

Faculty of Biosciences, Fisheries and Economics Department of Arctic and Marine Biology

# **Singers of the High Arctic; Seasonal acoustic presence of Spitsbergen bowhead whales (***Balaena mysticetus***) around Svalbard, Norway**

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> **BIO-3950 (60 ECTS) Master's Thesis in Biology**

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**Singers of the High Arctic; Seasonal acoustic presence of Spitsbergen bowhead whales (***Balaena mysticetus***) around Svalbard, Norway**

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#### **Abstract**

Marine mammals throughout the circumpolar Arctic are facing profound levels of environmental change due to climate warming. Among them is the bowhead whale (*Balaena mysticetus*), an Arctic endemic cetacean that spends its entire life in Arctic waters and lives in tight association with sea ice habitats. The Spitsbergen bowhead whale population resides in the Northeast Atlantic, where they were hunted to near extinction during commercial whaling in the previous centuries. In this study, Passive Acoustic Monitoring (PAM) was used to analyse their seasonal and spatial trends at six different sites around the Svalbard Archipelago, Norway. A total of 47,232 audio files, recorded between 2017 and 2022, were analysed for bowhead whale vocalizations. The analyses focused on data collected between October and May, using a combination of Long-Term Spectral Averages (LTSA's) and visual/auditory verification. These findings were subsequently correlated to seasonal changes in environmental conditions. Bowhead whale vocalizations were detected at all study sites, but with significant variation between locations as well as some interannual variation. The consistent and high detection rates of singing west and east of Svalbard suggest that these sites may serve as key areas for bowhead whale overwintering and breeding. In contrast, the lower and fluctuating detection rates in the area north of Svalbard suggest that it serves as a movement corridor between regions. Significant positive correlations were found between bowhead whale acoustic activity and high sea ice concentrations, emphasizing their highly ice-affiliated nature. This study provides novel information on the distribution and habitat use of Spitsbergen bowhead whales and raises concern for the recovery of this population in an Arctic that faces rapid sea ice habitat loss.

**Keywords:** Arctic whales · East Greenland-Svalbard-Barents Sea Population · Passive Acoustic Monitoring · Phenology · Sea Ice · Climate Change · Song

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### <span id="page-5-0"></span>**1 Introduction**

The Arctic features some of the most unique and remote ecosystems on the planet and is home to some highly specialized species of marine mammals. Arctic ecosystems are currently facing profound environmental changes due to global warming. A phenomenon called 'Arctic amplification' is driving a rapid rate of change in this area, which is warming nearly four times faster than the global average (Rantanen et al., 2022). One of the principal results is a rapid rate of sea ice loss, which creates dark surfaces that reduce albedo, further accelerating the rate of warming (Kim et al., 2016). The annual minimum sea ice extent is currently decreasing by 13% per decade, relative to the average extent from 1981 to 2010 (Druckenmiller et al., 2021). The impacts of these changes are causing great concern for all Arctic endemic marine mammals, because of their limited ability to adapt to rapidly changing environmental conditions (Kovacs et al., 2021). Natural selection for adaptive genotypes is too slow for most High Arctic species because of their long generation times, and phenological changes are not always feasible (Gilg et al., 2012). For many species, conditions at the southern limits of their original ranges might no longer meet their ecological needs (Laidre et al., 2008), resulting in northward shifts in distribution, migration endpoints or foraging grounds (Storrie et al., 2018; Bengtsson et al., 2022; Chambault et al., 2022; Vacquié-Garcia et al., 2024). Information on species' geographical ranges and their habitat use is fundamental for understanding their ecology, and for predicting their response to environmental change (Gaston & Fuller, 2008). However, this information is still lacking for some Arctic marine mammal populations, and it is especially challenging to obtain for highly mobile and cryptic species such as Arctic endemic cetaceans.

The bowhead whale (*Balaena mysticetus*) is the largest and longest-lived cetacean that resides in the Arctic. It is the only baleen whale that spends its entire life in Arctic waters, and it possesses behavioural, physiological and morphological adaptations to live within this harsh climate (George, 2009). Their large body size and thick blubber layer insulate them from the cold (Rugh & Shelden, 2009) and allow them to store large amounts of energy. This is critical, because food availability is highly seasonal in the polar environment (Ferguson et al., 2010a). Furthermore, they lack a dorsal fin and can use their massive head to break through sea ice up to 60 cm thick for breathing. These adaptations allow them to occupy areas with high ice concentrations (George et al., 1989), which is important because bowhead whales are a highly ice-affiliated species. Sea ice habitats provide a spatially extensive environment which is virtually disease-free and low in competition, and it offers a seasonally rich food supply (Vacquié-Garcia et al., 2017). Sea ice also provides shelter from rough seas, as well as protection from the bowhead whales' only natural predator - the killer whale (*Orcinus orca*) (Matthews et al., 2020).

Based on both their geographic distribution as well as genetic analyses, bowhead whales can be subdivided into four distinct populations: one in Sea of Okhotsk Sea; one in the Bering-Chukchi-Beaufort seas; one in the East Canada-West Greenland area; and one in the East Greenland-Svalbard-Barents Sea area (hereafter referred to as the Spitsbergen population) (Baird & Bickham, 2021). While all four of these recognized populations were reduced greatly by commercial whaling during the  $17<sup>th</sup>$  to  $19<sup>th</sup>$  centuries, the Spitsbergen population was most dramatically impacted. Initially, this was one of the biggest bowhead whale populations, estimated to number well over 50,000 adult individuals in 1611 (Allen & Keay, 2006). However, after extensive exploitation this population was deemed 'virtually extinct' by 1911, with only tens of individuals estimated to be left (Christensen et al., 1992). Over the last two decades, several studies have suggested that the population is somewhat larger than previously thought (Stafford et al., 2012; Vacquié-Garcia et al., 2017) and that a gradual recovery might be taking place (Boertmann et al., 2015; Tervo et al., 2023). Abundance surveys indicate that the current size of the Spitsbergen population is more likely to comprise several hundred individuals, although data are still lacking for meaningful trend assessments.(Boertmann et al., 2015; Kovacs et al., 2020)

The Spitsbergen bowhead whale population occupies waters of the northern Barents Region, between East Greenland and Franz Josef Land in Russia (Kovacs et al., 2020). While all other bowhead whale populations have distinct seasonal migration patterns that track the receding ice edge northwards towards the High Arctic in summer and southwards again when ice formation starts in late fall or early winter (Heide-Jørgensen et al., 2006; Quakenbush et al., 2010; Szesciorka & Stafford, 2023), the Spitsbergen population exhibits a different pattern. They are found at the northernmost latitudes of their range in winter and move southwards in summer (Lydersen et al., 2012). Some individuals spend the winter in almost completely ice-covered areas, up to hundreds of kilometres inside the ice edge, where they likely make use of polynyas (areas of open water surrounded by sea ice) as well as cracks and leads in the ice to breathe. It is not precisely known why their migratory behaviour differs so radically from their conspecifics in the Bering-Chukchi-Beaufort Seas and East Canada-West Greenland region (Kovacs et al., 2020). Possible factors that might play a role in the habitat preference of the Spitsbergen bowhead whales include seasonal food availability (Wiig et al., 2007), sea ice conditions and their history with extensive human exploitation; animals that showed a strong preference for ice-affiliation were those that survived commercial whaling (Kovacs et al., 2020).

Bowhead whales feed primarily on pelagic and epibenthic zooplankton (e.g. copepods, euphausiids, mysids and amphipods) filtered from the water with their long baleen plates. It is assumed that most of their feeding is done during summer, as this is the period when highdensity prey is most readily available (Ferguson et al., 2010a). However, several studies suggest that some feeding also takes place outside the summer months (Lowry et al., 2005; Heide-Jørgensen et al., 2013). Little is known about the diet and feeding behaviour of Spitsbergen bowhead whales. Food availability in this area is driven by primary production in the marginal ice zone, polynyas and melt ponds. Oceanic currents also play an important role in the input of nutrients and biomass in this area (Wold et al., 2011). Warm, nutrient-rich Atlantic water is transported into the Arctic Ocean via the West-Spitsbergen Current, where it meets cold, icefilled Arctic water from the East Greenland Current, flowing southwards out of the Arctic Ocean (Vernet et al., 2019). This frontal region creates conditions for high productivity, resulting in large aggregations of copepods that bowhead whales can feed on (Wiig et al., 2007).

Page **3** of **55** To understand more about bowhead whale habitat selection, behaviour, and distribution in relation to their environment, several studies have been performed using sighting data (Moore, 2000; Shpak & Paramonov, 2018) or satellite tracking (Ferguson et al., 2010a; Lydersen et al., 2012; Kovacs et al., 2020; Citta et al., 2023). Satellite tracking is currently the most common method to track an individual's movements over long distances. However, there are methodological and technical challenges with bowhead whale tagging operations, and tagging is (at least mildly) invasive (Robbins et al., 2013). Furthermore, satellite tracking studies are constrained by limited sample sizes, due to the logistic and financial costs of the satellite tags and tagging operations. Visual observations are limited through accessibility in ice-covered areas, as well as extreme seasonal variation in light conditions and surface weather conditions. Therefore especially vessel-based surveys often represent an underestimation of the actual number of individuals present (Charif & Clark, 2009). Because bowhead whales prefer areas with high ice concentrations, which are less accessible than those typically covered by most vessel-based surveys, they are rarely surveyed. For the same reason, they are rarely reported in citizen science sightings databases, such as the Marine Mammal Sightings Database (MMSD) for Svalbard (Bengtsson et al., 2022). An alternative method for studying vocal species of whales makes use of passive acoustic monitoring (PAM). PAM involves deploying hydrophones to detect and record vocalizations of marine mammals. Although most

vocalizations do not occur at a constant rate and thus the absence of acoustic detections does not guarantee that no individuals were present, PAM still allows for autonomous, non-invasive monitoring of acoustic presence over large spatial and temporal scales (Menze, 2020). It has proven to be a useful tool for studying distributions and habitat use of marine mammals, and it has been successfully used to study relationships between phenology and environmental variables for many Arctic species (e.g. Ahonen et al., 2019; Stafford et al., 2021; Szesciorka & Stafford, 2023). Since bowhead whales have an extensive and varied acoustic repertoire and often reside in inaccessible ice-covered habitats, they are excellent subjects for passive acoustic studies.

Following the classification of the acoustic repertoire of bowhead whales described by Stafford et al. (2012), their vocalizations can be divided into three broad types; simple calls, call sequences and song. Simple calls are generally described as low frequency moans, with most of their acoustic energy under 500 Hz. They can be both frequency-modulated (FM) or amplitude-modulated (AM) and are produced without a distinct pattern. Simple calls are believed to be used for socializing and communication between individuals, and are produced year-round (Stafford et al., 2012). When simple calls are repeated in bouts of similar calls every 2 to 5 s, they are referred to as a call sequence (Clark & Johnson, 1984; Stafford et al., 2008). The duration of these regularly spaced, repeated sequences can vary, from less than one minute to many minutes (Blackwell et al., 2007). In winter, call sequences can be repeated for several weeks at a time (George & Thewissen, 2021). Compared to both simple calls and call sequences, song is much more complex. It consists of closely spaced 'song notes', which can be combinations of repetitive, broadband FM and AM calls. The frequency range of song can be up to 5 kHz and singing can last for hours at a time. Bowhead whales possess the unique ability to produce both high- and low-frequency and FM and AM sounds simultaneously, which is referred to as 'two-voiced singing' (Stafford et al., 2012). Songs are produced seasonally and are thought to be produced by male bowhead whales, serving as an acoustic display to compete with rival males and attract candidate mates (Diogou et al., 2023). In a recent study on the Spitsbergen bowhead population it was found that there is extraordinary intra- and inter-annual variability in these songs, with 184 different songs recorded over a 3-year period (Stafford et al., 2018a).

Page **4** of **55** Due to advances in sensor technology and increasing knowledge of bowhead whale acoustic behaviour within the last few decades, PAM has become a useful method to reveal more about distribution, migration patterns and behavioural ecology (Moore et al., 2010; Charif et al., 2013; Diogou et al., 2023). Recent studies on bowhead whale occurrence in western Greenland, western Fram Strait and through the Bering Strait (Ahonen et al., 2017; Chambault et al., 2018; Szesciorka & Stafford, 2023) have effectively used PAM to monitor populations and found correlations between their occurrence and environmental factors. Such studies are becoming increasingly important in the context of global warming and rapid environmental change in the Arctic.

This study investigates the acoustic presence of Spitsbergen bowhead whales across regions west, north and east of Svalbard during fall, winter and spring. PAM data from six different locations was used to (1) study seasonal and spatial trends of bowhead whale acoustic presence and singing behaviour and (2) investigate the correlation between both acoustic presence and song presence and seasonal changes in environmental factors, such as sea ice cover.

# <span id="page-10-0"></span>**2 Methods**

## <span id="page-10-1"></span>**2.1 Acoustic data collection**

The passive acoustic data used in this study was collected at six different locations around the Svalbard Archipelago, between 78.8° to 81.4° N and 5° W to 32.3° E (Figure 1). At four of these locations (Fram Strait, Atwain, M1 and M2), an Autonomous Underwater Recorder for Acoustic Listening (AURAL M2/M3, Multi-Électronique Inc.; HTI-96-MIN hydrophone with receiving sensitivity of  $-164 \pm 1$  dB re 1V  $\mu$ Pa – 1) was deployed on an oceanographic mooring. These four moorings were deployed and maintained by the Norwegian Polar Institute. At the remaining two study locations (13E and 26E), the acoustic data was collected via an M5-V30- 370 hydrophone (GeoSpectrum Inc.; hydrophone sensitivity of  $-164.2 \pm 1$  dB re 1V  $\mu$ Pa) attached to an AMAR-G3-UD recording instrument. These two moorings were deployed and maintained by the Norwegian Defence Research Establishment. The six locations in this study were chosen to provide coverage of different regions across the geographical range of Spitsbergen bowhead whales, including the western, northern, and eastern areas of the Svalbard Archipelago, which encompass a wide range of environmental conditions.



*Figure 1. Study area and mooring locations around Svalbard, indicated by the red dots. Bathymetric dataset from GEBCO 2023 under-ice bathymetry, accessed via: https://www.gebco.net/data\_and\_products/gridded\_bathymetry\_data/.*

To capture the singing season of the bowhead whales, which typically starts in late October or early November and ends in April or early May (George & Thewissen, 2021), acoustic data was analysed for an 8-month period between October and May. For the Fram Strait, M1 and M2 locations, two sampling periods were available for analyses, while for 13E, 26E and Atwain only one sampling period was available, resulting in a total of nine sampling periods. Between all nine sampling periods, the data spanned from October 2017 until May 2022. For 26E (2018- 2019) and M1 and M2 (2019-2020), the sampling periods did not cover the full 8-month period but started later or ended earlier. Due to the limiting effects of battery life and hard drive capacity, the duty cycles and sampling rates varied slightly between sampling periods. The duty cycles ranged between 6 and 20 minutes recorded every hour, and sampling rates varied between 16 and 128 kHz. Notably, even the lowest sampling rate in this range is sufficient to capture the entire bandwidth of bowhead whale vocalizations (Szesciorka & Stafford, 2023). For locations 13E and 26E, the hourly duty cycle alternated between two consecutive low frequency recordings, followed by one high frequency recording. Full deployment details for each sampling period are presented in Table 1.

*Table 1. Mooring metadata. Data sources: 1 = Norwegian Polar Institute, 2 = Norwegian Defence Research Establishment. \* indicates alternating sampling, where two low frequency recordings were followed by one high frequency recording.*

Location	Recording	Recording	Latitude	Longitude	<b>Deployment</b>	<b>Bottom</b>	<b>Sample</b>		<b>Duty Cycle Total number</b>	Data
	<b>Start</b>	End			Depth (m)		Depth (m) Rate (kHz)	(min/h)	of audiofiles	<b>Source</b>
	Fram Strait 01/10/2018 31/05/2019		78,84 N	5.00 W	81	1022	32	12	5832	
	Fram Strait   01/10/2018 31/05/2022		78,84 N	5.00 W	81	1022	128	6	5832	
13E		01/10/2019 31/05/2020	80,45N	13.20 E	840	1050	16/32*	20	5856	$\overline{2}$
26E		19/10/2018 31/05/2019	81,30 N	26,00 E	1155	1365	16/64*	20	5422	2
Atwain		01/10/2017 31/05/2018	81.41 N	31,24 E	55	206	32	12	5832	1
M1		18/11/2019 08/02/2020	79,58 N	28,07 E	60	252	32	12	2104	
M1		01/10/2021 31/05/2022	79.58 N	28,07 E	60	252	32	12	5818	1.
M <sub>2</sub>		18/11/2019 31/05/2020	79,68 N	32,31 E	67	350	32	12	4704	
M <sub>2</sub>		10/01/2020 31/05/2021	79.68N	32.31 E	67	350	32	12	5832	

### <span id="page-11-0"></span>**2.2 Acoustic data analysis**

Prior to the scoring of the 47,232 collected audio files, Long-Term Spectral Averages (LTSA's) were created to investigate the contribution of bowhead whale vocalizations to the overall soundscape. The LTSA's spanned the entire length of each sampling period (i.e. from the first recording to the last recording) and were made using the PAMGuide analysis tool in MATLAB (1 Hz resolution, 60 s time averaging, 50% overlap, Hanning window) (Merchant et al., 2015). The LTSA's were investigated for the presence of increased sound levels in frequencies that represent bowhead whale vocalizations.

In the next analytical phase, shorter 12-hour LTSA's were used for the detection of bowhead whale acoustic presence and song presence in each individual audio file, as this has been proven to be a successful method for investigating the presence of bowhead whale vocalizations (Szesciorka & Stafford, 2023). With the use of the open-source bioacoustics software PAMGuard (version 2.02.07; available at http:/www.pamguard.org) (Gillespie et al., 2009), all acoustic files were pre-processed for LTSA construction. After manually testing the settings for LTSA creation and visualization, the optimal settings for detecting bowhead whale vocalizations were determined and applied: Fast Fourier Transform (FFT) with a length of 4,096 data points, 75% overlap and Hanning window, with LTSA settings at an averaging interval of 5 seconds. For sampling periods where the duty cycle alternated between high and low frequency recordings, the high frequency audio files were down-sampled to match the sampling rate of the low frequency files, using the decimator module in PAMGuard. Additionally, for the sampling period where the sampling rate was 128 kHz, audio files were down-sampled to 32 kHz, in order to reduce processing time and match the frequency range of most other sampling periods. All down-sampling was performed using a low pass IIR Chebyshev filter, with a cut off frequency of 0.8 times the Nyquist frequency (0.4 times the sampling rate).

After processing the audio files in PAMGuard, 12-hour LTSA's were plotted using MATLAB (version R2023a), with a frequency range of  $0 - 4,000$  Hz and colour limits set to 40 - 150. Subsequently, these LTSA's were visually assessed, and each hour was scored for the presence of bowhead whale vocalizations. When bowhead whale acoustic presence was found that consisted of simple units, without any broadband components or two-voiced singing, hours were scored positive for acoustic presence. Hours that contained repeated, complex units with at least one broadband component were scored positive for both acoustic presence and song presence. An example of song that is visible for 12 consecutive hours of an LTSA can be found in Figure 2a. An example of a simple, repeated call sequence that is visible for four consecutive hours of an LTSA can be found in Figure 2b.



*Figure 2. Long-Term Spectral Average (LTSA) depicting a) 12 hours of bowhead whale song, recorded at Fram Strait, 3 January 2022 and b) bowhead whale call sequences (indicated by the red box), recorded at M2, 20 April 2020. Black dashed lines indicate zoomed-in spectrograms showing more detailed depictions of the vocalizations.*

Hours that contained: 1) sounds of overlapping vocalizing marine mammals (e.g. humpback whales in early fall or bearded seals in spring); or 2) interfering noise from e.g. ice formation or hydrophone strumming; or 3) sounds of interest that were either too faint or short to be definitively scored as bowhead whale were marked for later verification. Verification of these files took place through both visual and auditory assessment of spectrograms in Raven Pro 1.5 (Bioacoustics Research Program, Cornell Lab of Ornithology). No quantitative assessments were done during the scoring process, only the hourly presence or absence of bowhead whales and the presence of song were documented.

### <span id="page-14-0"></span>**2.3 Environmental data collection**

Daily sea ice concentration data were retrieved from sea ice remote sensing datasets of the University of Bremen, a service component of the GMES Polar View project and the Arctic Regional Ocean Observing System (ArcticROOS). Sea ice concentrations were retrieved by applying the ARTIST Sea Ice (ASI) algorithm to satellite-derived microwave radiometer data, obtained through the Advanced Microwave Scanning Radiometer 2 (AMSR-2) sensor. These data were organized into a polar stereographic grid with a spatial resolution of  $3.125 \text{ km}^2$ (Spreen et al., 2008). Sea ice concentrations, ranging from 0 (open water) to 100 (complete sea ice cover) were computed daily for each mooring location and sampling period in the Statistical Software R (v4.4.1), using the *sp* and *raster* packages (v2.1.4; Pebesma et al., 2005 and v3.6.26; Hijmans, 2023 respectively). Based on estimated propagation rates of bowhead whale vocalizations (Bonnel et al., 2014), ice concentrations were averaged over a 30 km radius around each mooring location.

Sea ice extent data were retrieved from the National Snow and Ice Data Center (NSIDC, Boulder, Colorado), where satellite passive microwave-derived data are used for calculating the Sea Ice Index. This Sea Ice Index data has a spatial resolution of  $25 \text{ km}^2$ , wherein a grid cell is considered 'ice' at ice concentrations of 15% or higher. Therefore, the ice edge is defined by the 15% concentration contour (Fetterer et al., 2008). Daily GeoTIFF files depicting the sea ice extent for the Northern Hemisphere were retrieved for each sampling period. The daily minimum distance (km) from each mooring to the ice edge was computed in R using the *rgdal* (v1.6.7; Bivand et al., 2023) and *raster* packages. These distances were subsequently transformed so that a positive distance to the ice edge indicates an ice-covered mooring, whereas a negative distance to the ice edge means that the mooring was in open water.

Other environmental data were retrieved from reanalysis datasets of the EU Copernicus Marine Service. Mass concentration of chlorophyll a  $(mg/m<sup>3</sup>)$  was obtained from the Global Ocean Biogeochemistry Hindcast, with a spatial resolution of 0.25° x 0.25°. Mass content of zooplankton expressed as carbon in sea water  $(g/m^2)$  was obtained from the Global Ocean Low and Mid Trophic Levels Biomass Content Hindcast, with a spatial resolution of 0.083° x 0.083°. Sea surface temperature (°C) was obtained from the OSTIA global sea surface temperature reprocessed product, with a spatial resolution of 0.05° x 0.05°. For all these variables, daily values were retrieved for each study location and sampling period in R, using *sp* and *raster* packages. Similar to the sea ice concentration data, daily means were calculated over a 30 km radius around each mooring location.

### <span id="page-15-0"></span>**2.4 Data exploration and statistical analyses**

Before exploring the statistical relationships between the environmental variables and bowhead whale acoustic presence or song presence, visual comparisons between collected environmental data and acoustic detections were conducted. Because the acoustic analyses focused on data from fall, winter and spring, the levels of zooplankton and chlorophyll a mass were very low across all study sites, with almost no variation. These variables were therefore only visually inspected but excluded from the statistical analyses. To examine the effects of the remaining environmental variables on the acoustic presence and singing behaviour, Generalised Additive Models (GAMs) were fitted, using the *mgcv* package (v1.9.1; Wood et al., 2011) in R. Due to the high variability in environmental conditions across the different study locations and initial visual data exploration indicating significant differences in the responses to environmental variables, the GAMs were fitted separately for each location. Furthermore, separate GAMs were used to examine the degree to which the environmental variables influenced either acoustic presence or song presence.

Before fitting the models, the predictors sea surface temperature (SST), sea ice concentration (SIC) and distance to ice edge (DTI) were checked for collinearity, both through the Pearson Correlation Coefficient, using the *stats* package (v4.4.1) in R, as well as using the *vif* function from the *car* package (v3.1.2; Fox et al., 2019). For most locations, a strong negative correlation was found between SST and SIC, SST and DTI, as well as a strong positive correlation between DTI and SIC. Because high collinearity can affect both model performance and interpretation, only SIC was kept as a predictor variable.

Daily acoustic presence and daily song presence (0-24 hrs/day) were transformed to daily proportional acoustic presence and daily proportional song presence (0-1) and SIC values were scaled. The sampling period 2019-2020 at M1 was excluded from the statistical analysis, due to the considerably shorter period with acoustic data available. Predictors SIC and month were included as smooth terms with a smoothness degree (k) of 3, which was determined as part of the model fitting process. The models were fitted using restricted maximum likelihood (REML) estimation, to ensure robust and efficient parameter estimation. The corAR1 term from the *nlme* package (v3.1.164; Pinheiro et al., 2024) was included in the model, to account for potential

autocorrelation. For the locations with two sampling periods, interaction terms between the covariates and the sampling period were included. This allowed for the effects of SIC and month to vary per sampling period, accounting for other uncaptured environmental differences between the two periods. The full models for these locations were specified as:

*acoustic presence* =  $_{s1}$ (SIC, *by sampling period*) +  $_{s2}$ (month, *by sampling period*) *+ sampling period*

*song presence* =  $_{s}$ *(SIC, by sampling period)* +  $_{s}$ <sub>2</sub> $(month, by sampling period)$ *+ sampling period*

and the full models for locations with a single sampling period were specified as

*acoustic presence* =  $_{s1}(SIC) + _{s2}(month)$ 

*song presence* =  $_{s1}(SIC) + _{s2}(month)$ 

where  $_{s1}$  and  $_{s2}$  are smooth functions to be estimated.

During the model fitting process, models were checked for dispersion issues by calculating the ratio of the residual deviance to the residual degrees of freedom. For all locations the model residuals were under-dispersed  $(0.15 - 0.56)$ , indicating less variability in the acoustic data than expected by the model. This was most likely caused by zero/one-inflation issues (Udistribution), because the acoustic presence and song presence were heavily inflated with days without any detections, or days with 24 hours of detections. To address this issue, models were compared using either the Tweedie family (Tweedie, 1984), because this is a flexible distribution suitable for zero-inflated data (Wood et al., 2016), or using a quasi-family; quasipoisson for count data (0-24) and quasi-binomial for proportional data (0-1), because these families add a dispersion parameter to the model (Zuur et al., 2009). The comparison showed a slightly better model fit when using the quasi-binomial family, therefore this was chosen for the final models.

After fitting the models, predicted values for presence and song were obtained using the predict function from the *mgcv* package, and plotted using the *ggplot2* package (v3.5.1; Wickham 2016). Model outcome details and residual plots can be found in Appendix A.

# <span id="page-17-0"></span>**3 Results**

## <span id="page-17-1"></span>**3.1 Acoustic energy contribution to the overall soundscape**

Across all LTSA's created for investigating the contribution of bowhead whales to the overall soundscape, bowhead whale vocalizations were detected in eight out of the nine sampling periods. In Fram Strait 2018-2019, a cloud of increased energy levels that reflects broadband bowhead whale vocalizations (hereafter referred to as song cloud) was observed from late December until late January (Appendix Figure B1a). In Fram Strait 2021-2022 a song cloud started in late November and continued until at least mid-January (Appendix Figure B1b). At 26E 2018-2019, a short song cloud was observed late-January (Appendix Figure B3). At Atwain 2017-2018, some increased acoustic energy around 300 Hz was detected between mid-November and mid-January reflecting lower frequency bowhead whale vocalizations; however, no clear song cloud was seen (Appendix Figure B4). During both sampling periods at M1, a short song cloud was observed from mid to late November (Appendix Figure B5). At M2 2019- 2020, a song cloud was seen from mid-November to early December (Appendix Figure B6a). Additionally, a clear band of increased acoustic energy around 250-300 Hz was noted, reflecting lower frequency bowhead whale vocalizations. Sometimes these vocalizations appeared to be accompanied by acoustic energy in the higher frequencies, although no clear song cloud was present. At M2 2020-2021, a very clear song cloud was seen from early December until early February (Appendix Figure B6b).

## <span id="page-17-2"></span>**3.2 Acoustic detection**

A total of 3,936 12-h LTSA's were generated and visually assessed for the hourly presence of bowhead whale vocalizations. Bowhead whale acoustic presence and song presence were detected in all nine sampling periods (Figure 3).



*Figure 3. Daily acoustic detections for nine sampling periods across six study locations. Daily counts of song (light blue) and non-song (dark blue) detections are stacked, as song vocalizations also count as bowhead whale acoustic presence. Only the analysed period, from October to May, is shown on the x-axis.*

### <span id="page-18-0"></span>*3.2.1 Bowhead whale acoustic presence*

In total, 20,617 hours containing bowhead whale acoustic presence (either song or non-song vocalizations) were detected across all sampling periods, yielding an overall detection rate of 43.8%. The detection rate of bowhead whale acoustic presence varied across locations and years. The highest detection rates were observed at the M2 and Fram Strait moorings, with bowhead whale vocalizations detected in 74% and 63% of recorded hours, respectively.

Across all sites, acoustic presence was predominantly found between November and April, peaking in December and January (Appendix Figure C1). Few vocalizations were detected in October and May. For both of the Fram Strait sampling periods, as well as the M1 2021-2022 and M2 2020-2021 sampling periods, a clear pattern can be seen wherein vocal activity increases until a period of relatively constant high presence is reached, followed by a gradual decrease (Figure 4). In the sampling periods 13E 2019-2020, 26E 2018-2019 and Atwain 2017- 2018, vocal activity was much more sporadic, with many gaps in the detections.



*Figure 4. Average daily detections of bowhead whale acoustic presence for each sampling period. Colour intensity indicates the average daily detections (0-24) of bowhead whale acoustic presence per week. Grey boxes indicate weeks without available acoustic data.* 

#### <span id="page-19-0"></span>*3.2.2 Bowhead whale song*

Bowhead whale song was detected in 9,776 hours across all sampling periods, yielding an overall detection rate of 20.8%. The earliest song detection occurred on the 25<sup>th</sup> of October, at Fram Strait in 2021. The latest song presence was detected on the 22<sup>nd</sup> of May, at 13E in 2020. While the predominant singing period varied across locations and years, most of the hours containing song were detected in December and January, and little to no song was detected in October and May (Appendix Figure C1).

The two sampling periods in Fram Strait showed a similar pattern in song presence, with a relatively constant period of high singing activity mid-winter (Figure 5). However, some variation between the two sampling periods can be seen in the duration and intensity of singing; detection rates in 2021-2022 were higher than in 2018-2019. The duration of the singing period, i.e. the time between the first and last song detected, was 190 days for 2021-2022 and 143 days for 2018-2019. In both years, short 'gaps' were present within the otherwise relatively constant singing period. The locations 13E, 26E and Atwain, which are all located north of Svalbard, showed variable patterns in song presence (Figure 5). Compared to Fram Strait, much less singing was detected at these locations. Furthermore, the days containing singing were much more sporadic throughout the analysed period, with little to no consistent singing period. Large intervals between days with song were found; for example, at 13E there is a period of 115 days without singing between two detections of song. For both locations north-east of Svalbard, M1 and M2, data was analysed for two sampling periods. At M1, all song detections occurred within the same four-week period in November – early December in both sampling periods (Figure 5). In contrast, the two sampling periods at M2 showed varying patterns of song presence; in 2019-2020 song detections were spread out from mid-November until early April, whereas in 2020-2021, a more concentrated singing period was observed from December to

early February. This singing period was followed by a 72-day period without song detections, after which a few hours containing song were detected in late April. Note that the sampling period started on 18 November in 2019-2020 at both M1 and M2, leaving part of the fall without data. Furthermore, the sampling period ended on 08 February 2020 for M1, leaving less than 3 months recorded.



*Figure 5. Average daily detections of bowhead whale song for each sampling period. Colour intensity indicates the average daily detections (0-24) of bowhead whale song per week. Grey boxes indicate weeks without available acoustic data.* 

### <span id="page-21-0"></span>**3.3 Presence and song in relation to environmental cues**

#### <span id="page-21-1"></span>*3.3.1 Fram Strait*

During both the 2018-2019 (Figure 6a) and 2021-2022 (Figure 6b) sampling periods at Fram Strait, sea ice concentrations were consistently high. The mooring remained ice-covered and sea surface temperatures were low, ranging between -1 and -1.9 °C. During the period between November and March, gaps in vocal presence and song can be seen in both sampling periods, some of which were correlated with periods of lower ice concentrations. Zooplankton and Chlorophyll a biomass were very low throughout both sampling periods.



*Figure 6. Bowhead whale acoustic presence in relation to environmental variables at Fram Strait in 2018-2019 (a) and 2021- 2022 (b). Top panel: bowhead whale daily acoustic presence (hrs/day) divided into total presence and song presence. Middle panel: sea ice concentration (%) (grey shaded area) and distance to ice edge (km). The dotted line represents mooring position relative to the ice edge, with negative distance indicating that the mooring is in open water and positive distance indicating*  ice-cover. Bottom panel: zooplankton (g/m<sup>2</sup>) and chlorophyll a (mg/m<sup>3</sup>) concentrations and sea surface temperature (°C).

The models showed a significant effect of SIC and month on both acoustic presence ( $R^2 = 0.73$ ) and song presence  $(R^2 = 0.69)$ . A significant positive correlation between SIC and acoustic presence, as well as song presence, were detected for ice concentrations of approximately 80% and higher for the 2021-2022 sampling period (Figure 7). In 2018-2019 this positive effect is less strong, but still present. For both sampling periods, the model showed a bell curve for the effect of month on presence, with the peaks for acoustic presence and song presence in January.



*Figure 7. Effects of Sea Ice Concentration (SIC) and month on (a) predicted acoustic presence and (b) predicted song presence at Fram Strait. Predicted values were derived from Generalized Additive models (GAMs) and plotted as dots. Red lines represent estimated splines for the 2018-2019 sampling period, blue lines represent the estimated splines for the 2021-2022 sampling period. These splines illustrate the smoothed relationship between the predictors (SIC and month) and the predicted values. Shaded areas represent the 95% confidence intervals.*

#### <span id="page-22-0"></span>*3.3.2 13E*

Ice concentrations at 13E were relatively low from October until mid-February, with few peaks of increased concentration (Figure 8). During this time, the mooring was mostly in open water, close to the ice edge. Vocalizations occurred sporadically, with little correlation to any of the collected environmental variables. From mid-February, sea surface temperature dropped, and ice concentrations increased to almost full ice cover until mid-May, during which time the mooring was situated deep within the ice. A small cluster of vocalizations, many of which were song, occurred at the end of April, again without any clear correlation with the environmental variables. Chlorophyll a biomass was close to zero throughout the whole sampling period. Zooplankton mass declined between October and February but seemed to have no impact on the detection of bowhead whale acoustic presence or song presence.



*Figure 8. Bowhead whale acoustic presence in relation to environmental variables at 13E in 2019-2020. Top panel: bowhead whale daily acoustic presence (hrs/day) divided into total presence and song presence. Middle panel: sea ice concentration (%) (grey shaded 'area) and distance to ice edge (km). The dotted line represents mooring position relative to the ice edge,*  with negative distance indicating that the mooring is in open water and positive distance indicating ice-cover. Bottom panel: *zooplankton (g/m<sup>2</sup> ) and chlorophyll a (mg/m<sup>3</sup> ) concentrations and sea surface temperature (°C).*

The models showed a small but significant effect of SIC and month on acoustic presence ( $R^2$  = 0.09), but no significant effects were found for song presence ( $\mathbb{R}^2 = 0.01$ ). A slight negative relationship between acoustic presence and SIC was found (Figure 9a).



*Figure 9. Effects of Sea Ice Concentration (SIC) and month on (a) predicted acoustic presence and (b) predicted song presence at 13E, in 2019-2020. Predicted values were derived from Generalized Additive Models (GAMs) and plotted as dots. Blue lines represent estimated splines from the GAMs. These splines illustrate the smoothed relationship between the predictors (SIC and month) and the predicted values. Shaded areas represent the 95% confidence intervals.*

#### <span id="page-24-0"></span>*3.3.3 26E*

At the 26E study location, ice formation did not start until mid-December, leaving the mooring in open water for the first few months of the sampling period (Figure 10). During this time, some scattered acoustic presence occurred from mid-November to early December. In late December and January, the temperature decreased and two large peaks in ice concentration occurred, resulting in the mooring being ice-covered. These peaks coincided with increased acoustic presence, and a period of song presence in late-January. In early February, ice concentrations decreased with increasing temperatures, leaving the mooring in open water. This coincided with a period of little acoustic presence. From mid-February ice concentrations increased once more, resulting in the mooring being deep inside the ice edge for the rest of the sampling period. During this time, scattered acoustic presence and song presence occurred until mid-April. Zooplankton and chlorophyll a biomass were both consistently low throughout the whole sampling period.



*Figure 10. Bowhead whale acoustic presence in relation to environmental variables at 26E in 2018-2019. Top panel: bowhead whale daily acoustic presence (hrs/day) divided into total presence and song presence. The grey area indicates days without acoustic data. Middle panel: sea ice concentration (%) (grey shaded area) and distance to ice edge (km). The dotted line represents mooring position relative to the ice edge, with negative distance indicating that the mooring is in open water and positive distance indicating ice-cover. Bottom panel: zooplankton (g/m<sup>2</sup> ) and chlorophyll a (mg/m<sup>3</sup> ) concentrations and sea surface temperature (°C).*

The models showed significant effects of SIC and month on acoustic presence ( $\mathbb{R}^2 = 0.49$ ) and song presence ( $\mathbb{R}^2 = 0.16$ ). Both acoustic presence and song presence increased steadily with increasing ice concentrations, until approximately 60% (Figure 11). After this concentration level, SIC had a negative effect on acoustic presence and song presence. The effect of month

on acoustic presence was bell-shaped, with a peak in late-January. This relationship was similar for song presence, but less pronounced.



*Figure 11. Effects of Sea Ice Concentration (SIC) and month on (a) predicted acoustic presence and (b) predicted song presence at 26E, in 2018-2019. Predicted values were derived from Generalized Additive Models (GAMs) and plotted as dots. Blue lines represent estimated splines from the GAMs. These splines illustrate the smoothed relationship between the predictors (SIC and month) and the predicted values. Shaded areas represent the 95% confidence intervals.*

#### <span id="page-25-0"></span>*3.3.4 Atwain*

During the entire sampling period, ice concentration fluctuated highly at Atwain, without extended periods of high ice concentrations (Figure 12). The mooring was ice covered from mid-November until February, and from mid-March until early-May. The rest of the time, the mooring was in open water. Acoustic presence and song presence also fluctuated, with acoustic detections during both periods of high and low ice concentration. Zooplankton and chlorophyll a biomass were both close to zero for the entire sampling period.

![](_page_26_Figure_0.jpeg)

*Figure 12. Bowhead whale acoustic presence in relation to environmental variables at Atwain in 2017-2018. Top panel: bowhead whale daily acoustic presence (hrs/day) divided into total presence and song presence. Middle panel: sea ice concentration (%) (grey shaded area) and distance to ice edge (km). The dotted line represents mooring position relative to the ice edge, with negative distance indicating that the mooring is in open water and positive distance indicating ice-cover. Bottom panel: zooplankton (g/m<sup>2</sup> ) and chlorophyll a (mg/m<sup>3</sup> ) concentrations and sea surface temperature (°C).*

Despite the high variability, the models showed highly significant effects of SIC and month on acoustic presence ( $\mathbb{R}^2 = 0.47$ ) and song presence ( $\mathbb{R}^2 = 0.51$ ). Acoustic presence increased steadily with increasing SIC (Figure 13a). The same positive effect of SIC on song presence was seen for ice concentrations above approximately the 30% concentration level (Figure 13b). A clear seasonal peak in acoustic presence occurred in January. Song presence also peaked in January, but the seasonal pattern was less distinct.

![](_page_26_Figure_3.jpeg)

*Figure 13. Effects of Sea Ice Concentration (SIC) and month on (a) predicted acoustic presence and (b) predicted song presence at Atwain, in 2017-2018. Predicted values were derived from Generalized Additive Models (GAMs) and plotted as dots. Blue lines represent estimated splines from the GAMs. These splines illustrate the smoothed relationship between the predictors (SIC and month) and the predicted values. Shaded areas represent the 95% confidence intervals.*

#### <span id="page-27-0"></span>*3.3.5 M1*

At M1 in the 2019-2020 sampling period, ice concentrations increased in late-October and remained high throughout most of the remaining period, resulting in continuous ice cover over the mooring (Figure 14). In 2021-2022, ice concentrations started to increase slightly later, in mid-November. The singing period coincided with the increasing ice concentrations, when the mooring went from being in open water to being ice covered. Whether this was the case for the 2019-2020 sampling period cannot be determined because no acoustic data were collected before mid-November (at which time the ice was already established over the mooring).

![](_page_27_Figure_2.jpeg)

*Figure 14. Bowhead whale acoustic presence in relation to environmental variables at M1 in (a) 2019-2020 and (b) 2021- 2022. Top panel: bowhead whale daily acoustic presence (hrs/day) divided into total presence and song presence. The grey area indicates days without acoustic data. Middle panel: sea ice concentration (%) (grey shaded area) and distance to ice edge (km). The dotted line represents mooring position relative to the ice edge, with negative distance indicating that the mooring*  is in open water and positive distance indicating ice-cover. Bottom panel: zooplankton (g/m<sup>2</sup>) and chlorophyll a (mg/m<sup>3</sup>) *concentrations and sea surface temperature (°C).*

Because the 2019-2020 sampling period at M1 was significantly shorter than all other sampling periods in this study, this year was not included in the statistical analyses. The model for acoustic presence in 2021-2022 showed a significant ( $\mathbb{R}^2 = 0.69$ ), but small increase of presence with increasing SIC (Figure 15). Furthermore, a significant relationship between month and acoustic presence was found, with peak acoustic presence in November and December, after which a gradual decline took place until mid-April. The model for song presence in 2021-2022 did not converge, and thus could not be used for interpreting the effects of SIC and month on the presence of song at this location.

![](_page_28_Figure_1.jpeg)

*Figure 15. Effects of Sea Ice Concentration (SIC) and month on predicted acoustic presence at M1, in 2021-2022. Predicted values were derived from Generalized Additive Models (GAMs) and plotted as dots. Blue lines represent estimated splines from the GAMs. These splines illustrate the smoothed relationship between the predictors (SIC and month) and the predicted values. Shaded areas represent the 95% confidence intervals.*

### <span id="page-28-0"></span>*3.3.6 M2*

At M2 in the 2019-2020 sampling period, ice concentrations increased in mid-October and remained consistently high throughout the rest of the sampling period (Figure 16). In 2020- 2021, temperatures remained high for much longer during fall, causing late ice formation; ice concentrations started to rise only in mid-December. This corresponded with a later start of the singing period in 2020-2021 compared to 2019-2020. It is not known when the acoustic presence or song presence started in 2019-2020, because acoustic data were not available before mid-November.

![](_page_29_Figure_0.jpeg)

*Figure 16. Bowhead whale acoustic presence in relation to environmental variables at M2 in (a) 2019-2020 and (b) 2020- 2021. Top panel: bowhead whale daily acoustic presence (hrs/day) divided into total presence and song presence. The grey area indicates days without acoustic data. Middle panel: sea ice concentration (%) (grey shaded area) and distance to ice edge (km). The dotted line represents mooring position relative to the ice edge, with negative distance indicating that the mooring is in open water and positive distance indicating ice-cover. Bottom panel: zooplankton (g/m<sup>2</sup> ) and chlorophyll a (mg/m<sup>3</sup> ) concentrations and sea surface temperature (°C).*

The models showed significant effects of SIC and month on acoustic presence ( $\mathbb{R}^2 = 0.83$ ) and song presence ( $\mathbb{R}^2 = 0.65$ ). A positive effect of ice concentration on presence was found for the 2019-2020 sampling period (Figure 17a). A similar positive trend could be seen for 2020-2021, although no significant relationship was established ( $p=0.09$ ). A significant, but fluctuating effect of SIC on song presence was found for the 2020-2021 sampling period (Figure 17b). The effect of month on presence and song was significant for both sampling periods. The 2020- 2021 sampling period showed a bell curve with peak acoustic presence and song presence in

January. In 2019-2020, presence peaked in January, after which it decreased with month. Song presence had a linear negative relationship with month from November to May.

![](_page_30_Figure_1.jpeg)

*Figure 17. Effects of Sea Ice Concentration (SIC) and month on (a) predicted acoustic presence and (b) predicted song presence at M2. Predicted values were derived from Generalized Additive Models (GAMs) and plotted as dots. Red lines represent estimated splines from the 2019-2020 sampling period, blue lines represent the estimated splines from the 2020-2021 sampling period. These splines illustrate the smoothed relationship between the predictors (SIC and month) and the predicted values. Shaded areas represent the 95% confidence intervals.*

## <span id="page-31-0"></span>**4 Discussion**

This study aimed to identify the seasonal and spatial trends of acoustic presence and singing behaviour of Spitsbergen bowhead whales throughout their core range. Additionally, it aimed to investigate the correlation between environmental factors, such as sea ice cover, and the acoustic presence and song activity. Bowhead whales were present and sang during each of the nine sampling periods. However, there were notable differences between the locations and years in terms of the length and intensity of periods with acoustic presence, as well as the patterns seen in the presence of song. Furthermore, significant but varying correlations were found between bowhead whale acoustic activity and sea ice concentration.

Acoustic presence at Fram Strait was characterized by a steady period of detected vocalizations throughout the winter season. Most of the detected vocalizations were song, thought to be emitted by male bowhead whales as a reproductive display. This constant and loud presence of bowhead whale song indicates that numerous bowhead whales were present near this sampling site throughout the winter (Stafford et al., 2012), and strengthens the theory that Fram Strait is a key breeding area for bowhead whales in this region. Ahonen et al. (2017) documented acoustic detections at this location between 2008 and 2014. Their work showed similar patterns of consistent and high bowhead whale presence during the winter months, although slightly more vocalizations were detected during fall and spring compared to the current study. This might be due to the limited ability to detect faint or short simple calls in LTSA's. These less prominent vocalizations could be underrepresented in this study, particularly in the months preceding and following the singing period. Furthermore, the duty cycle at Fram Strait during the 2021-2022 sampling period was 6 min/h, meaning there was potentially a slightly lower chance of bowhead whale vocalizations being detected compared to sampling periods with higher duty cycles. However, it is unlikely that the length of the duty cycle had a significant effect on the results reported herein, since the Fram Strait 2021-2022 sampling period showed the second highest detection rate for acoustic presence and the highest detection rate for song presence thus far reported in literature, despite the lower duty cycle.

Interannual differences in bowhead whale detections at this location are likely related to yearto-year differences in environmental conditions. The Fram Strait mooring was located approximately 340 km west of Svalbard and 270 km east of Greenland, situated on the continental shelf slope at a bottom depth of 1,022 m. Cold, nutrient-poor and relatively fresh water is exported southwards out of the Arctic Ocean at this location, via the East Greenland

Current (EGC). The EGC also exports substantial amounts of sea ice from across the Arctic Ocean, resulting in a heavy sea ice cover during winter, especially in Western Fram Strait (Hunkins, 1990). These environmental conditions, combined with the low amount of anthropogenic disturbance in the soundscape during the winter season (Ahonen et al., 2017) make for a highly suitable habitat and breeding ground for bowhead whales. The positive correlations between sea ice concentrations and acoustic presence as well as song presence further support that bowhead whales prefer habitats with high ice concentration for breeding.

The strong and consistent period of acoustic detections at Fram Strait stands in stark contrast to the sparse and variable acoustic presence detected north of Svalbard, especially at locations 13E and 26E. These two sites have not been studied previously with respect to bowhead whale acoustic presence. At both locations, the duty cycle was 20 min/h, meaning there was a slightly higher chance of detecting acoustic presence compared to sampling periods where duty cycles were lower. Despite this, these locations still showed the lowest level of acoustic presence and song. Detections occurred sporadically, with little indication that bowhead whales were present in these areas for extended periods of time. The detection rates for both acoustic presence and song were higher at Atwain, although the patterns remained irregular, with periods of high vocal activity interrupted by brief periods without vocalizations being detected.

Page **28** of **55** The 13E, 26E and Atwain moorings were all situated along the continental shelf slope north of Svalbard. In this region there is a large inflow of relatively warm, salty and nutrient rich Atlantic water coming from the West Spitsbergen Current (WSC). This sub-surface current plays a large role in determining regional environmental conditions (Lundesgaard et al., 2022; Wold et al., 2023). Ice conditions at these sites mainly consist of drift-ice and are highly variable due to fluctuating temperatures, as well as the effects of currents and wind on the ice pack. For large parts of the winter these moorings shifted back and forth between being ice-covered or situated in open water. These environmental conditions could explain the sparse and sporadic patterns in bowhead whale detections, both in terms of acoustic presence and song detections. Despite being located only  $\pm$  90 km apart, the higher detection rate at Atwain compared to 26E might be partly attributable to differences in bottom and deployment depth. While the 13E and 26E moorings were situated at bottom depths well over 1,000 m and deployment depths of 840 m and 1155 m respectively, the Atwain mooring was deployed in significantly shallower waters, at a bottom depth of 206 m and a deployment depth of 55 m. However, other environmental parameters could also have played a role. Although a slightly negative correlation between sea ice and presence was found at 13E, much stronger positive correlations were found at 26E and especially at Atwain. This might indicate that the bowhead whales north of Svalbard still make use of the sea ice habitats, despite the fluctuating and unpredictable ice conditions here.

The study locations to the east of Svalbard (M1 and M2) demonstrated high levels of acoustic presence with a clear period of extended bowhead whale site use, especially at M2. High levels of acoustic presence and song presence occurred in both sampling periods at M2, suggesting that this site may serve as another important area for bowhead whales and potentially a second breeding site for the Spitsbergen population. These results are similar to previous findings of bowhead whale acoustic presence in this area. Llobet et al. (2023) manually detected bowhead whale presence from the same acoustic data between November 2019 and September 2020, thus covering the 2019-2020 sampling period analysed in this study at M2. The high level of similarity between acoustic presence detected by Llobet et al. (2023)'s manual analysis, compared to using LTSA's, supports the methodologies used herein for detecting bowhead whale acoustic presence in a more time-efficient manner. A more modest acoustic presence was found at M1, compared to M2. This could be because M1 was situated slightly closer to the coast of Svalbard, further from the shelf edge and potentially exposed to slightly more ship traffic. The M2 study site was located slightly further off-shore and closer to the coastal polynyas around Franz Josef Land, which is another important area for Spitsbergen bowhead whales based on reported observations from the Russian archipelago (Wiig, 2006; Gavrilo, 2015). This could explain the higher detections rates of acoustic presence and song presence at M2, compared to M1. At M2 in the 2019-2020 sampling period, a clear band of high energy levels around 250-300 Hz can be seen in the LTSA spanning the full sampling period. This band reflects a continuous 'hum' of lower frequency bowhead whale calls. Since calls are produced relatively infrequently (Stafford 2022), this clear continuous band of call sequences can only be produced by multiple individuals overlapping their vocalizations with each other. This band is visible for nearly three months, from mid-December to early March, indicating a continuous presence of multiple individuals within the vicinity of the M2 mooring during this time.

Both M1 and M2 were situated on the continental shelf, in the northern part of the Barents Sea. These moorings were located downstream of two deep troughs, that act as 'gateways' for Atlantic Water from the WSC to be advected into the Barents Sea east of Svalbard. However, this region is also heavily influenced by sea ice drifting southwards between the Arctic Ocean and the Barents Sea (Lundesgaard et al., 2022). This causes a relatively stable ice cover at these study locations, but with large interannual variability in the timing of when the drift ice arrives.

During the 2019-2020 sampling periods at both M1 and M2, sea ice arrived early, in mid- to late October. Although no acoustic data was available until late November for both locations, bowhead whale song was detected immediately upon the start of each sampling period, suggesting an early start of the singing period. In contrast, during the 2020-2021 sampling period at M2, sea ice arrived much later, in December. This significant delay in ice cover appears to have caused a corresponding delay in the start of the singing period. Additionally, while the 2019-2020 sampling period at this location was characterized by approximately five months of intermittent singing, a much shorter but more continuous period of song took place in the following year. A similar pattern can be seen at M1: the singing period in 2021-2022 started late, corresponding with the delayed ice-arrival compared to 2019-2020, and was also restricted to a much shorter, but continuous 1-month window. The relationship between sea ice and bowhead whale acoustic presence at M1 was not very clear. There were no bowhead whale detections between February and May, whilst ice concentrations during this time were high. At M2, the relationship between sea ice and presence was slightly more positive, although for song the effect of sea ice in 2020-2021 fluctuated and was highest for intermediate ice concentrations. This was likely due to the singing period coinciding with ice arrival, but not continuing into the following period of consistently high ice concentrations.

The differences in acoustic presence and singing patterns observed across the six study locations, combined with the environmental differences between these regions, suggest that the area north of Svalbard serves as a movement corridor between the regions west and east of Svalbard, which seem to be the preferred areas for Spitsbergen bowhead whales. While tracking studies have shown that this population spends their winters in the northern-most latitudes of their geographical range, followed by southward movements towards the end of winter and in spring, less is known about their east-west movement patterns. Some tagged individuals have moved eastward from Fram Strait over to Franz Josef Land in Russia (Kovacs et al., 2020). A deeper understanding of social structure and potential site fidelity could probably be achieved by analysing song structure. Studies on song structure have been done for bowhead whales overwintering in Northeast Greenland coastal waters (Erbs et al., 2021), as well as humpback whales in Northern Norway (Tyarks et al., 2022). Some studies have suggested that bowhead whale song is not shared at the population level, but rather similar song structures occur within clusters of animals (Tervo et al., 2011; Johnson et al., 2015). Examining the temporal and spatial distribution of specific structures west and east of Svalbard might give some insight into

whether bowhead whales in this population associate differentially with some clusters of animals.

The modelling results in this study showed that acoustic presence peaked in mid-winter at most locations, with a gradual increase until January, followed by a subsequent gradual decrease toward the spring. For song presence, a similar pattern was notable at Fram Strait and M2, where most singing was observed. Consistent with the results for acoustic presence, song presence also peaked during mid-winter at most locations. At M2 in 2019-2020, the effect of month on song presence was not bell-shaped but song presence declined gradually over the course of the sampling period. This could be attributed to the fact that this sampling period did not span the full eight months between October and May; it lacked the initial fall period, when presence and song were generally low at this site in the other sampling period, as well as at other sites.

Statistical analyses showed that sea ice concentration was correlated with both the presence of bowhead whales and how much singing they displayed. This fits well with the ice-affiliated nature of bowhead whales (George & Thewissen, 2021). Periods of song often coincided with periods of sea ice formation or high sea ice cover. Apart from providing shelter and seasonally pulsed food supplies (Ferguson et al., 2010a), sea ice habitats also provide a suitable acoustic habitat for the transmission and reception of bowhead whale song, since a dense canopy of ice can enhance the propagation of sound beneath it (Diachok & Winokur, 1974). Therefore, higher ice concentrations might be preferred by singing bowhead whales over loose pack-ice or open water conditions, as it allows their song to be carried over greater distances and thus increases their chances of being heard by other individuals.

An important consideration in the detection of bowhead whale vocalizations is that the distinction between song and non-song vocalizations can sometimes be ambiguous. Low frequency sounds can travel further from the emitter than high frequency sounds (Browning et al., 2017), thus distant bowhead whale song might sometimes have been classified as non-song acoustic presence, because the higher frequency components of the song were not detectable. This could have led to false negative detections of song. Additionally, human sampling bias cannot be excluded as a source of false negative or false positive detections, when it comes to the manual assessments of LTSA's.

The variable strength of the relationship between sea ice concentration and acoustic presence or song presence, indicates that there are endogenous rhythms (Hunt et al., 2022) and likely also other environmental cues that play important roles in determining bowhead whale behaviour and habitat selection. While sea surface temperature and distance to the ice edge were excluded from the statistical analyses due to high collinearity with sea ice concentration, they likely do contribute to bowhead whale acoustic phenologies. The distance to the ice edge can be difficult to interpret, since sea ice extent can differ greatly regionally and bowhead whales likely also make use of coastal polynyas and flaw lead systems (Kovacs et al., 2020), which are not considered in the sea ice extent data. Other environmental variables such as oceanic currents, wind, bathymetry, or anthropogenic disturbances such as vessel presence or seismic blasting might also play a role in where bowhead whales are found at a given time.

The satellite-derived chlorophyll and zooplankton biomass were low and too consistent to contribute to explaining the variance in acoustic presence and song presence of bowhead whales in this study. It is assumed that bowhead whales feed primarily during the daylight period, while this study is centered around the winter season, when productivity is generally very low and zooplankton communities are deep and dormant. However, it is important to note that remote sensing satellite data is limited by sea ice and cloud cover, which potentially affected the accuracy of biomass estimates in this study. Additionally, some studies have provided evidence of winter feeding in other bowhead whale populations (Pomerleau et al., 2014; Citta et al., 2015; Moore, 2016; Pomerleau et al., 2018). Since certain copepod species occupy intermediate depths during winter in the Barents Sea (Hirche & Kosobokova, 2011), this could facilitate some winter feeding for Spitsbergen bowhead whales as well. Furthermore, the advection of Atlantic zooplankton has a large peak of advected biomass (mainly consisting of copepod species) in December in the northern Barents Sea region (Wold et al., 2023), further facilitating potential winter feeding. Therefore, although feeding is not considered to be a primary activity during the winter season, prey availability might still play a role in bowhead whale habitat preference.

Page **32** of **55** Bowhead whales across the entire Arctic are facing extreme environmental changes due to climate warming, which are happening at extraordinarily fast rates. Declines in sea ice thickness and seasonal sea ice extent, as well as changes in the timing of seasonal sea ice formation and retreat are impacting their habitats (George & Thewissen, 2021). The changes in sea ice conditions, along with increasing temperatures, have already been found to correlate to changes in bowhead whale migration patterns, with both earlier migration in the spring (Noongwook et al., 2007; Szesciorka & Stafford, 2023) and later migrations in fall (Stafford et al., 2021; Szesciorka et al., 2024) reported in recent decades, for some bowhead whale populations. Furthermore, there are large changes occurring in the Arctic food webs. Less sea ice allows for deeper light penetration and a longer growing season for phytoplankton (as long as nutrients are available) (Arrigo et al., 2008; Arrigo & van Dijken, 2015), which leads to an increased abundance of zooplankton. Combined with increased upwelling and higher levels of advection of copepods, these increasing foraging opportunities have resulted in increased body condition of bowhead whales in the Beaufort Sea (George et al., 2015). However, Arctic zooplankton species are being rapidly replaced by less nutritious boreal species, which has potentially negative consequences for upper trophic level animals (Mueter et al., 2021). In addition, many migratory marine mammal and fish species are expanding their period in Arctic waters and shifting their migratory endpoints northwards, due to changing ice conditions and a longer open-water season (Storrie et al., 2018; Lydersen et al., 2020; Ahonen et al., 2021; Bengtsson et al., 2022; Pöyhönen et al., 2024). This can lead to intensified competition for prey (Kovacs et al., 2011), as well as for acoustic niche space (Duarte et al., 2021). Whether bowhead whales can adapt their foraging strategies following altered species composition and prey abundance and increased competition, remains uncertain (Fortune et al., 2020). In addition to food-web changes, another important consequence of decreased ice cover is the increased vulnerability of bowhead whales to predation. In the Canadian High Arctic and Pacific Arctic the expansion of the range and seasonal presence of killer whales has already been documented (Ferguson et al., 2010b; Stafford, 2018b). Increased presence of killer whales could potentially regulate habitat preference, or even population growth of bowhead whales in an Arctic with less sea ice, as has already been observed in Hudson Bay (Higdon & Ferguson, 2010). Lastly, anthropogenic disturbances such as vessel traffic in previously inaccessible ice-covered areas are expected to increase (AMSA, 2009), further contributing to changes and stressors that bowhead whales are facing. All these challenges are a cause of concern for the recovery of Spitsbergen bowhead whales. Their impact will depend on the resilience and behavioural plasticity of these highly ice-affiliated Artic endemic cetaceans.

# <span id="page-38-0"></span>**Conclusion**

This study has provided new insight regarding the seasonal acoustic presence of Spitsbergen bowhead whales around the Svalbard Archipelago. Bowhead whale acoustic presence was detected at all recording sites, with the highest detection rates at locations west and east of Svalbard. The predominance of song at specific sites highlights the importance of these key areas for bowhead whale overwintering and likely breeding. Furthermore, this study demonstrated significant correlations between sea ice concentration and bowhead whale presence and singing behaviour. These results contribute to our knowledge of bowhead whale distribution and habitat selection, but also highlight the necessity of gaining more information and knowledge on bowhead whale phenology in a rapidly changing ecosystem. Future work should be continued with PAM in this region, which in combination with satellite tracking could provide information on migratory patterns, potential changes in habitat use and the impacts of environmental variables on bowhead whale distribution. Such knowledge is essential for effective climate change and anthropogenic disturbance mitigation strategies, in order to ensure the conservation of the Spitsbergen bowhead whale population.

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## <span id="page-47-0"></span>**Appendix A: GAM model summaries and residual plots**

![](_page_47_Picture_372.jpeg)

*Table A1. Model output for effects of Sea Ice Concentration (SIC) and month on acoustic presence at Fram Strait (n=484).*

*Table A2. Model output for effects of Sea Ice Concentration (SIC) and month on song presence at Fram Strait (n=484).*

![](_page_47_Picture_373.jpeg)

![](_page_48_Figure_0.jpeg)

*Figure A1. Residual plots for GAMs (Generalized Additive Models) of (a) acoustic presence and (b) song presence of bowhead whales at Fram Strait (n=484). Showing Histogram of Residuals, Q-Q plot, Response vs Fitted Values and Residuals vs Linear Predictor.*

![](_page_49_Picture_328.jpeg)

*Table A3. Model output for effects of Sea Ice Concentration (SIC) and month on acoustic presence at 13E (n=244).*

*Table A4. Model output for effects of Sea Ice Concentration (SIC) and month on song presence at 13E (n=244).*

![](_page_49_Picture_329.jpeg)

![](_page_49_Figure_4.jpeg)

*Figure A2. Residual plots for GAMs (Generalized Additive Models) of (a) acoustic presence and (b) song presence of bowhead whales at 13E (n=244). Showing Histogram of Residuals, Q-Q plot, Response vs Fitted Values and Residuals vs Linear Predictor.*

![](_page_50_Picture_304.jpeg)

*Table A5. Model output for effects of Sea Ice Concentration (SIC) and month on acoustic presence at 26E (n=225).*

*Table A6. Model output for effects of Sea Ice Concentration (SIC) and month on song presence at 26E (n=225).*

![](_page_50_Picture_305.jpeg)

![](_page_50_Figure_4.jpeg)

*Figure A3. Residual plots for GAMs (Generalized Additive Models) of (a) acoustic presence and (b) song presence of bowhead whales at 26E (n=225). Showing Histogram of Residuals, Q-Q plot, Response vs Fitted Values and Residuals vs Linear Predictor.*

![](_page_51_Picture_307.jpeg)

*Table A7. Model output for effects of Sea Ice Concentration (SIC) and month on acoustic presence at Atwain (n=243).*

*Table A8. Model output for effects of Sea Ice Concentration (SIC) and month on song presence at Atwain (n=243).*

![](_page_51_Picture_308.jpeg)

![](_page_51_Figure_4.jpeg)

*Figure A4. Residual plots for GAMs (Generalized Additive Models) of (a) acoustic presence and (b) song presence of bowhead whales at Atwain (n=243). Showing Histogram of Residuals, Q-Q plot, Response vs Fitted Values and Residuals vs Linear Predictor.*

Family	Link <b>Function</b>		Formula	Adjusted $\mathbb{R}^2$	<b>Deviance</b> <b>Explained</b>							
Quasibinomial	Logit		Presence $\sim$ s(SIC, k = 3) + s(month, $k = 3$ )	0.688	60.8%							
<b>Parametric Coeffficients</b>												
		<b>Estimate</b>	<b>Std. Error</b>	<b>T</b> value	Pr(> t )							
(Intercept)		$-1.6930$	0.1942	$-8.717$	5.22e-16***							
<b>Approximate Significance of Smooth Terms</b>												
		edf	Ref.df.	F	p-value							
s(SIC)		1.963	1.997	36.64	$<$ 2e-16***							
s(month)		1.686 1.900		65.38	$<$ 2e-16 <sup>***</sup>							
Signif.codes: $0^{***}$ , 0.001 <sup>**</sup> , 0.01 <sup>*</sup> , 0.05 <sup>*</sup> , 0.1 <sup>0</sup> 1												

*Table A9. Model output for effects of Sea Ice Concentration (SIC) and month on acoustic presence at M1 (n=240).*

![](_page_52_Figure_2.jpeg)

*Figure A4. Residual plots for GAMs (Generalized Additive Models) of acoustic presence of bowhead whales at Atwain (n=243). Showing Histogram of Residuals, Q-Q plot, Response vs Fitted Values and Residuals vs Linear Predictor.*

![](_page_53_Picture_356.jpeg)

*Table A10. Model output for effects of Sea Ice Concentration (SIC) and month on acoustic presence at M2 (n=439).*

*Table A11. Model output for effects of Sea Ice Concentration (SIC) and month on song presence at M2 (n=439).*

![](_page_53_Picture_357.jpeg)

![](_page_54_Figure_0.jpeg)

*Figure A6. Residual plots for GAMs (Generalized Additive Models) of (a) acoustic presence and (b) song presence of bowhead whales at M2 (n=439). Showing Histogram of Residuals, Q-Q plot, Response vs Fitted Values and Residuals vs Linear Predictor.*

<span id="page-55-0"></span>![](_page_55_Figure_0.jpeg)

![](_page_55_Figure_1.jpeg)

*Figure B1. Long-Term Spectral Average (LTSA) for Fram Strait, between (a) 01-10-2018 and 31-05-2019 and (b) 01-10-2021 and 31-05-2022. LTSA's illustrate the concentration of sound energy along the frequency band 10-4000 Hz (logarithmic scale). Red ellipses indicate sound energy from bowhead whale vocalizations.* 

![](_page_56_Figure_0.jpeg)

*Figure B2. Long-Term Spectral Average (LTSA) for 13E, between 01-10-2019 and 31-05-2020. LTSA illustrates the concentration of sound energy along the frequency band 10-4000 Hz (logarithmic scale).*

![](_page_56_Figure_2.jpeg)

*Figure B3. Long-Term Spectral Average (LTSA) for 26E, between 19-10-2018 and 31-05-2019. LTSA illustrates the concentration of sound energy along the frequency band 10-4000 Hz (logarithmic scale). Red ellipse indicates sound energy from bowhead whale vocalizations.*

![](_page_56_Figure_4.jpeg)

*Figure B3. Long-Term Spectral Average (LTSA) for Atwain, between 01-10-2017 and 31-05-2018. LTSA illustrates the concentration of sound energy along the frequency band 10-4000 Hz (logarithmic scale). Red ellipse indicates sound energy from bowhead whale vocalizations.*

![](_page_57_Figure_0.jpeg)

*Figure B5. Long-Term Spectral Average (LTSA) for M1, between (a) 18-11-2019 and 08-02-2020 and (b) 01-10-2021 and 31- 05-2022. LTSA's illustrate the concentration of sound energy along the frequency band 10-4000 Hz (logarithmic scale). Red ellipses indicate sound energy from bowhead whale vocalizations.* 

![](_page_58_Figure_0.jpeg)

*Figure B6. Long-Term Spectral Average (LTSA) for M2, between (a) 18-11-2019 and 31-05-2020 and (b) 01-10-2020 and 31- 05-2021. LTSA's illustrate the concentration of sound energy along the frequency band 10-4000 Hz (logarithmic scale). Red ellipses indicate sound energy from bowhead whale vocalizations.* 

![](_page_59_Figure_0.jpeg)

<span id="page-59-0"></span>**Appendix C: Detection details**

*Figure C1. Total number of detections per month for acoustic presence and song presence, across all analysed data.*

![](_page_60_Picture_0.jpeg)