presence of natural and seismic airgun survey noise. J. Acoust. Soc. Am. 147, 2061–2080. https://doi.org/10.1121/10.0000935.

Tsagris, M., Athineou, G., Adam, C., Sajib, A., Amson, E., Waldstein, M.J., Tsagris, M.M., 2022. Package ' Directional .' Doi: 10.1007/s11222-017-9756-4>.

Tsujii, K., Otsuki, M., Akamatsu, T., Amakasu, K., Kitamura, M., Kikuchi, T., Fujiwara, A., Shirakawa, H., Miyashita, K., Mitani, Y., 2021. Annual variation of oceanographic conditions changed migration timing of bowhead whales Balaena mysticetus in the southern Chukchi. Polar Biol. 44, 2289–2298. https://doi.org/10.1007/s00300-021-02960-y.

Venables, W.N., Ripley, B.D., 2002. Modern applied statistics with S, 4th ed. Springer, New York, New York.

Walkusz, W., Williams, W.J., Harwood, L.A., Moore, S.E., Stewart, B.E., Kwasniewski, S., 2012. Composition, biomass and energetic content of biota in the vicinity of feeding bowhead whales (Balaena mysticetus) in the Cape Bathurst upwelling region (south eastern Beaufort Sea). Deep. Res. Part I Oceanogr. Res. Pap. 69, 25–35. https://doi.org/10.1016/j.dsr.2012.05.016.

Wang, M., Overland, J.E., 2009. A sea ice free summer Arctic within 30 years? Geophys. Res. Lett. 36, 2–6. https://doi.org/10.1029/2009GL037820.

Weingartner, T.J., Okkonen, S.R., Danielson, S.L., 2021. Chapter 25. Physical Oceanography, in: The Bowhead Whale. INC, pp. 381-402. Doi: 10.1016/B978-0-12-818969-6.00025-X.

Weydmann, A., Zwolicki, A., Muś, K., Kwaśniewski, S., 2015. The effect of temperature on egg development rate and hatching success in Calanus glacialis and C. finmarchicus. Polar Res. 34, 1–8. https://doi.org/10.3402/polar.v34.23947.

Woodgate, A.R., Peralta-Ferriz, C., 2021. Warming and reshening of the Pacific inflow to the Arctic From 1990–2019 implying dramatic shoaling in Pacific winter water ventilation of the Arctic water column. Geophys. Res. Lett. 48, 1–11. https://doi.org/10.1029/2021GL092528.

Wursing, B., Clark, C.W., 1993. Behaviour. In: Burns, J.J., Montague, J.J., C., C. (Eds.), The Bowhead Whale. The Society for Marine Mammalogy, pp. 157-199.

Zuur, A., Ieno, E., Walker, N., Saveliev, A., Smith, G., 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY. https://doi.org/10.1016/B978-0-12-387667-6.00013-0.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.

Møller, A.P., Jennions, M.D., 2002. How much variance can be explained by ecologists and evolutionary biologists? Oecologia 132, 492–500. https://doi.org/10.1007/s00442-002-0952-2. I add it here because I do not seem to be able to edit the text.

JASCO, 2009. Appendix A. Automated detection and classification of marine mammal vocalizations, Northeastern Chukchi Sea Joint Acoustic Monitoring Program 2009-2010.

Further reading

Stafford, K.M., Castellote, M., Guerra, M., Berchok, C.L., 2018a. Seasonal acoustic environments of beluga and bowhead whale core-use regions in the Pacific Arctic. Deep Res. Part II Top. Stud. Oceanogr. 152, 108–120. https://doi.org/10.1016/j.dsr2.2017.08.003.