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Acoustic presence and vocal repertoire of bowhead whales (*Balaena mysticetus*) in eastern and central Fram Strait

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Bowhead whales (*Balaena mysticetus*) of the East Greenland-Svalbard-Barents Sea (Spitsbergen) population are still considered endangered, but knowledge on spatio-temporal distribution patterns and behavioral aspects remains scarce, yet crucial for this population's conservation. Long-term passive acoustic recordings were collected at five locations in central and eastern Fram Strait (78-79°N, 0-7°E) as part of the Ocean Observing System FRAM (Frontiers in Arctic Marine Monitoring). Data recorded in 2012 and 2016/2017 were analyzed for the acoustic occurrence of bowhead whales at hourly resolution using a combination of automated and manual analyses. Bowhead whales were acoustically present from autumn throughout the winter months (October-February) and occasionally in spring (March-June), supporting hypotheses that Fram Strait is an important overwintering area. Acoustic presence peaked between mid-November and mid-December with bowhead whale calls recorded almost daily, often hourly for several consecutive days. The observed peak in acoustic presence coincided with the presumed mating period of bowhead whales, starting in late winter, indicating that Fram Strait may also serve as a mating area. Detailed analyses of recordings of a single year and location revealed eight distinct bowhead whale song types, comprising simple songs and call sequences. No bowhead whales were recorded in summer (July-September), indicating that they had migrated to summering areas or resided outside the detection range. Compared to previous studies in western Fram Strait, bowhead whale detections in our recordings were less frequent and recorded songs were less complex. The observed regional differences in bowhead whale acoustic behavior across Fram Strait suggest that eastern Fram Strait may represent a less favorable part of the bowhead whale overwintering area.

KEYWORDS

bowhead whales, Arctic Ocean, distribution range, wintering ground, passive acoustic monitoring, song type analysis, LFDCS automated detection

1 Introduction

Beginning in 1611, centuries of commercial whaling greatly reduced the global bowhead whale (*Balaena mysticetus*) population with the East Greenland-Svalbard-Barents Sea population (hereinafter referred to as the Spitsbergen population) being depleted to near extinction (Reeves, 1980; Woodby and Botkin, 1993; Shelden and Rugh, 1995). Despite becoming protected in the early 1930s, the Spitsbergen population does not show signs of recovery and is still listed as 'endangered' by the IUCN Red List of Threatened Species (Cooke and Reeves, 2018). The population size prior to commercial whaling has been estimated to have ranged between 33,000 and 65,000 individuals (Allen and Keay, 2006). Today, it is believed to range up to 343 individuals (Vacquié-Garcia et al., 2017; Cooke and Reeves, 2018), which accounts for only 0.5–1% of the pre-whaling population size. Given the scarcity of Spitzbergen bowhead whales, detailed knowledge on population parameters including abundance, population trend and spatio-temporal patterns remains lacking (Cooke and Reeves, 2018).

Many early reports on bowhead whale distribution stem from observations of whalers and zoologists, having been published since the 19th century (e.g. Scoresby, 1820; Eschricht and Reinhardt, 1866; Gray, 1889; as cited in Reeves, 1980). These historic whaling records suggest that Fram Strait, located between Greenland and Svalbard, was a key area for this population (Woodby and Botkin, 1993). Being the only deep-water connection between the Arctic Ocean and the Nordic Seas, Fram Strait is thus the most important gateway for the exchange of water masses (e.g., Fahrbach et al., 2001). The dynamic hydrological conditions within Fram Strait create large productive areas with high zooplankton abundance (Blachowiak-Samolyk et al., 2007), likely providing favorable feeding conditions for bowhead whales. During commercial whaling, bowhead whales were caught extensively in the Fram Strait area between 76°N and 80°N in early spring, which whalers referred to as the 'Northern Whaling Ground' (Moore and Reeves, 1993). Recent sightings suggest that the Spitsbergen population still occupies most of their previous range, at least during the spring and summer months (Wiig et al., 2007; de Boer et al., 2019; Kovacs et al., 2020). Acoustic surveys in the western part of Fram Strait reported extensive acoustic activity from bowhead whales between October and April (Moore et al., 2012; Stafford et al., 2012). These observations suggested that western Fram Strait provides an important wintering area for the Spitsbergen bowhead whale population (Stafford et al., 2012). While the western Fram Strait seems to be used regularly by bowhead whales (Ahonen et al., 2017; Stafford et al., 2018; Kovacs et al., 2020), detailed information about the extent of their distribution in eastern Fram Strait and the Svalbard archipelago is still limited (but see Stafford et al. (2012) for central Fram Strait).

Updated knowledge on the distribution patterns and population trends of Spitsbergens' bowhead whales is highly relevant in the context of a rapidly changing Arctic Ocean. While Fram Strait appears to be a hotspot area for bowhead whales and other cetacean species (Storrie et al., 2018), it is undergoing severe and rapid environmental changes due to climate change (Laidre et al., 2015). Rising water temperatures and declining sea ice concentrations are likely to lead to severe habitat loss for Spitsbergen's bowhead whale population, given their preference for cold and ice-covered waters (Kovacs et al., 2020). The changing sea ice conditions and the resulting increases in anthropogenic activities add additional threats to the already vulnerable Spitsbergen stock (Reeves et al., 2014; Thomas et al., 2016). Such threats include elevated noise levels from ship traffic, drilling and seismic surveys (Ahonen et al., 2017) but also an increasing risk of ship strikes (e.g. George et al., 2017). This might particularly affect Spitsbergen bowhead whales in eastern Fram Strait, which is - compared to western Fram Strait – already a rather easily accessible region due its low sea ice concentrations during most of the year (e.g. Grosfeld et al., 2016). An improved knowledge on bowhead whale abundance, spatio-temporal occurrence and behavior, such as their migratory and acoustic behavior, is required to predict how the population may react to these threats (Laidre et al., 2008; Moore and Huntington, 2008; Kovacs et al., 2011). Moreover, such information is of particular importance to establish effective conservation and management strategies, e.g., to mitigate noise disturbance or prevent potential ship strikes from increasing anthropogenic activities (Reeves et al., 2014).

The remarkably diverse vocal behavior and repertoire of bowhead whales, along with their often inaccessible ice-covered habitats, makes them highly suited for being studied by passive acoustic monitoring. Bowhead whales produce a variety of sounds, from simple calls to complex songs differing between populations and evolving over time, and are able to produce two sounds simultaneously (e.g., Würsig and Clark, 1993; Tervo et al., 2011a; Stafford and Clark, 2021). Calls are usually frequency-modulated sounds within a limited repertoire of different call types, produced year-round mainly in the frequency range between 50 and 500 Hz (e.g., Würsig and Clark, 1993; Stafford and Clark, 2021; Stafford, 2022). Bowhead whale songs, in contrast, are produced seasonally mainly during winter and spring months and are highly variable both intra- and inter-annually with manifold songs being sung by a population within one season (e.g. Tervo et al., 2009; Tervo et al., 2011b; Johnson et al., 2015; Stafford et al., 2018).

The present study assesses temporal patterns in the acoustic occurrence of bowhead whales at different locations in eastern and central Fram Strait, using long-term passive acoustic recordings collected during two sampling periods, one in 2012 and one in 2016-2017. Furthermore, we aimed at describing the vocal repertoire of Spitzbergen bowhead whales within a 1-year period from July 2016 to July 2017.

TABLE 1 Locations and recording parameters of passive acoustic recorders deployed in Fram Strait in 2012 and in 2016/2017. Deployment and recording period are given in the format MM/YYYY. Hydrophone sensitivity is based on a factory calibration of each sensor, using a pistonphone calibration at 251 Hz. System gain was assessed at 251 Hz using a Brüel and Kjær pistonphone calibrator for either a pre-deployment or a post-deployment (underlined in Table 1, in case a pre-deployment calibration was not possible) calibration.

ID	Mooring ID	Recorder Serial Number	Latitude	Longitude	Deployment Depth [m]	Water Depth [m]	Sampling Frequency [Hz]	Gain [dB]	Hydrophone Sensitivity [dB]	Deployment Period	Recording Period	Operational Period [d]
C-2012	ARKF16-09	SV1021	78° 49.76′ N	0° 25.77′ E	800	2,525	5,333	<u>45.6</u>	−193.5	06/2012–09/2014	06/2012–11/2012	151
C-2016	ARKR02-01	SV1091	78° 50.01′ N	0° 00.09′ E	806	2,587	48,000	40.7	−192.8	07/2016–07/2018	07/2016–07/2017	360
E-2012	ARKF04-15	SV1026	78° 50.01′ N	6° 59.99′ E	743	1,420	5,333	<u>46.9</u>	−193.4	06/2012–06/2015	06/2012–11/2012	147
E-2016	ARKF05-17	SV1088	79° 00.02′ N	5° 40.12′ E	808	2,100	48,000	41.0	−193.1	07/2016–09/2018	07/2016–07/2017	361
S-2016	ARKR01-01	SV1097	78° 10.21′ N	0° 00.04′ E	799	3,013	48,000	41.2	−192.8	08/2016–07/2018	08/2016–08/2017	361

2 Materials and methods

2.1 Data collection

Passive acoustic data were collected by five recorders (type Sono.Vault, manufactured by develogic GmbH, Hamburg, Germany), with two recorders deployed in 2012 and three recorders deployed in 2016 (Table 1). All recorders were attached to oceanographic moorings in Fram Strait, in the framework of the Ocean Observing System FRAM (Frontiers in Arctic Marine Monitoring, Soltwedel et al., (2013); Figure 1; Table 1). All recorders were assigned an ID representing their relative location within this study's recording area (i.e. with "C" representing central Fram Strait, "E" used for eastern Fram Strait and "S" for the data set located in the southern part of central Fram Strait), as well as a number representing the (start of the) respective recording period for each recorder (Table 1).

Two recorders were located in central Fram Strait (recorders C-2012 and C-2016), one in southern Fram Strait (S-2016) and two in eastern Fram Strait (E-2012 and E-2016). All recorders were moored at depths around 800 m. All recorders were scheduled to record continuously at sample rates of either 5,333 Hz or 48,000 Hz, resulting in effective bandwidths of 8–2,666 Hz or 8–24,000 Hz (Table 1). Recordings were stored internally on memory cards in 5-min or 10-min long sound files (with a sampling resolution of 24-bit). The study period comprised two recording periods: i) from June to November 2012 for the recorders deployed in 2012 and ii) July/August 2016 to July/August 2017 for the recorders deployed in 2016 (Table 1). The recorders deployed in 2012 stopped recording prior to recovery due to battery exhaustion, thus only covered the second half of 2012. Moreover, one of these (recorder E-2012) lacks 12 days of data in October due to a defective memory card. Recorders deployed in 2016 were scheduled to record for about 1 year given limitations in storage capacity, hence yielded passive acoustic recordings for 360 or 361 days.

Prior to analysis, recordings originally sampled at 48,000 Hz were downsampled to a sampling rate of 5,333 Hz, resulting in an analyzed bandwidth from 8 to 2,666 Hz, to match the sampling rate of the recordings from C-2012 and E-2012 in order to allow for comparison of results among all recorders. Furthermore, all acoustic data were converted to a 16-bit sampling resolution to follow the requirements of the automated detection software.

2.2 Acoustic data analysis

Acoustic data analyses comprised an estimation of the hourly acoustic presence of bowhead whales using an automated detection and classification algorithm as well as an assessment of the vocal repertoire by manual classification of songs based on descriptive song characteristics.

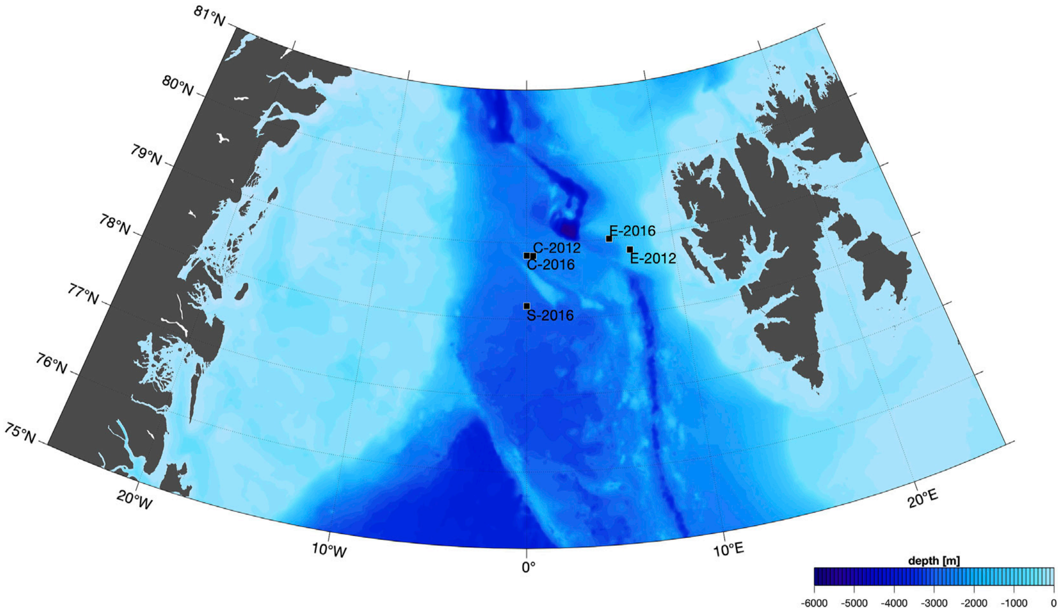

FIGURE 1
Deployment locations of the five recorders in Fram Strait between Greenland and Svalbard. Recorder C-2012 and E-2012 were recording in 2012, while C-2016, S-2016 and E-2016 were recording year-round in 2016/17. C-2012 and C-2016 belong to the central recording site, S-2016 to the southern and E-2012 and E-2016 to the eastern recording site.

2.2.1 Automated detection of hourly acoustic bowhead whale presence

Bowhead whale vocalizations were automatically detected and classified based on a user-developed call library in the Low-Frequency Detection and Classification System (LFDCS) (Baumgartner and Mussoline, 2011). The LDFCS software created spectrograms of each data file with a frame of 1,024 samples and 80% overlap using Fast Fourier Transformation (FFT). Pitch tracks detected by LFDCS are classified based on the similarity between characteristic attributes (such as start and end frequency, frequency range, duration as wells as slope of frequency variation) of the pitch track to those of a predefined set of call types contained in a call library, using quadratic discriminant function analysis (Baumgartner and Mussoline, 2011). Similarity is rated by Mahalanobis distance and measures the deviation of a detected call from the assigned call type, with lower Mahalanobis distance values representing closer matches of a detected (call) event to its assigned call type (Baumgartner and Mussoline, 2011).

The call library used in this study contained a set of exemplary bowhead whale (both song and non-song) calls obtained from acoustic data collected in Fram Strait in 2012 (C-2012) and 2016/17 (S-2016). Taking into account potential spatio-temporal variations in bowhead whale calls (e.g., Delarue et al., 2009; Tervo et al., 2009; Stafford et al., 2018), the exemplar calls comprised calls from two locations as well as from several months and daytimes to ensure that different individuals and call variations were covered. Building a new call library requires a data set to be processed by LFDCS beforehand. For that purpose, several sections containing potential exemplars were manually selected from acoustic data collected by C-2012 and S-2016. Chosen data sections were processed with LFDCS to generate pitch tracks. The spectrogram view of LFDCS allows to browse through the pitch tracks, select and populate them into the call library via built-in commands. Only calls that were accurately pitch-tracked were selected as exemplars. Exemplar calls were categorized into 13 call types according to their spectrographic shape, duration and frequency range, containing between 24 and 554 exemplars per call type (see Supplementary Material Table SA1). Moreover, the call library also contained exemplary ice sounds, to reduce the risk of misclassifying sounds of spectrographically similar ice tremors as bowhead whales. For more information on the call library and LFDCS detection details, see Supplementary material S1 (containing a parameter file for LFDCS detection, as well as the LFDCS call library used in the present study).

Detector performance was evaluated by manually assessing hourly acoustic presence of bowhead whales in a subset of the data recorded at the central recording site (C-2016) of the 2016/17 sampling period (which were not used to build the LFDCS call library). This reference data set contained 12 non-consecutive days of acoustic data from October throughout March of the C-2016 recordings, comprising the first and the 15th day of each month. The reference data set thereby covered the period, when bowhead whales are likely to be present in Fram Strait (Stafford et al., 2012; Ahonen et al., 2017). Manual review entailed visual inspection of spectrograms (window size: 2.5 min; frequency range: 8–1,300 Hz; spectrogram settings: FFT 1,024, overlap 90%, Hann window), using Raven Pro 1.5 (Bioacoustics Research Program, Cornell Lab of Ornithology), supplemented by aural review of potential calls. The resulting hourly acoustic presence data was considered the ground truth to which the output of LFDCS was compared. Based on pre-analyses, a (comparatively low) Mahalanobis distance threshold of 1.5 and a SNR threshold of 8 dB were chosen as detection criteria in the LFDCS processing routine to ensure a high precision of the LFDCS detector. However, higher precision values may be accomplished at the cost of a lower recall rate (i.e. increasing the amount of missed calls, leading to an underrepresentation of the species of interest).

In a post-processing approach, all automated detection events of bowhead whales were manually reviewed on an hourly basis in terms of a false-positive control. Each hour was visually reviewed in spectrograms (initial settings: window size: 2.5 min; frequency range: 8–1,300 Hz; spectrogram settings: FFT 1,024, overlap 90%, Hann window) for the presence of at least one bowhead whale call by a single trained analyst, using Raven Pro 1.5 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, United States). If needed, spectrogram settings were optimized, e.g. by zooming into the respective time or frequency range, and potential call events were aurally examined for verification of bowhead whale acoustic presence. In case the analyst did not confirm the presence of bowhead whales in a particular hour, all automated detections during this hour were considered false positive events and bowhead whales were regarded as acoustically absent within that particular hour. Additionally, hours that did not contain automated detections, but bowhead whale acoustic presence was confirmed in previous and consecutive hours, were reviewed. The probability of acoustic presence was considered reasonably high within these hours since bowhead whales often vocalize for several hours (Würsig and Clark, 1993; Stafford et al., 2008; Stafford et al., 2012). Bowhead whale calls were identified based on published descriptions of their spectrographic signatures (Würsig and Clark, 1993; Delarue et al., 2009; Johnson et al., 2015), and online sound libraries (e.g., Macaulay Library of The Cornell Lab of Ornithology; Discovery of Sound in the Sea, www.dosits.org).

Automated acoustic presence results were compared to daily acoustic presences assessments from manual, i.e. visual and aural, analyses for data sets from E-2016, C-2016 and C-2012. Data recorded by E-2016 and C-2016 were decimated to 3,000 Hz before manual exploration. Manual analysis was conducted by trained analysists on a daily basis (for C-2012) or for every second day (for C-2016 and E-2016) using Raven Pro 1.5 (using initial spectrogram settings: FFT 2500 points for C-2012 and FFT 1536 points for E-2016 and C-2016, overlap 50%, Hanning window, window size: 10 min, which were optimized in terms of frequency or time resolution whenever needed). To ensure comparability of the post-processed automated results and the manual detections of daily acoustic presence, acoustic presence estimates from both analysis approaches were visualized based on the number of analyzed recording days per month.

2.2.2 Vocal repertoire assessment

For the assessment of the acoustic repertoire of bowhead whales within a 1-year period from July 2016 to July 2017, acoustic data recorded by E-2016 in eastern Fram Strait were analyzed. Spectrograms were visually checked for the presence of bowhead whale songs. In this study, the term ‘song’ comprised both call sequences and *true* songs, thereby following the differentiation of Stafford et al. (2012). By definition, true songs are composed of different calls, named ‘units’ (or ‘notes’), combined into phrases (Würsig and Clark, 1993). Call sequences, in contrast, are a series of repeated similar calls (Blackwell et al., 2007). Apart from songs, there were many other signals recorded from bowhead whales including constant calls, moans or individual down- and upsweeps that did not show any repetitive pattern, thus were not included in the song repertoire analysis. Only true songs and call sequences that were clearly distinguishable against the background noise and repeated at least three times within a day were considered for song repertoire analysis. Classification of songs was done manually, based on descriptive song characteristics, such as spectral structure of units, the arrangement of units and their frequency range.

2.3 Sea ice data

Sea ice coverage in the study area was derived from satellite data (Spreen et al., 2008). Daily sea ice concentration data with a $6.25 \times 6.25\ \text{km}^2$ resolution were downloaded from a database provided by the University of Bremen[1]. Mean daily sea ice concentrations were calculated from all data points within a 35 km radius around each recording location. Bowhead whale vocalizations have been estimated to propagate over distances of up to 35 km (Bonnel et al., 2014). In accordance, Stafford et al. (2012) did not find any overlap in bowhead whale call recordings between two recorders in western and central Fram Strait, deployed ca. 95 km apart, concluding a detection range of less than 45 km for bowhead whale sounds. Hence, in the present study, a radius of 35 km was considered representative of the sea ice conditions within the respective recording area. The relationship between sea ice concentration within the 35 km radius and the number of hours with bowhead

1 (available at: https://seaice.uni-bremen.de/data/amsr2/asi_daygrid_swath/n6250/).

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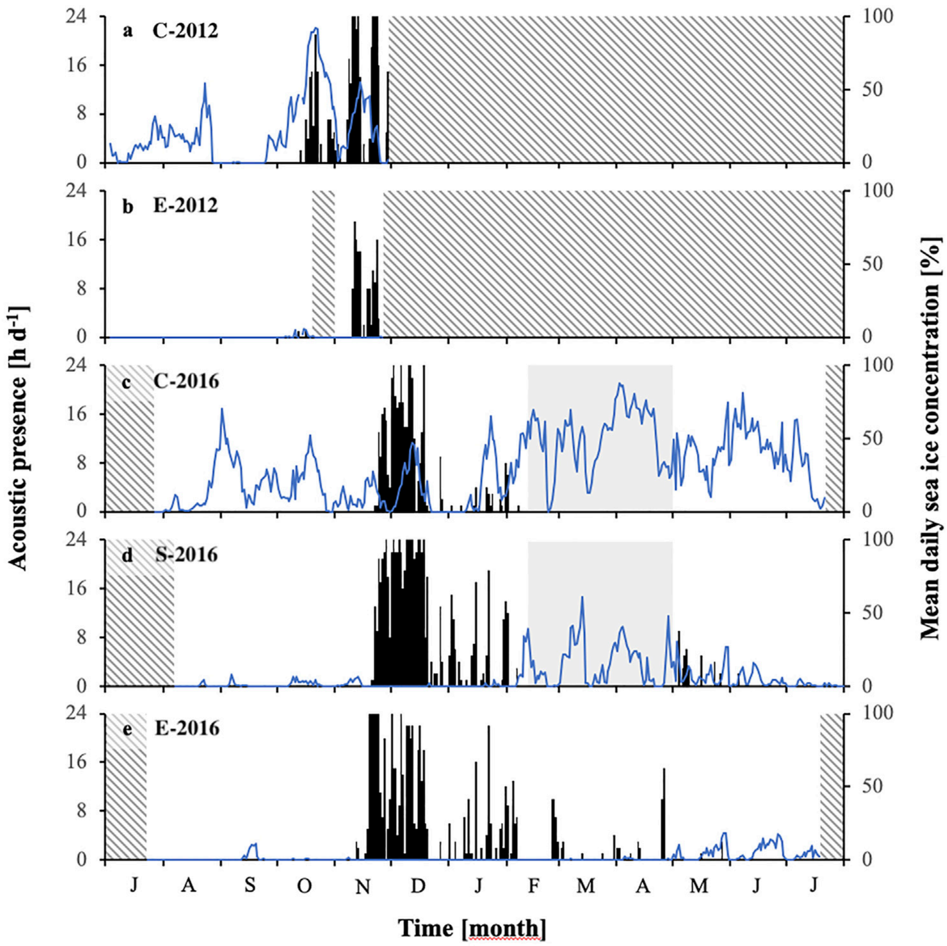

FIGURE 2
Acoustic presence of bowhead whales in Fram Strait in 2012 (panels **A, B**) and 2016/17 (panels **C–E**), with recorders C-2012 **(A)**, E-2012 **(B)**, C-2016 **(C)**, S-2016 **(D)** and E-2016 **(E)**. Number of hours per day [h d^{-1}] with acoustic presence of bowhead whales (left *y*-axis, black bars) and mean daily sea ice concentration [%] within a 35 km radius around each recording location (right *y*-axis, blue lines). Hatched areas illustrate periods without recording data. Light grey, shaded areas indicate the time period between mid-February and April 2017 when no bowhead whale calls were detected due to prevailing sounds of breaking ice masking large parts of the spectrogram at the central and southern recording sites. Please note that for easier comparisons between recorders from different sampling periods (which differed in the months of deployment and recovery), the *x*-axes range from July to July, hence comprising 13 months.

whale acoustic presence per day was tested using Poisson regression.

3 Results

3.1 Temporal patterns in the acoustic presence of bowhead whales

Bowhead whale sounds were detected at all recording sites and during both sampling periods in 2012 and 2016/17 (Thomisch, 2022a). The acoustic presence of bowhead whales was highly seasonal. Bowhead whales were acoustically present from autumn throughout winter (October/November-February) and occasionally in spring (March-June), but acoustically absent in summer (July-September; Figure 2). In both sampling periods, bowhead whales started to be acoustically present in autumn. While bowhead whales in 2012 started to call already in mid-October in central Fram Strait, first detections of bowhead whales, including both song and simple calls, did not occur until mid-November in the recordings of 2016/17 (Figure 2). The observed seasonal patterns are in accordance with those of daily acoustic presence estimates by manual analyses (see Supplementary Material Figure SA1).

The ground truth data set to which the LFDCS performance was compared contained bowhead whale calls in 86 h out of 288 h within 12 non-consecutive days. Using a Mahalanobis distance threshold of 1.5 combined with a SNR threshold of

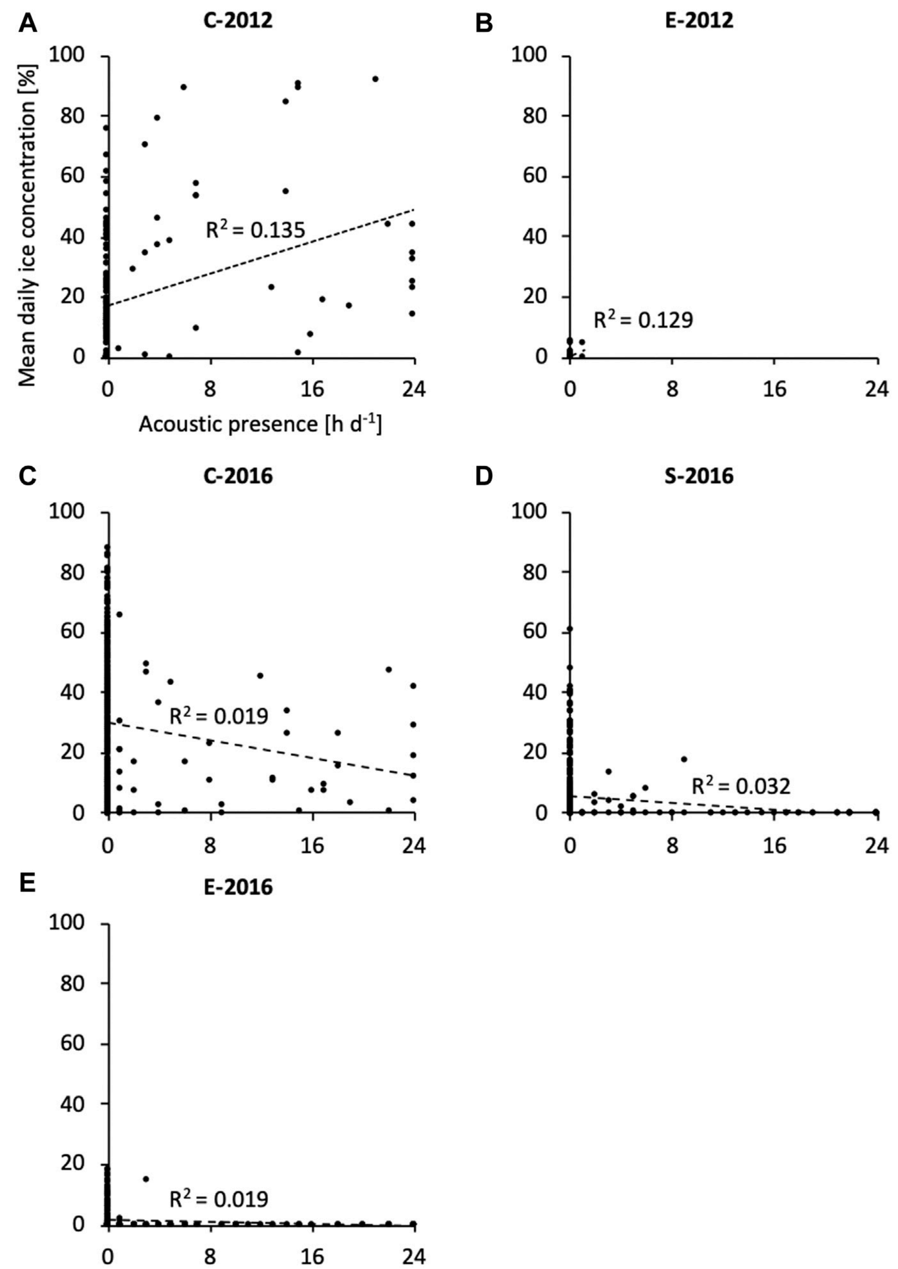

FIGURE 3
Relationship between acoustic presence of bowhead whales [h d^{-1}] in Fram Strait and mean of daily sea ice concentration [%] within a 35 km radius around each recording location based on Poisson regression, expressed by the coefficient of determination R^2. Data were recorded in 2012 **(A,B)** and 2016/17 **(C–E)** with recorders C-2012 **(A)**, E-2012 **(B)**, C-2016 **(C)**, S-2016 **(D)** and E-2016 **(E)**.

8 dB, the LFDCS detector yielded a recall of 32.6% (i.e. detecting bowhead whale calls in 31 h, as compared to 86 h with acoustic presence in the ground truth data set) and a precision of 90.3% (i.e. correctly identifying acoustic presence in 28 of the 31 h).

In 2012, acoustic presence occurred in distinct blocks, each lasting around a week, from mid-October until the end of November when recordings stopped (Figures 2A,B). Hourly acoustic presence increased from October to November. This increase was only apparent in the data of the central recording site (C-2012), since the eastern recording site (E-2012) was missing a crucial time period of twelve recording days in late October.

Between 2016 and 2017, bowhead whales were recorded at any recording sites from late autumn throughout winter

(November-February), and occasionally during spring (March-May) at the southern and eastern recording sites (S-2016, E-2016; Figures 2D,E). No bowhead whales were detected from July to November 2016 and in July 2017 at all recording sites (Figures 2C–E). Acoustic presence peaked between mid-November and mid-December when bowhead whales were recorded almost daily, often hourly for several days in a row (Figures 2C–E). The period from mid-November to mid-December thereby marked the peak-period of bowhead whale call detections in the 2016/17 recording period, with 68% of all hours with bowhead whale detections occurring during this period. Highest acoustic presence of bowhead whales was detected at the southern recording site. Subsequently, acoustic presence considerably decreased, but continued in patches, each lasting mostly between 2 and 4 d, throughout January and into February (Figures 2C–E). Due to prevailing noise of breaking ice, no bowhead whales were detected (confirmed by manual post-processing) at the central (C-2016) and southern (S-2016) recording sites from mid-February throughout April (Figures 2C,D). However, the absence of bowhead whale vocalizations from mid-February throughout April in the recording sites in central Fram Strait in 2017 matches further preliminary manual analyses where also no bowhead whales were detected in recordings from C-2016 within this period (see also Supplementary Material Figure SA1). While bowhead whales were sporadically recorded again at the southern recording site in May and June, no further acoustic detections occurred at the central recording site during these months. At the eastern recording site, acoustic presence of bowhead whales continued in patches, each lasting 2-4 d, until the end of May (Figure 2E).

Sea ice concentrations were highly variable among the recording sites, with sea ice concentrations being highest at the central, and lowest at the eastern recording sites throughout both sampling periods (Figure 2). Although there seemed to be a vague tendency of acoustic presence of bowhead whales to be increased in the absence of sea ice at some recording sites (Figures 2B–D), the relationship between sea ice concentrations and bowhead whale acoustic presence was inconclusive using Poisson regression (Figure 3).

3.2 Vocal repertoire of bowhead whales in winter 2016–2017

Within a 1-year period from July 2016 to July 2017, eight distinct bowhead whale song types were identified, providing the first description of the acoustic repertoire of bowhead whales in eastern Fram Strait (recorder E-2016) (Thomisch, 2022b). The song types were divided into five *true*, but simple songs (types 1, 3, 5, 6, 7) and three call sequences (types 2, 4, 8, Figure 4, see also Supplementary Material Figure SA2, for spectrographic examples of each song type variant). Some song types (1, 2, 3, and 6) displayed up to six different variants, while for other song types (4, 5, 7, and 8) only one variant was recorded. No complex songs, according to the definition of Stafford et al. (2012), were found.

Songs were recorded on 58 out of 76 days (76%) with acoustic presence of bowhead whales in eastern Fram Strait in 2016/17. The number of different song types was greatest when acoustic presence peaked in late autumn and early winter (November-December) and during winter (January-February; Figure 5). Fewer song types were recorded between March and May (Figure 5). Song type 2 occurred most frequently and persisted throughout the whole period with bowhead whale acoustic presence except for May, while other song types appeared for a shorter time period and then disappeared over time.

There was an overall trend that song types and variants thereof occurred in succession over the season, even though several song types coexisted at the same time (Figure 5). Song type 1 was only recorded at the very first days of bowhead whale acoustic presence in mid-November. Song type 2 was almost omnipresent over the entire season, occurring from mid-November until mid-April. Song type 3 was predominantly observed in November, and on three other occasions in each December and February. Type 4 was occasionally recorded in mid-December and in the second half of January, and type 5 was observed on two consecutive days in January. At the end of January, song type 6 was recorded throughout the days with acoustic presence in February and was then only recorded again on 1 day at the beginning of March. Song type 7 was only observed on 2 days in late April, and type 8 was only detected at the end of the season during 2 days in May (Figure 5).

4 Discussion

Vocalizations of bowhead whales were recorded from late autumn onwards at all recording sites and in both sampling periods. Acoustic presence continued throughout winter until spring in the 2016/17 sampling period. No conclusions on bowhead whale acoustic presence are possible for the 2012 sampling period due to instrument failure in November 2012. No bowhead whale sounds were detected during the summer months from mid-June to September in either recording period. This seasonal pattern in acoustic occurrence is in accordance with previous acoustic studies on bowhead whale presence in Fram Strait (Moore et al., 2012; Stafford et al., 2012; Ahonen et al., 2017; De Vreese et al., 2018).

Given the variability of bowhead whale sounds and their remarkably high diversity in vocal repertoire over time (e.g. Tervo et al., 2011b; Stafford et al., 2018), bowhead whale vocalizations are hard to detect using automated detection algorithms. Nevertheless, the low recall of the LFDCS detector quantified in this study is suspected to be caused mainly by a

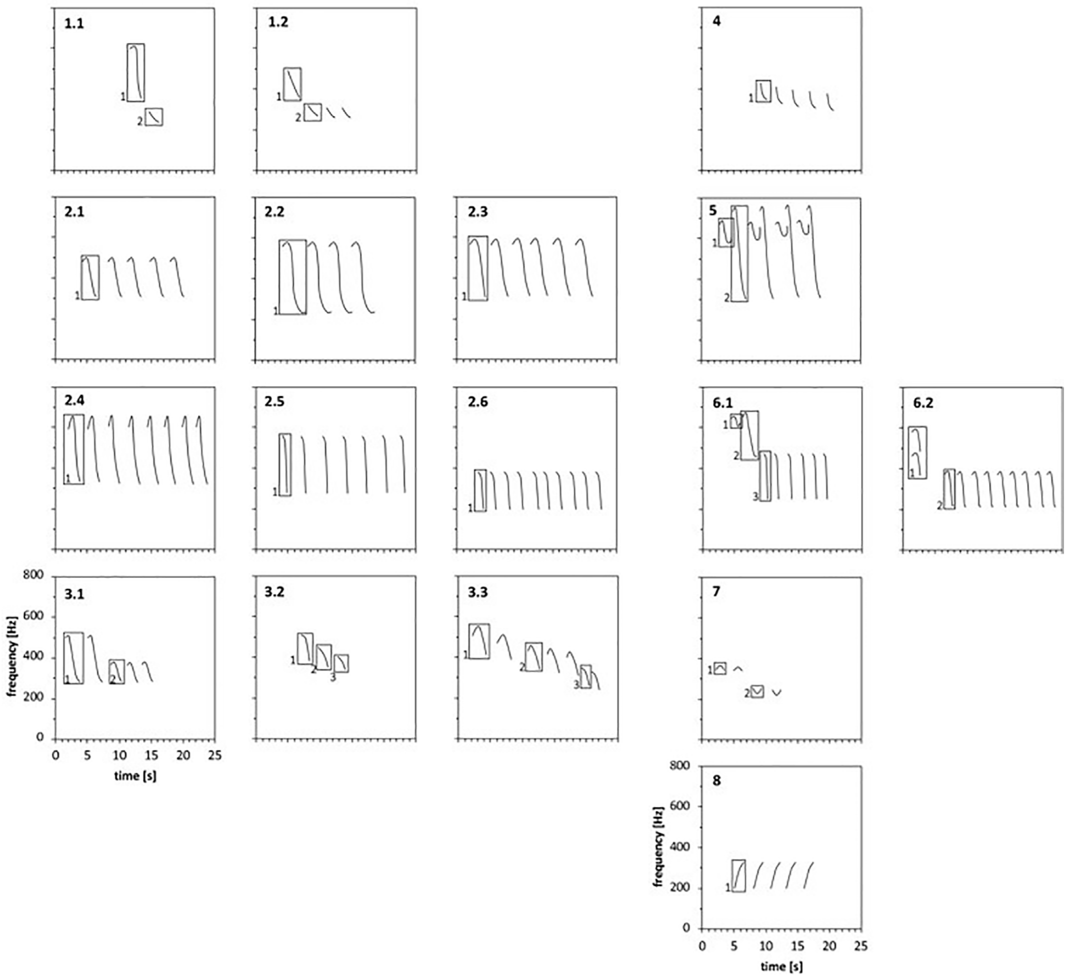

FIGURE 4
Idealized representations of the song types of bowhead whales recorded by E-2016 in eastern Fram Strait (79° 00.02′ N, 5° 40.12′ E) from November through May 2016/17. Song types (in rows, except for song type 2 which spans two rows) were numbered in their order of first occurrence, and variants (in columns) of the song types are assigned a sub-number. Different song units are encompassed by different boxes. Please note that for each sub-figure, the *x*-axis comprises a time interval of 25 s and the *y*-axis represents the frequency range from 0 to 800 Hz.

combination of the test data set characteristics and the LFDCS detector settings. LFDCS was set to only detect calls above the SNR threshold of 8.0 dB. However, bowhead whale calls contained in the test data set were comparatively quieter thus harder to detect, with an empirically estimated mean SNR of 3.0 dB (±1.6, $n = 87$), using the "Inband Power" measurements of Raven Pro. Hence, LFDCS is likely to have missed a large proportion of the bowhead whale calls contained in the manually annotated data set which did not meet the SNR requirements for detection, yielding a low recall of the detector. Leroy et al. (2018) emphasize the difficulties of comparing manual and automated detector performances based on human annotations and automatic detections, respectively. Compared to automated detection approaches, human analysts are much better at detecting faint calls within a spectrogram as they are able to adapt their sensitivity to the prevailing acoustic conditions (Leroy et al., 2018). Hence, the presence of mainly faint bowhead whale calls in the present study further hampers the comparability of an automated detectors' performance to a manually analyzed ground truth data set.

In this study, we chose a rather conservative attempt (i.e. using a low Mahalanobis distance of 1.5 and a SNR of 8 dB) to assess bowhead whale acoustic presence in Fram Strait. During post-processing, all false positive detections of the automated detector were discarded after visual and/or aural inspection. In turn, an over-representation of bowhead whales in the present study can be excluded. However, the rather low recall of the LFDCS detector implied that the acoustic presence of bowhead

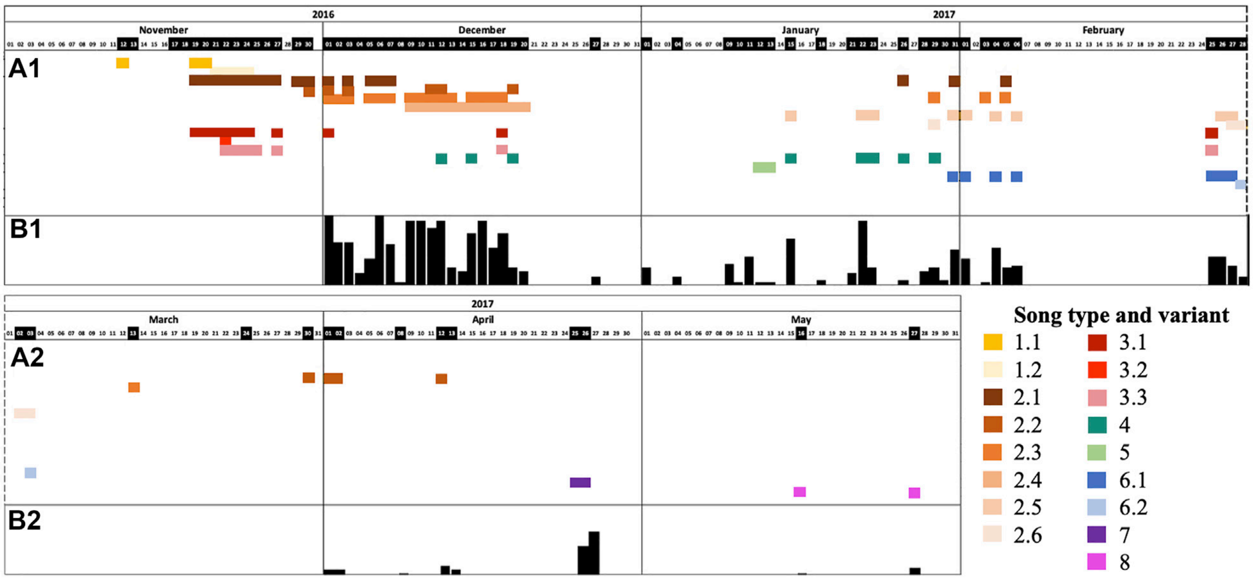

FIGURE 5
Temporal patterns in the occurrence of bowhead whale song types in eastern Fram Strait (79° 00.02′ N, 5° 40.12′ E) between November 2016 and May 2017. Calendar days on which distinct song types of bowhead whales were recorded in eastern Fram Strait by E-2016 from November 2016 until February 2017 **(A1)** and March until May 2017 **(A2)**. Black bars indicate the number of hours per day [h d^{-1}] with acoustic presence of bowhead whales from November 2016 until February 2017 **(B1)** and March until May 2017 **(B2)**. Variants of the song types are assigned a sub-number.

whales is likely to be under-represented in this study in comparison to a manually annotated data set. This is particularly relevant in the context of assessing acoustic presence during periods with few or faint bowhead whale vocalizations, not meeting the SNR criterion of the LFDCS detector, e.g. when animals arrive in or leave the area. However, results on daily acoustic presence of bowhead whales based on manual analyses showed the same overall seasonal patterns than automated analyses. This in turn provides first evidence that the LFDCS detector may underestimate acoustic occurrence, particularly during periods with less frequent or more faint bowhead whale vocalizations, but does not misrepresent patterns in bowhead whale acoustic presence in eastern and central Fram Strait. Nevertheless, future studies based on PAM data from the Fram Strait recording array should also consider more sensitive analysis methods to better represent acoustic presence of bowhead whales during periods with many faint bowhead whale calls.

According to historic whaling records, Fram Strait has consistently been an important habitat for bowhead whales (Moore and Reeves, 1993), serving as a summering area for those animals that had overwintered in the southwestern Greenland Sea near Iceland (Ross, 1993). Before 1818, whaling concentrated in Fram Strait between 76°N and 80°N. The preferred whaling ground for bowhead whales was considered to be located at 79°N, 150-200 km west of Spitsbergen (Moore and Reeves, 1993), which considerably overlaps with the sampling area of this study. Recent satellite-tracking data from 13 individuals show that Spitsbergen's bowhead whales still inhabit (western) Fram Strait during summer and autumn and overwinter in waters off Northeast Greenland or Franz Josef Land (Kovacs et al., 2020). Recent passive acoustic monitoring studies suggest that Fram Strait is also a wintering area for the population (Stafford et al., 2012; Ahonen et al., 2017, this study). Bowhead whales are known to vocalize year-round (e.g. Clark et al., 2015). Hence, the observed acoustic absence of bowhead whales during summer months in the present study implies an actual absence of individuals in the study area during summer. Although an under-representation of bowhead whale acoustic presence due to missed detections cannot be excluded in this study, the absence of vocalizations during summer months implies that eastern Fram Strait might not be used intensively as a summer habitat during the study period. While Fram Strait was a known summering area for bowhead whales during the whaling era, seasonal and regional occurrence patterns of the population may have shifted over time in response to long-term climatic changes or alterations in habitat suitability (Ross, 1993). This is in accordance with the observation that tagged bowhead whales were not observed in eastern Fram Strait throughout the period from June 2017 to May 2018 (Kovacs et al., 2020). There is evidence that changes in sea surface temperatures might affect bowhead whale habitat selection and movement patterns (Chambault et al., 2018; Citta et al., 2018; Citta et al., 2021; Tsujii et al., 2021). Nevertheless, increasing predation pressure by killer whales in increasingly ice-free Arctic habitats is likely to be the major driver of habitat preferences of bowhead whales towards sea ice covered areas as a predator refuge (Matthews et al., 2020). Hence, eastern Fram Strait may not constitute a suitable bowhead whale summer habitat possibly due to a lack of sea ice as a refuge and related predation risk.

Acoustic presence continued from autumn until spring. It was most intense during winter when vocalizations of bowhead whales were detected almost daily, often persisting over the entire day, for several weeks. The acoustic behavior during winter has been described for bowhead whales in Disko Bay, western Greenland (Tervo et al., 2009) where they observed multiple individuals singing simultaneously, with songs being more frequent in winter than in spring. Stafford et al. (2012) showed similar results for the western part of Fram Strait where songs of bowhead whales were recorded almost constantly between November and April. Singing is assumed to be a form of sexual display performed by males to attract females (Würsig and Clark, 1993). As intense singing coincided with the presumed mating period of bowhead whales, starting in late winter (Koski et al., 1993), Stafford et al. (2012) concluded that Fram Strait might be a mating area for the Spitsbergen bowhead whale population.

Apart from being an overwintering and potential mating area, bowhead whales may also seasonally occupy Fram Strait for feeding. Bowhead whales commonly occur in 'oceanographically complex' areas (e.g. Lowry, 1993; Okkonen et al., 2011; Citta et al., 2018; Hofmann et al., 2021) where bathymetric and oceanographic features cause favorable feeding conditions (Finley, 2001; Falk-Petersen et al., 2015; Ashjian et al., 2021; Citta et al., 2021). Fram Strait is such an area, influenced by a large-scale water mass exchange and sea ice transport between the Arctic Ocean and the Nordic Seas (e.g. Rudels and Quadfasel, 1991; Rudels et al., 1999). Fram Strait carries cold, Arctic water and sea ice southwards with the East Greenland Current in the west and warm, Atlantic water northwards with the West Spitsbergen Current in the east (e.g. Quadfasel et al., 1987; Rudels et al., 1995). Large amounts of zooplankton of Atlantic origin are transported with the Atlantic inflow into Fram Strait in the east (Smith, 1988; Blachowiak-Samolyk et al., 2007). Bowhead whales filter-feed on zooplankton including calanoid copepods and euphausiids (Lowry et al., 2004; Ashjian et al., 2010; Moore et al., 2010; Ashjian et al., 2021). During spring and early summer, bowhead whales have been reported to preferentially stay in productive areas above bottom slopes (Moore, 2000; Moore et al., 2000; Lydersen et al., 2012; de Boer et al., 2019). In contrast, during autumn, bowhead whales migrate into shelf habitats where shallow waters may provide better opportunities to encounter copepods, which descend into deeper waters after the spring bloom (Boertmann et al., 2009; Citta et al., 2015). The presence of sea ice coupled with bathymetric features that promote upwelling may cater for optimal feeding conditions for bowhead whales in Fram Strait during spring.

The observed decline in acoustic presence in spring may relate to a shift in behavior from mating to feeding (Tervo et al., 2009). However, bowhead whales are known to feed in winter (e.g. Citta et al., 2015 for the Bering-Chukchi-Beaufort population). Furthermore, bowhead whales do sing extensively during winter months (e.g. Delarue et al., 2009; Tervo et al., 2009; Stafford et al., 2012; Clark et al., 2015), indicating that singing and feeding behaviors are not exclusive in bowhead whales. Hence, the declining acoustic presence in spring and an acoustic absence in summer likely represents the migration of bowhead whales from eastern Fram Strait to summering areas. This is in accordance with sighting data reported by Bengtsson et al. (2022) indicating a shift in the Spitzbergen bowhead whale summer distribution from the area west off Svalbard to the waters north of the archipelago. Further knowledge on the seasonal migration of bowhead whales from the Spitsbergen population stems from a limited number of satellite-tracked bowhead whales (Lydersen et al., 2012; Kovacs et al., 2020). The tracked movement patterns for Spitsbergen's bowhead whales from north to south in summer is reverse to what has been described for other bowhead whale populations. Bowhead whales from the East Canada-West Greenland and the Bering-Chukchi-Beaufort population follow the retreating ice edge northwards in summer and move southwards again in winter with the advancing ice edge (Reeves et al., 1983; Heide-Jørgensen et al., 2006; Quakenbush et al., 2010). Even though the conclusions about the seasonal movement of Spitsbergen's bowhead whales stem from a limited number of individuals, they are in accordance with historic records from whaling operations centuries ago (Moore and Reeves, 1993; Lydersen et al., 2012). Considering what is known about the summer migration of bowhead whales combined with the decrease in acoustic activity from early spring onwards, bowhead whales might have left eastern Fram Strait for summer. However, bowhead whales have been sighted approximately 150 km to the north (Wiig et al., 2007; Wiig et al., 2010) and approximately 300 km to the southwest (de Boer et al., 2019) of this study's central recording sites during summer in past years. Hence, it cannot be excluded that bowhead whales were present in eastern Fram Strait during summer but remained undetected by the automated detector. Alternatively, bowhead whales might have inhabited parts of eastern Fram Strait that were outside the recording area.

To our knowledge, this study provides the first description of the acoustic repertoire of bowhead whales in eastern Fram Strait. During a 1-year period in 2016/17, eight distinct bowhead whale song types were identified, with the acoustic repertoire exclusively consisting of single calls, simple songs and call sequences. This contrasts observations in western Fram Strait where a multitude of distinct (complex) songs were recorded (Stafford et al., 2012;

Stafford et al., 2018). Stafford et al. (2012) noted considerable differences in song complexity between different recording sites in the western and central part of Fram Strait, with extensive singing activity in the west, and comparatively simple calls and call sequences in the central part, which is in accordance with the acoustic repertoire described here. However, the vocal repertoire of bowhead whales seems to change almost entirely between years (e.g. Tervo et al., 2011b; Stafford et al., 2018), implying that the song repertoire presented here may be only representative for the 2016/2017 winter season. Continued passive acoustic monitoring by the Fram Strait recording array will provide further insights into temporal and spatial patterns in song diversity of Spitzbergen bowhead whales in eastern Fram Strait.

The production of multiple songs within a season has previously been observed, e.g. for the Eastern Canada-West Greenland population (Stafford et al., 2008; Tervo et al., 2011b), or the Bering-Chukchi-Beaufort population (Delarue et al., 2009; Johnson et al., 2015). Additionally, an extremely high diversity in the songs of bowhead whales from the Spitsbergen population was observed in western Fram Strait (Stafford et al., 2018). Despite the fact that multiple songs are produced each year, it remains unclear whether the population as a whole has a repertoire of multiple songs, or whether different individuals or groups sing different songs (see also Tervo et al., 2009; Johnson et al., 2015). However, there is evidence for song sharing among bowhead whales (Stafford et al., 2008; Tervo et al., 2011b; Johnson et al., 2015).

Besides the presence of multiple distinct song types, there was also a succession of the song types observed with the progressing season, with song types appearing and eventually disappearing after being recorded for a certain time period. Similarly, seasonal changes in the song type repertoire of bowhead whales have been observed in western Fram Strait (Stafford et al., 2018), in the Bering-Chukchi-Beaufort population during their annual migrations through the Chukchi Sea (Delarue et al., 2009; Johnson et al., 2015), and for bowhead whales during the spring and winter months in Disko Bay, western Greenland (Tervo et al., 2009). In contrast to the emergence of new song types due to gradual changes in the acoustic repertoire as observed in humpback whales, *Megaptera novaeangliae* (Noad et al., 2000), gradual (seasonal) changes from one song type to another does not seem to have occurred for bowhead whales in the present study. However, such changes might have remained undetected due to the relatively low amplitude of the bowhead whale sounds and the small sample size. Alternatively, song types may be specific to different individuals or sub-groups of a population. Hence, song types may appear and disappear because different individuals or groups of whales producing different songs were passing through the recording area (see also Delarue et al., 2009; Johnson et al., 2015). The recording site in eastern Fram Strait is not known to coincide with a migratory route for bowhead whales, as it was the case for the acoustic studies conducted in the Chukchi Sea where a clear succession of song types was evident (Johnson et al., 2015). However, whales overwintering elsewhere in the Fram Strait area might have temporarily moved into or passed the detection range of the recording device, hence causing the temporary occurrence of a certain song type.

Interestingly, one song type (i.e. song type 2) formed an exception among all other song types as it was recorded throughout almost the entire period with bowhead whale acoustic presence. This persistent presence or use of this song type might indicate that this song type could hold a basic communicative function common to all individuals, or at least a large part of the population. What this function could be, however, remains speculative. Bowhead whales are known to produce repeated call sequences, often referred to as 'simple song', which have been recorded on wintering and feeding grounds as well as during migration (e.g. Würsig and Clark, 1993; Stafford and Clark, 2021). Apart from bowhead whales, simple frequency-modulated downsweep sounds – resembling the calls which song type 2 is composed of – are also known to be produced by several other baleen whale species, such as blue whales, *Balaenoptera musculus* (e.g., McDonald et al., 2001), fin whales, *B. physalus* (e.g., Thompson et al., 1992), Antarctic minke whales, *B. bonaerensis* (Dominello and Širović, 2016), sei whales, *B. borealis* (Calderan et al., 2014), and humpback whales (Darling, 2015). In blue whales, the production of such frequency-modulated downsweep calls has generally been associated with group feeding behavior (Oleson et al., 2007), but was also reported in the context of escorting behavior (Schall et al., 2020). In long-finned pilot whales (*Globicephala melas*), repeated call sequences, which make up a large portion of their vocal repertoire, may act as a form of contact call (Zwamborn and Whitehead, 2017). Maintaining acoustic contact and cohesion between individuals that are not within visual range of each other is of particular importance in mother-calf relationships and during migration. The persistent occurrence of song type 2 was not restricted to a specific time period. Combined with the different behavioral contexts in which call sequences of other cetacean species have been recorded, this could hence imply a more basic function of song type 2 in Spitsbergen's bowhead whale population. Persisting passive acoustic monitoring in eastern Fram Strait will shed further light on the temporal patterns in the song diversity and repertoire of Spitzbergen bowhead whales.

Differences in the acoustic behavior of bowhead whales between the western and eastern part of Fram Strait could reflect regional differences in habitat suitability. In western Fram Strait, nearly continuous loud singing during winter months and a remarkably high diversity in bowhead whale song type repertoire was observed. More than 180 different songs were recorded over a 3-year period, with a progression of songs appearing and disappearing after variable periods of time (Stafford et al., 2012; Stafford et al., 2018). Compared to the extensive and loud singing of bowhead whales in western Fram Strait, the acoustic signals of bowhead whales in eastern Fram Strait (this study) were considerably less frequent and loud. Such latitudinal differences between eastern/central and western Fram Strait are also evident from the acoustic observations reported by Stafford et al. (2012), where bowhead whale sounds were considerably less common in a recorder located in central Fram Strait at ~78°N, 0°E. Even though the recording sites in western, central and eastern Fram Strait were only a few hundreds of kilometers apart, the western part of Fram Strait seems to be preferred by bowhead whales over the central and eastern parts. One possible reason for this may be the difference in sea ice cover between western and eastern Fram Strait. While the eastern part of Fram Strait is a region with low sea ice concentrations, the western part of Fram Strait is ice-covered almost year-round (Nöthig et al., 2015). Bowhead whales are known to live in close association with sea ice, but animals are also known to inhabit open water areas far off the marginal ice edge, particularly during summer months (Lydersen et al., 2012; Citta et al., 2015; George et al., 2015; de Boer et al., 2019). Sea ice is thought to provide shelter from killer whale (*Orcinus orca*) predation, offer feeding opportunities (Ferguson et al., 2010) and may be beneficial for the transmission and reception of acoustic signals (Stafford et al., 2012). Additionally, the presence of sea ice leaves western Fram Strait inaccessible for anthropogenic activities, thus undisturbed for most parts of the year (Ahonen et al., 2017). Considering that sea ice concentrations were low in eastern Fram Strait, bowhead whales may have spent less time in the region or were less vocally active because of the potential risk of killer whale predation as suggested by Stafford et al. (2012). Habitat selection for bowhead whales might also be a matter of sex or age, as has been described for bowhead whales of the Eastern Canada-West Greenland population (Heide-Jørgensen et al., 2010; Fortune et al., 2020). The presence of sea ice as a predator refuge might be particularly important for juveniles or females with calves (Fortune et al., 2020; Matthews et al., 2020). In turn, adult individuals may be more flexible in their habitat selection, since there may be less threatened by killer whale predation. Furthermore, habitats might also be selected in the context of energetics, with larger (older) animals inhabiting more productive areas as they require a larger total amount of prey compared to smaller (younger) individuals (Fortune et al., 2020). Hence, eastern Fram Strait might be inhabited by different cohorts, e.g. younger individuals not exhibiting the full vocal repertoire as compared to adults, than western Fram Strait, possibly providing an additional explanation for the observed differences in vocal behavior and song repertoire between these study sites. Irrespective of potentially low habitat suitability (either for all individuals or for some sexes and age classes), bowhead whales were detected for several months around the recording sites in eastern Fram Strait. Therefore, our mooring locations in eastern Fram Strait still represent a (possibly lesser frequented) part of the bowhead whale overwintering area. Recordings from other, e.g. more eastern, sites in Fram Strait would be required to further define and localize distribution range boundaries of Spitzbergen bowhead whales.

Ongoing climate change-related sea ice decline in the Arctic Ocean will directly affect ice-associated bowhead whales due to a progressive loss of their habitat, as sea ice provides feeding opportunities and shelter from killer whale predation (Ferguson et al., 2010). Also, indirect effects represent additional threats to bowhead whales, e.g., by increasing risk of predation and competition for prey, as well as increased risk of ship strikes or noise pollution from anthropogenic activities (Reeves et al., 2014; Moore and Reeves, 2018; Halliday, 2020a; Halliday, 2020b; Halliday et al., 2021). With reductions in sea ice, distribution patterns of bowhead whales are likely to change. Such shifts may occur as a consequence of increasing predation pressure by killer whales (Kovacs et al., 2011), driving habitat preferences of bowhead whales towards sea ice covered areas as a predator refuge (Matthews et al., 2020). Bowhead whales from the Bering–Chukchi–Beaufort population were observed to overwinter on their summer feeding ground in the eastern Beaufort Sea and Amundsen Gulf for the first time in winter 2018/19, with an underlying phenological shift in the species' migratory behavior possibly directly linked to climate change (Insley et al., 2021). Climate-change related shifts in bowhead whale distribution or habitat usage may also occur in Fram Strait, where sea ice likely is an important factor driving differences in bowhead whale distribution (Stafford et al., 2012; Ahonen et al., 2017; this study). Furthermore, due to increasingly ice-free Arctic regions, subarctic species, which seasonally move into Arctic waters to feed, will likely tend to arrive earlier or stay longer on these feeding grounds (e.g. Brower et al., 2018; Stafford, 2019; Willoughby et al., 2022). In turn, changes in distribution and phenology of subarctic species will increase the competition for prey with Arctic endemic species (Laidre et al., 2008; Moore and Reeves, 2018) or the risk of predation by killer whales which is an increasing threat for several bowhead whale populations (e.g. George et al., 2017; Shpak and Paramonov, 2018; Willoughby et al., 2020). In addition, sea ice loss facilitates anthropogenic activities in formerly inaccessible, ice-covered areas of the Arctic Ocean, with increasing underwater noise levels being of major concern for marine mammals as they strongly rely on sound for communication and navigation purposes (Reeves et al., 2014). Bowhead whales are likely to be particularly affected by low-frequency sounds (<1 kHz) from large vessels and seismic surveys, which significantly overlap with the bowhead whale vocalization frequency range (Ahonen et al., 2017) and can be transmitted over large distances to areas remote from industrial activities and shipping lanes (Nieukirk et al., 2012). In Fram Strait, airgun signals were recorded year-round (Moore et al., 2012), whereas shipping noise occurred mainly during the summer months and in the eastern part of Fram Strait where shipping is more extensive (Klinck et al., 2012). Bowhead whales from the Bering-Chukchi-Beaufort population have been observed to increase rate of calling and call source levels in the presence of weak seismic survey activity (Thode et al., 2020) but stop vocalizing in the presence of loud airgun pulses (Blackwell et al., 2015). Nevertheless, long-term effects of increased anthropogenic noise on bowhead whales are still unknown. Increased risk of predation, competition for prey or anthropogenic threats may also be particularly threatening the Spitzbergen bowhead whale population that – although whaling ceased almost a century ago - does not show signs of recovery from depletion by whaling to date.

This passive acoustic monitoring study provides essential knowledge on the (acoustic) occurrence of Spitsbergen's bowhead whale population and on spatial and temporal patterns in their distribution in eastern and central Fram Strait. Such additional information is particularly important in the light of a very small, relatively scarcely investigated and endangered population as the Spitzbergen bowhead whales. Further steps will include investigating the relationship of bowhead whale acoustic presence with prevailing sea ice conditions and other environmental factors to obtain a better understanding of the observed differences between western and eastern Fram Strait. A detailed identification and investigation of the contributors to the local soundscapes and of spatio-temporal patterns in their acoustic presence in eastern Fram Strait will improve our understanding of the study area's importance as a bowhead whale habitat as well as of the presence and persistence of anthropogenic sound sources as potential threats to marine life in Arctic waters.

Data availability statement

The datasets presented in this article are available at https://doi.org/10.1594/PANGAEA.945330 (Thomisch, 2022a; for data on hourly acoustic presence of bowhead whales) and https://doi.org/10.1594/PANGAEA.945404 (Thomisch, 2022b; for data on bowhead whale song repertoire) via the data repository PANGAEA.

Author contributions

KT, OB, and IVO designed the study. SS collected the passive acoustic data and compiled the metadata. KT and KH analyzed and validated the data and wrote the draft manuscript. KT, KH, EB, OB, SS, and IVO discussed the results and wrote the final manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frsen.2022.907105/full#supplementary-material

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