Patterns in the Acoustic Presence and Vocal Behaviour of Bowhead Whales *Balaena mysticetus* in Eastern Fram Strait

MASTER THESIS

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CONTENT

SUMMARY

Fram Strait, located between Greenland and Svalbard, provides a critical habitat to seasonally migrant and endemic cetaceans, including bowhead whales *Balaena mysticetus* of the Spitsbergen population. This population has been depleted close to the point of extinction by commercial whaling and still is considered as endangered. Due to its low abundance and the remoteness of its habitat, baseline knowledge on spatio-temporal distribution patterns and behavioural aspects are scarce, yet crucial for the conservation of this population.

Long-term passive acoustic recordings were collected at different locations in eastern Fram Strait (78-79°N, 0-7°E), contributing to the Ocean Observing System FRAM (Frontiers in Arctic Marine Monitoring). Data recorded during two sampling periods between 2012 and 2017 were analysed for the occurrence of bowhead whales using the Low-Frequency Detection and Classification System (LFDCS). Seasonal changes in their acoustic repertoire were investigated using recordings from a single year and location.

Bowhead whales were acoustically present from autumn throughout winter (October/November-February) and occasionally in spring (March-June), suggesting that Fram Strait is used as an overwintering area. Given that peak levels of acoustic presence coincided with the presumed mating period of bowhead whales, Fram Strait may also serve as a mating area. No bowhead whales were recorded in summer (July-September), indicating that they either were vocally inactive or had migrated to summering areas.

Eight distinct song types of bowhead whales were identified comprising simple songs and call sequences. Even though more than one song type was recorded at a given time, there was an overall trend that songs occurred in temporal succession. It remains speculative why songs appeared and subsequently disappeared with the progressing season, but the temporal succession possibly is related to the song types being used in different behavioural contexts. One song type formed an exception as it was recorded throughout almost the entire season and may hence serve a communicative function common to all individuals, or at a least a large part of the population.

In contrast to previous studies on bowhead whales in western Fram Strait, the recorded bowhead whale detections were less frequent and, in addition, less complex. Bowhead whales appear to preferentially occupy the western part of Fram Strait where sea ice concentrations are generally higher. Due to the observed regional differences in the acoustic behaviour between eastern and western Fram Strait, eastern Fram Strait may represent the easterly distribution range boundary of the bowhead whale overwintering area.

The findings of this study further highlight the importance of Fram Strait as a habitat for the endangered Spitsbergen bowhead whale population. In the light of rapid changes in the Arctic region, an improved understanding of distribution patterns and the acoustic behaviour is of particular relevance for developing effective conservation and management strategies, but also for assessing potential effects on the bowhead whale population resulting from climate-induced environmental changes.

1 INTRODUCTION

The bowhead whale *Balaena mysticetus* is the only baleen whale that resides in Arctic waters year-round (Moore and Reeves 1993). As such, bowhead whales are highly adapted to live in close association with sea ice (e.g., Ferguson et al. 2010). Five populations of bowhead whales are traditionally acknowledged by the Scientific Committee of the International Whaling Commission based on their geographic distribution (Figure 1): (i) Hudson Bay-Foxe Basin (East Canada), (ii) Davis Strait-Baffin Bay (West Greenland), (iii) East Greenland-Svalbard-Barents Sea (hereinafter referred to as the "Spitsbergen population"), (iv) Bering-Chukchi-Beaufort Seas, and (v) Okhotsk Sea population (Cooke and Reeves 2018a, 2018b; IWC 1992; Rugh et al. 2003). However, recent data indicate to re-assess the population structure since the Hudson Bay and Davis Strait population might consist of a single population referred to as East Canada-West Greenland population (Cooke and Reeves 2018a; Heide-Jørgensen et al. 2006).

Due to centuries of commercial whaling beginning in 1611, the global bowhead whale population was greatly reduced with the Spitsbergen population being depleted to near extinction (Jonsgård 1981; Reeves 1980; Shelden and Rugh 1995; Woodby and Botkin 1993). Despite becoming protected in the early 1930s, the Spitsbergen population does not show signs of recovery and still is considered as being "endangered" by the IUCN Red List of Threatened Species (Cooke and Reeves 2018b). The population size prior to commercial whaling has been estimated at 52,500 individuals (Allen and Keay 2006), while today it is believed to number in the range of 50-250 individuals (Cooke and Reeves 2018b). Given the low abundance of bowhead whales of the Spitsbergen population, baseline data on many population parameters, such as abundance, population trend and spatio-temporal distribution patterns, are still scarce to date.

Current knowledge about the spatial distribution of this population is mainly based on old whaling reports (Reeves 1980). The historic distribution of the Spitsbergen population extended from the Greenland Sea to Svalbard across the Barents Sea to Franz Josef Land, and as far east as Novaya Zemlya, possibly even to the Kara Sea (Moore and Reeves 1993; Reeves 1980; Rugh et al. 2003). Sighting data between 1940 and 2009, summarised by Wiig et al. (2010), showed that the Spitsbergen bowhead whale population still occurs in its former range. Historic whaling records suggest that Fram Strait, located between Greenland and Svalbard, was a key area for this population (Woodby and Botkin 1993). Fram Strait is the only deep-water connection, thus the most important gateway for the exchange of water masses between the Arctic Ocean and the Nordic seas (e.g., Aagaard et al. 1985; Fahrbach et al. 2001). The dynamic hydrological conditions within Fram Strait create large productive areas with high zooplankton abundance (Blachowiak-Samolyk et al. 2007), hence making this region a favourable habitat for the zooplankton-feeding bowhead whale. 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). Despite the overexploitation of bowhead whales in this area, recent sightings suggest that the Spitsbergen population still occupies these waters, at least during the spring and summer months (de Boer et al. 2019; Wiig et al. 2007).

In the Fram Strait area, the presence of dense ice cover, particularly in the western part, hampers visual surveys. In consequence, visual surveys are constrained mainly to the summer months resulting in a lack of winter observations of bowhead whales from this region. Since whaling operations also occurred outside the winter months, data on the presence of bowhead whales in Fram Strait during the winter are limited. The need for seasonally unbiased data to assess marine mammal occurrence and distribution year-round has emerged new techniques, such as passive acoustic monitoring (PAM) (Mellinger et al. 2007; Širović et al. 2004; Sousa-Lima 2013). PAM includes fixed or mobile hydrophones to record the underwater sound environment from which the recorded signals of interest then can be extracted. Since acoustic recorders can sample continuously over long periods of time – depending on battery and storage limitations –, PAM is capable to collect year-round, and hence seasonally unbiased data. In contrast to visual surveys, which are dependent on weather and sighting conditions, PAM is particularly useful in remote and seasonally inaccessible areas such as polar regions. Given that bowhead whales produce a remarkable variety of acoustic sounds ranging from simple calls to complex songs (Clark and Johnson 1984; Cummings and Holliday 1987; Ljungblad et al. 1982; Würsig and Clark 1993) makes them highly suitable for being studied using PAM.

Recently, 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). The results suggested that western Fram Strait provides an important wintering area for the Spitsbergen bowhead whale population (e.g., 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), virtually nothing is known about their occurrence in the eastern part of Fram Strait.

The present study aims to assess temporal patterns in the occurrence of bowhead whales at different locations in eastern Fram Strait, using long-term passive acoustic recordings collected during two sampling periods between 2012 and 2017. Given an extraordinarily high song diversity documented for the Spitsbergen population (Stafford et al. 2018), this study further wants to provide a first description of song types produced by bowhead whales in eastern Fram Strait and investigate potential seasonal changes in their acoustic repertoire, using recordings from a single year and location.

Updated knowledge of the *status quo* of bowhead whales is of high relevance in the context of a rapidly changing Arctic Ocean. Fram Strait appears to be a key area for bowhead whales and other cetacean species (Kovacs and Lydersen 2006), and is undergoing severe and rapid environmental changes associated with rising water temperatures and declining sea ice due to climate change (e.g., Laidre et al. 2015). The changing sea ice conditions and the resulting increases in anthropogenic activity add additional threats to the already vulnerable Spitsbergen population (Reeves et al. 2014; Thomas et al. 2016). An improved knowledge about their abundance, spatio-temporal occurrence and behavioural aspects, such as their migratory and acoustic behaviour, is required to predict how the population may react to these changes (Kovacs et al. 2011; Laidre et al. 2008; Moore and Huntington 2008). Moreover, such information is of particular importance to establish effective conservation and management strategies, e.g. to mitigate noise disturbance from anthropogenic activities (Reeves et al. 2014).

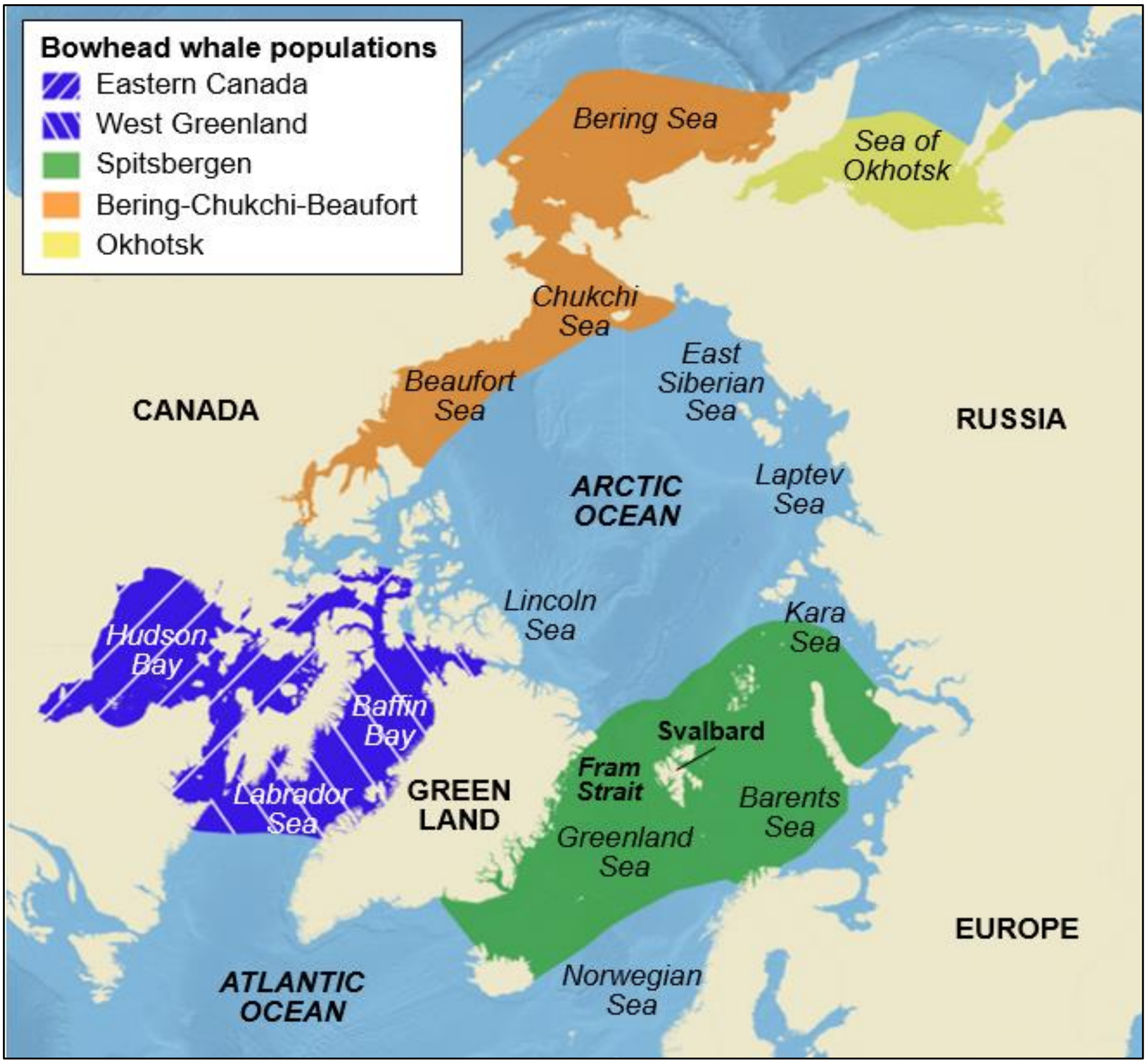


Figure 1. Circumpolar distribution of bowhead whale populations. Note that the Hudson Bay-Foxe Basin (East Canada) population and the Davis Strait-Baffin Bay (West Greenland) population may consist of a single population referred to as East Canada-West Greenland population. Source: NAMMCO, modified by adding names of the depicted geographic regions.

2 MATERIAL & METHODS

2.1 Data Collection

Passive acoustic data were collected by five Sono.Vault recorders (manufactured by develogic GmbH, Hamburg, Germany). The study period comprised two sampling periods between 2012 and 2017: June 2012-November 2012 and July/August 2016-July/August 2017 (Table 1). The recorders were attached to oceanographic moorings located in central (SV1021, SV1091), southern (SV1097) and eastern parts (SV1026, SV1088) of Fram Strait as part of the Ocean Observing System FRAM (Frontiers in Arctic Marine Monitoring, Soltwedel et al. 2013) (Figure 2, Table 1). The recorders were moored at depths around 800 m and scheduled to continuously record the underwater sound environment at sample rates of 5,333 Hz (SV1021 and SV1026) and 48,000 Hz (SV1091, SV1097 and SV1088; Table 1). Recordings were stored internally on memory cards in 5-min or 10-min long sound files with a 24 bit sampling resolution. Data quality was inspected using long-term spectrograms of the recordings. Two recorders (SV1021 and SV1026) stopped recording prior to recovery due to battery exhaustion, thus only cover the second half of 2012. Moreover, recorder SV1026 lacks twelve days of data in October due to a defective memory card.

Prior to analysis, recordings originally sampled at 48,000 Hz were downsampled to a sampling rate of 5,333 Hz to match the sampling rate of the recordings from SV1021 and SV1026 in order to allow comparison of results from different recorders. All acoustic data were converted to a 16 bit sampling resolution to follow the requirements of the automated detector.

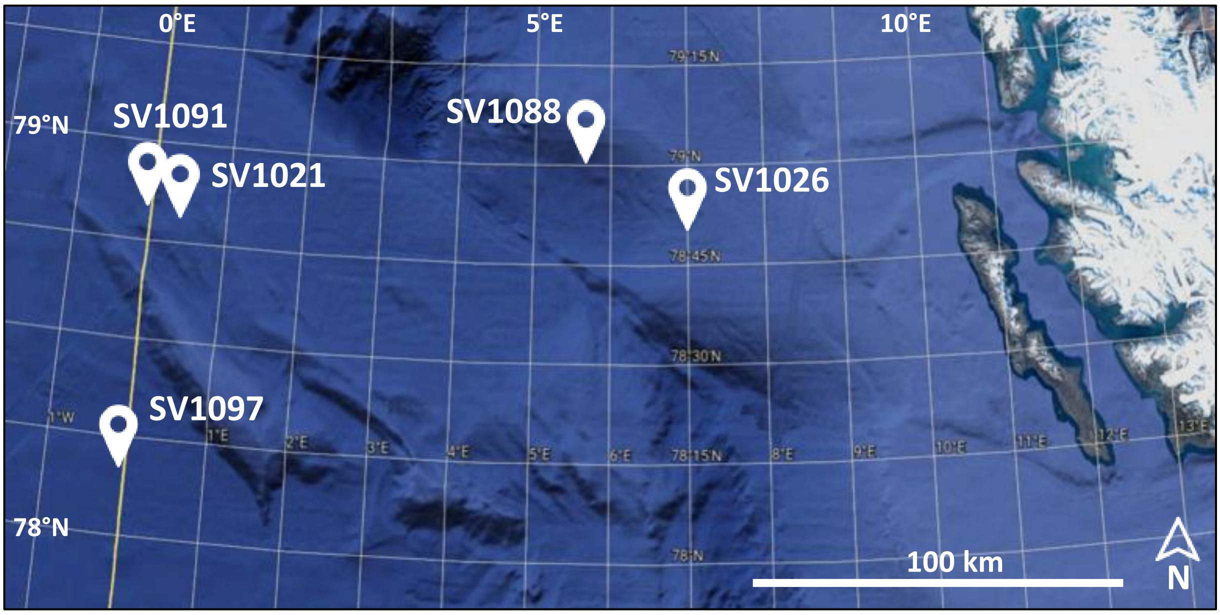


Figure 2. Deployment locations of the five recorders (white pins) in Fram Strait between Greenland and Svalbard. SV1021 and SV1026 were recording in 2012, while SV1091, SV1097 and SV1088 were recording year-round in 2016/17. SV1021 and SV1091 belong to the central recording site, SV1097 to the southern and SV1026 and SV1088 to the eastern recording site. Map source: Google Earth.

Table 1. Locations and recording parameters of passive acoustic recorders deployed in Fram Strait as part of the Ocean Observing System FRAM between 2012 and 2018. Deployment and recording period given as mm/yyyy.

Mooring ID	Recorder ID	Latitude	Longitude	Deployment period	Recording period	Operational period [d]	Deployment depth [m]	Original sampling frequency [Hz]
ARKF16-09	SV1021	78° 49.76’ N	0° 25.77’ E	06/2012-09/2014	06/2012-11/2012	151	800	5,333
ARKF04-15	SV1026	78° 50.01’ N	6° 59.99’ E	06/2012-06/2015	06/2012-11/2012	147	743	5,333
ARKR02-01	SV1091	78° 50.01’ N	0° 00.09’ E	07/2016-07/2018	07/2016-07/2017	360	806	48,000
ARKR01-01	SV1097	78° 10.21’ N	0° 00.04’ E	08/2016-07/2018	08/2016-08/2017	361	799	48,000
ARKF05-17	SV1088	79° 00.02’ N	5° 40.12’ E	07/2016-09/2018	07/2016-07/2017	361	808	48,000

2.2 Acoustic Analysis

2.2.1 Automated Detection

All acoustic data were processed using the automated detector Low-Frequency Detection and Classification System (LFDCS). LFDCS is a software that automatically detects and classifies low-frequency baleen whale calls (Baumgartner and Mussoline 2011). The software created spectrograms of each data file with a frame of 1,024 samples and 80 % overlap using Fast Fourier Transformation (FFT). Technical details controlling the behaviour of LFDCS during the automated detection process are predefined in a parameter file (Table A1). Briefly, the underlying algorithm of LFDCS determines the best path through each call in a spectrogram (Baumgartner and Mussoline 2011). Those paths are also referred to as pitch tracks (Figure 3). Seven attributes of a call are extracted from the pitch track and used for classification. Attributes include, for instance, start and end frequency, frequency range, duration as wells as slope of frequency variation (Baumgartner and Mussoline 2011). Classification is based on the similarity between attributes of the pitch track to those of a predefined set of call types contained in a call library using quadratic discriminant function analysis. Similarity is rated by Mahalanobis distance and measures the deviation of a detected call from the assigned call type. The lower the Mahalanobis distance value, the closer a call matches its assigned call type (Baumgartner and Mussoline 2011).

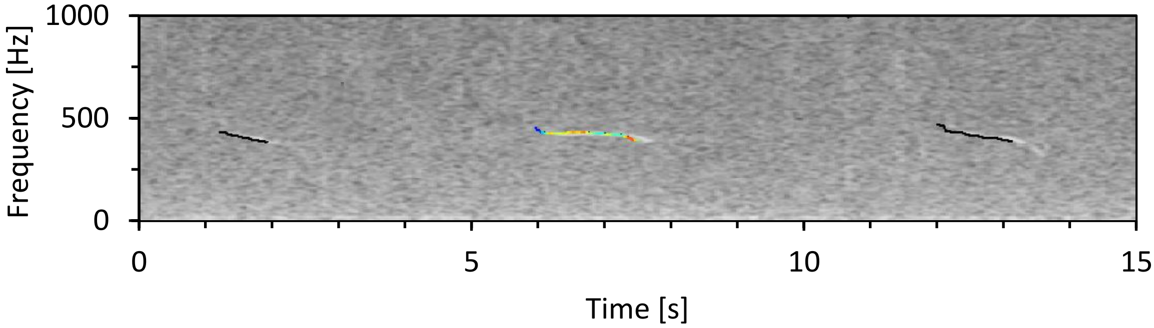


Figure 3. Spectrogram produced by the Low-Frequency Detection and Classification System (LFDCS) showing bowhead whale calls. Detected signals (pitch tracks) marked in black. Selected pitch track highlighted in colour representing the loudness (amplitude, dB) of the call relative to the background. Warmer colours indicate high amplitudes, while cooler colours indicate lower amplitudes. Recorded on 14 November 2012 in Fram Strait by SV1021 (78° 49.76’ N, 0° 25.77’ E).

2.2.2 Call Library

The call library used in this study contained a set of exemplary bowhead whale calls obtained from recording data collected in Fram Strait in 2012 (Hiemer 2018). Due to spatio-temporal variation in bowhead whale calls (e.g., Tervo et al. 2011; Stafford et al. 2018; Delarue et al. 2009), the call library described in Hiemer (2018) was expanded and improved by adding additional exemplar calls from the southern (SV1097) recording site of the 2016/17 sampling period. The exemplar calls comprised calls from several months and daytimes to ensure that different individuals and call variations were covered. Exemplar calls were categorised into 13 call types according to their spectrographic shape, duration and frequency range (Table 2, Figure 4).

Due to their spectrographic similarity to bowhead whale calls, sounds of ice tremors (also known as “singing” ice) are likely to mistakenly be classified by LFDCS as bowhead whales. To reduce the risk of misclassifying sounds of breaking ice as bowhead whales, the call library also contained exemplary ice sounds. Classification relies on the assumption that the exemplar calls within a call type follow a multivariate distribution and that the call types are as distinct as possible (Figure 5).

Table 2. Classification, description and frequency range [Hz] of bowhead whale calls within the call library; *n* refers to the number of exemplars in each call type. Values in the description column are given as means.

	Call type	**Description**	**Frequency range [Hz]**	***n***
01	Up-down call	Tonal up-down call of 0.7 s duration and a bandwidth of 37 Hz	200-700	144
02	Moan	Constant call of 0.6 s duration and a bandwidth of 14 Hz	300-600	132
03	Downsweep 1	Single downsweeping unit of 0.8 s duration and a bandwidth of 58 Hz	300-600	488
04	Downsweep 2	Single downsweeping unit of 0.6 s duration and a bandwidth of 38 Hz	200-400	145
05	Downsweep 3	Single downsweeping unit of 0.8 s duration and a bandwidth of 104 Hz	300-600	554
06	Steep Downsweep	Single steeply downsweeping unit of 0.7 s duration and a bandwidth of 204 Hz	200-800	101
07	Curved Downsweep	Constant call transitioning into a downsweep of 1.2 s duration and a bandwidth of 117 Hz	400-600	75
08	Upsweep	Single upsweeping unit of 0.8 s duration and a bandwidth of 65 Hz	600-700	60
09	Up- and Downsweep 1	Slight upsweep followed by downsweep of 1.0 s duration and a bandwidth of 172 Hz	400-700	181
10	Up- and Downsweep 2	Slight upsweep followed by downsweep of 0.8 s duration and a bandwidth of 122 Hz	300-600	154
11	Up- and Downsweep 3	Slight upsweep followed by downsweep of 1.6 s duration and a bandwidth of 292 Hz	300-600	37
12	Up- and Downsweep 4	Slight upsweep followed by downsweep of 1.4 s duration and a bandwidth of 403 Hz	300-800	24
13	"Wave"	Up-down-upsweep, resembles a wave, of 1.1 s duration and a bandwidth of 36 Hz	400-600	71

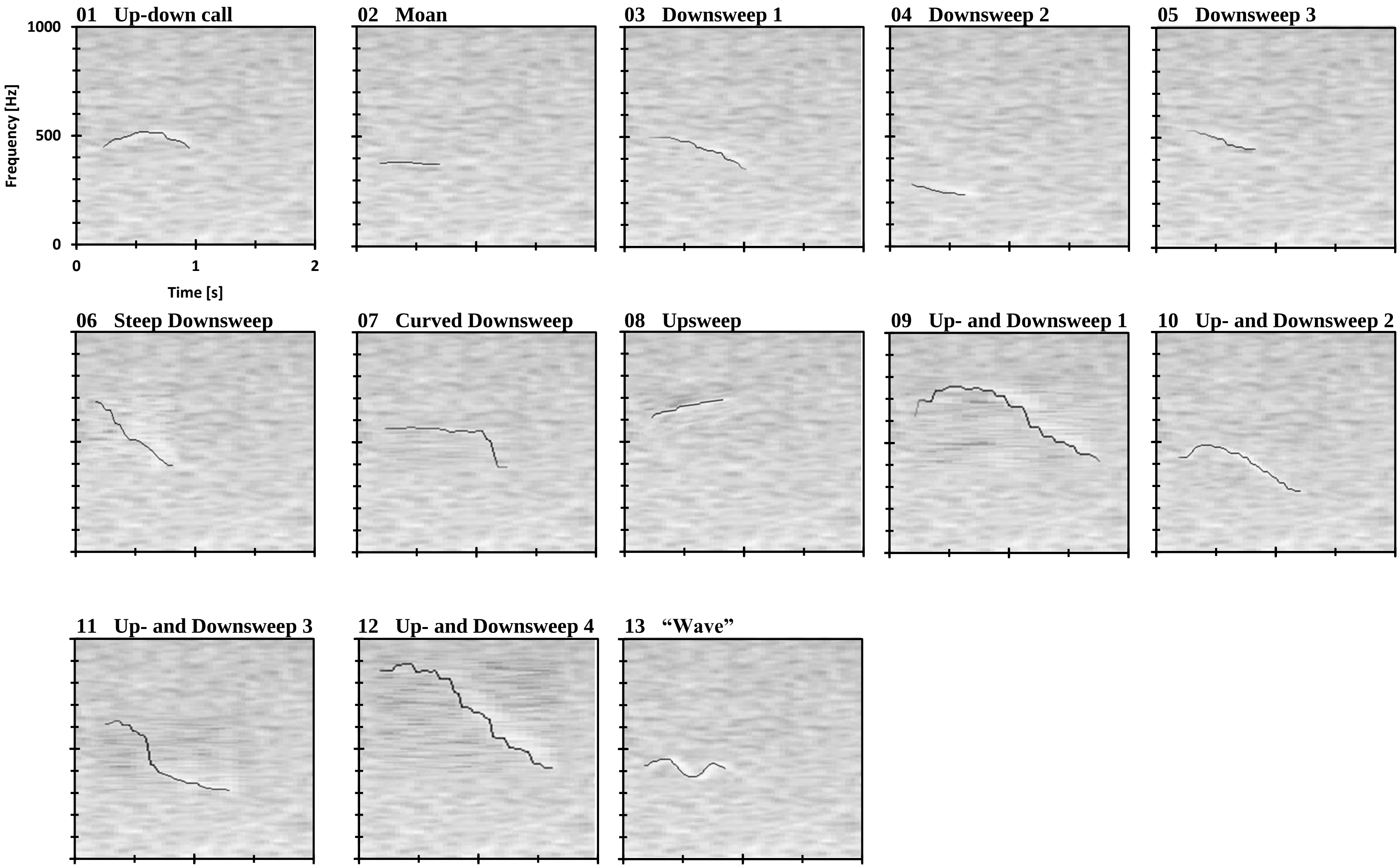


Figure 4. Exemplary pitch tracks of bowhead whale call types. Spectrogram settings: FFT 1,024, Hann window. The x-axis comprises a time interval of 2 s and the y-axis a bandwidth of 0-1,000 Hz for all exemplary pitch tracks.

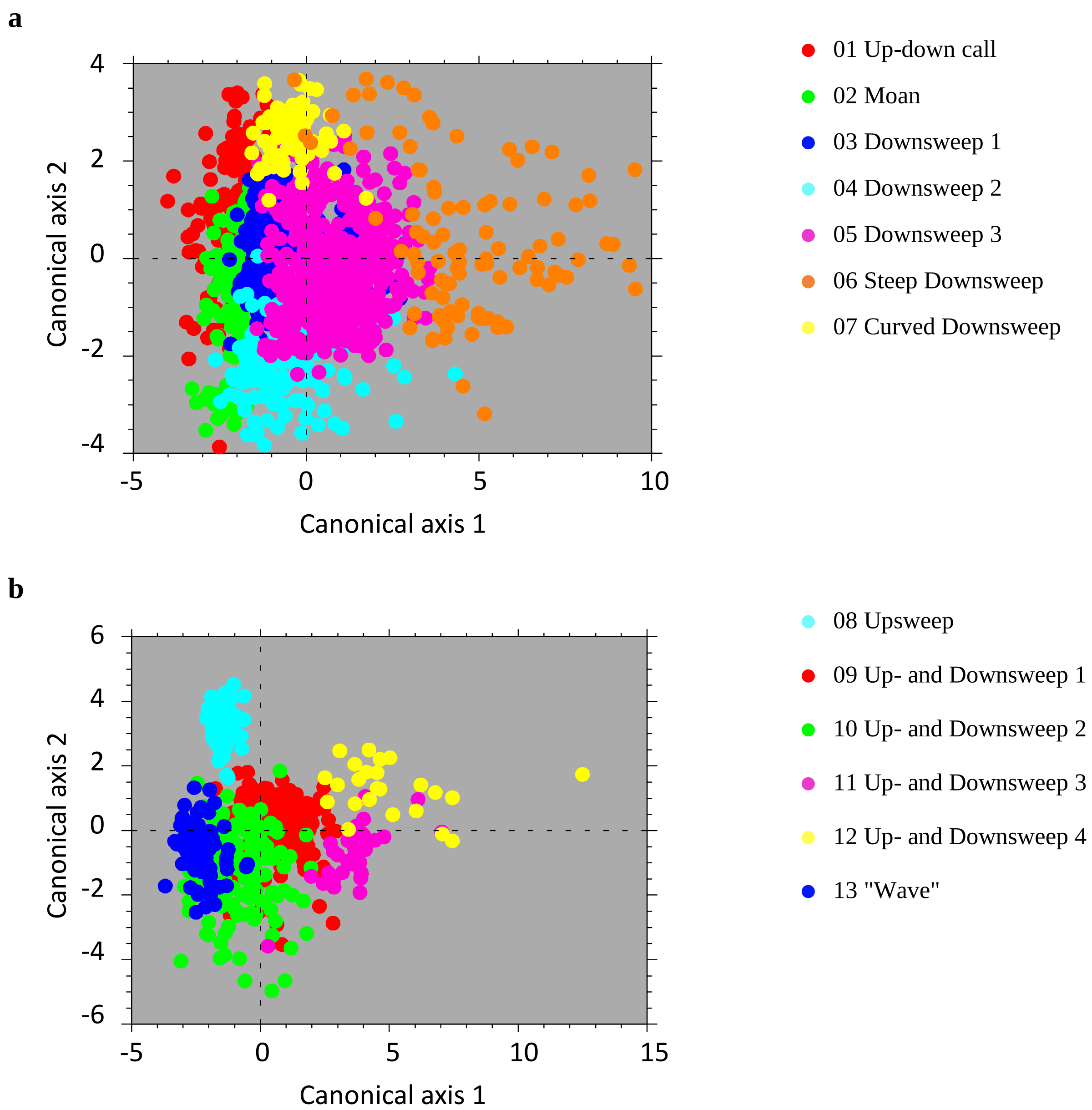


Figure 5. Canonical discriminant function analysis (CDFA) scatterplot of bowhead whale call types. CDFA seeks to reduce the seven attributes of each call type down to two dimensions in order to visualise which call types may interfere with one another (Baumgartner 2019). Thus, the canonical x- and y-axis represent the 7-dimensional distribution of the attributes for each call type. The more the call types are separated, the more different they are. Each call type is represented by a different colour explained in the legend on the right. (**a**) Scatterplot of call types 01-07. (**b**) Scatterplot of call types 08-13.

2.2.3 Detector Evaluation

Detector performance was evaluated to quantify whether LFDCS is likely to over- or underestimate hourly acoustic presence of bowhead whales. A data subset was manually reviewed for hourly acoustic presence of bowhead whales. This data set comprised 12 days of acoustic data from the central recordings site (SV1091) of the 2016/17 sampling period covering the late autumn, winter and early spring months (i.e. October-March) when bowhead whales are likely to be present in Fram Strait (Ahonen et al. 2017; Stafford et al. 2012). Within each month between October and March, the 1st and 15th day were analysed for hourly acoustic presence. Manual review entailed visually inspecting spectrograms (window size: 2.5 min; frequency range: 0-1,300 Hz; spectrogram settings: FFT 1,024, overlap 90 %, Hann window) created with Raven Pro 1.5 (Bioacoustics Research Program, Cornell Lab of Ornithology), supplemented by listening to potential calls. Hourly acoustic presence was determined as the presence of at least one bowhead whale call within a particular hour. The resulting data set was considered to be the ground truth against which the output of LFDCS was compared. Detector performance was quantified by calculating recall and precision. Recall (Eq. 1) measures how many of the hours with acoustic presence in the ground truth data set were also found by LFDCS. Complementarily, the miss rate (Eq. 2) states how many of the hours with acoustic presence were missed by LFDCS. Precision (Eq. 3) defines how many of the hours with acoustic presence detected by LFDCS were correct, i.e. were true positive.

(1) $$Recall = \frac{number\ of\ true\text{-}postive\ hours}{number\ of\ positive\ hours}$$

(2) $$Miss\ rate = \frac{number\ of\ false\text{-}negative\ hours}{number\ of\ positive\ hours} = 1 - Recall$$

(3) $$Precision = \frac{number\ of\ true\text{-}positive\ hours}{number\ of\ LFDCS\text{-}predicted\ positive\ hours}$$

2.2.4 Post-Processing of Automated Detections

Choosing appropriate detection thresholds is crucial to balance the trade-off between the number of false detections and the number of missed calls of an automated detector (Mellinger et al. 2007). In a previous study on the performance of LFDCS in determining hourly acoustic presence of bowhead whales, LFDCS provided both a reasonably high recall and precision when only detections with a Mahalanobis distance threshold of 1.5 combined with a SNR threshold of 8 dB were considered (Hiemer 2018). Using these thresholds to filter all calls detected by LFDCS in the acoustic recordings of this study, however, resulted in a large proportion of false positive hours. To eliminate the false positive hours, 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 (window size: 2.5 min; frequency range: 0-1,300 Hz; spectrogram settings: FFT 1,024, overlap 90 %, Hann window) created with Raven Pro 1.5 for the presence of at least one bowhead whale call validated by a trained analyst. 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 the hours before and after them, were reviewed. The probability of acoustic presence was considered reasonably high within these hours since bowhead whales often vocalise for several hours (e.g. 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), augmented aurally with the aid of online sound libraries (e.g., Macaulay Library of The Cornell Lab of Ornithology; Discovery of Sound in the Sea, www.dosits.org).

2.3 Sea Ice Concentration

Sea ice coverage in the study area was derived from satellite data (Spreen et al. 2008). Daily sea ice concentration data with a $6.25 \times 6.25\ km^2$ resolution were downloaded from https://seaice.uni-bremen.de/data/amsr2/asi_daygrid_swath/n6250/. Mean ice concentrations for every day were calculated from all data points within a 35 km radius around each recording location. As bowhead whale vocalisations are estimated to propagate distances of up to 35 km (Bonnel et al. 2014), a radius of 35 km was considered to be representative of the sea ice conditions within the respective recording area.

2.4 Acoustic Repertoire

The acoustic repertoire of bowhead whales within a one-year period was assessed from acoustic data recorded by SV1088in eastern Fram Strait. Sound files containing acoustic detections of bowhead whales were displayed as spectrograms created with Raven Pro 1.5 (window size 2.5 min; frequency range: 0-1,300 Hz; spectrogram settings: FFT 1,024, overlap 90 %, Hann window). Spectrograms were visually checked for the presence of bowhead whale songs. In this study, the term “song” comprises both call sequences and *true* songs, thereby following the differentiation of Stafford et al. (2012). Here, true songs are made up by different calls, called “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). Each song type was numbered based on its chronological order of appearance within the sampling period. Only songs 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 based on descriptive song characteristics, such as spectral structure of units, the arrangement of units and their frequency range. For a more robust classification system, song types were still considered the same type if the number of repetitions of units differed between songs, but the unit structure, arrangement of units and frequency range remained similar. In such cases, songs were considered a variant of the song type and assigned a sub-number, e.g. 1.1, 1.2 etc. for variants of song type 1.

3 RESULTS

3.1 Detector Performance

According to the ground truth data set, bowhead whale calls were identified in 86 h out of 288 h within 12 sampled days (Table A2a). Using the automated detector with a Mahalanobis distance threshold of 1.5 combined with a signal-to-noise (SNR) threshold of 8 dB, LFDCS detected a total of 504 bowhead whale calls. Regarding hourly acoustic presence, LFDCS detected bowhead whale calls within 31 h (Table A2b), i.e. only a fraction of the hours with acoustic presence was also found by LFDCS, resulting in a recall of 32.6 % (or a miss rate of 67.4%). Out of the 31 h with acoustic presence detected by LFDCS, 28 h (90.3 %) were correctly identified (precision) (Table 3, Figure A1).

Evaluating the performance of LFDCS at a daily resolution, LFDCS retrieved 57.1 % of the days with manually detected acoustic presence correctly and performed with 66.7 % precision.

For the acoustic presence analysis of the whole data set, a total of 33,230 h of acoustic recordings were processed by LFDCS. During post-processing, 3,911 h containing automated detection events of bowhead whales were manually reviewed in terms of a false-positive control, resulting in 2,292 h with confirmed acoustic presence. Consequently, LFDCS performed with only 58.6 % precision with regard to the whole data set, rather than 90.3 % as indicated by the ground truth data set.

Table 3. Performance of the automated detector Low-Frequency Detection and Classification System (LFDCS) in determining hourly acoustic presence of bowhead whales based on 12 sampled days.

	Ground truth data set (human analyst)	Automated detector (LFDCS)
Total hours sampled	288	288
Hours with presence	86	31
True positive hours		28 (9.7 %)
Missed hours		58 (20.1 %)
Recall		32.6 %
Miss rate		67.4 %
Precision		90.3 %

3.2 Acoustic Presence of Bowhead Whales

Bowhead whale sounds were detected at all recording sites and during both sampling periods in 2012 and 2016/17. In 2012, recordings covered only the second half of the year whereas the recordings from the 2016/17 sampling period provided year-round data between the summers of 2016 and 2017. Acoustic presence did not show any diel pattern (Figure 6) since detections were uniformly distributed across all daytimes (Figure A2). Instead, 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 7). In both sampling periods, bowhead whales started to be acoustically present in autumn (Figure 7). The onset of acoustic presence coincided with low levels of sun light due to polar night conditions (Figure 6). While bowhead whales in 2012 started to call already in mid-October, first detections of bowhead whales occurred not until mid-November in the recordings of 2016/17.

In 2012, acoustic presence occurred in distinct blocks, each lasting around a week, from mid-October until the end of November when recordings stopped (Figure 7a, b). Hourly acoustic presence increased from October to November. This increase was only apparent in the data of the central recording site (SV1021) since the eastern recording site (SV1026) was missing a crucial time period of twelve recording days in late October. For the central recording site, bowhead whales were present in 11 % of the recorded hours and in 4 % of the hours at the eastern recording site. Hence, acoustic presence was more than twice as high at the central recording site.

Between 2016/17, bowhead whales were recorded at all recording sites from late autumn throughout winter (November-February) and also occasionally during spring (March-May) at the southern and eastern recording site (SV1097, SV1088). No bowhead whales were detected from July to November 2016 and in July 2017 at all recording sites (Figure 7c-e). Acoustic presence peaked during polar night conditions between mid-November and mid-December when bowhead whales were recorded almost daily, often hourly for several days in a row (Figure 7c-e). During this period, 68 % (± 4.5, n=3) of all hours with bowhead whale detections occurred, with highest acoustic presence at the southern recording site. Subsequently, acoustic presence considerably decreased, but continued in patches, each lasting mostly between 2-4 d, through January until February. Due to prevailing noise of breaking ice, no bowhead whales were acoustically detected at the central (SV1091) and southern recording site from mid-February throughout April (Figure 7c, d). While bowhead whales were recorded again at the southern recording site at a few occasions 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.

Data suggested that there was no relationship between sea ice concentration in 35 km radius around the recording sites and bowhead whale acoustic presence for all years and recording sites (Figure 7, Figure A3). Sea ice concentrations were highly variable among the three recordings sites, with sea ice concentrations being highest at the central, and lowest at the eastern recordings site throughout the sampling period. In 2016/17, acoustic presence coincided with the absence of sea ice at the southern and eastern recording site (Figure 7c, d). No such trend was present in the data of the central recording site (Figure 7e).

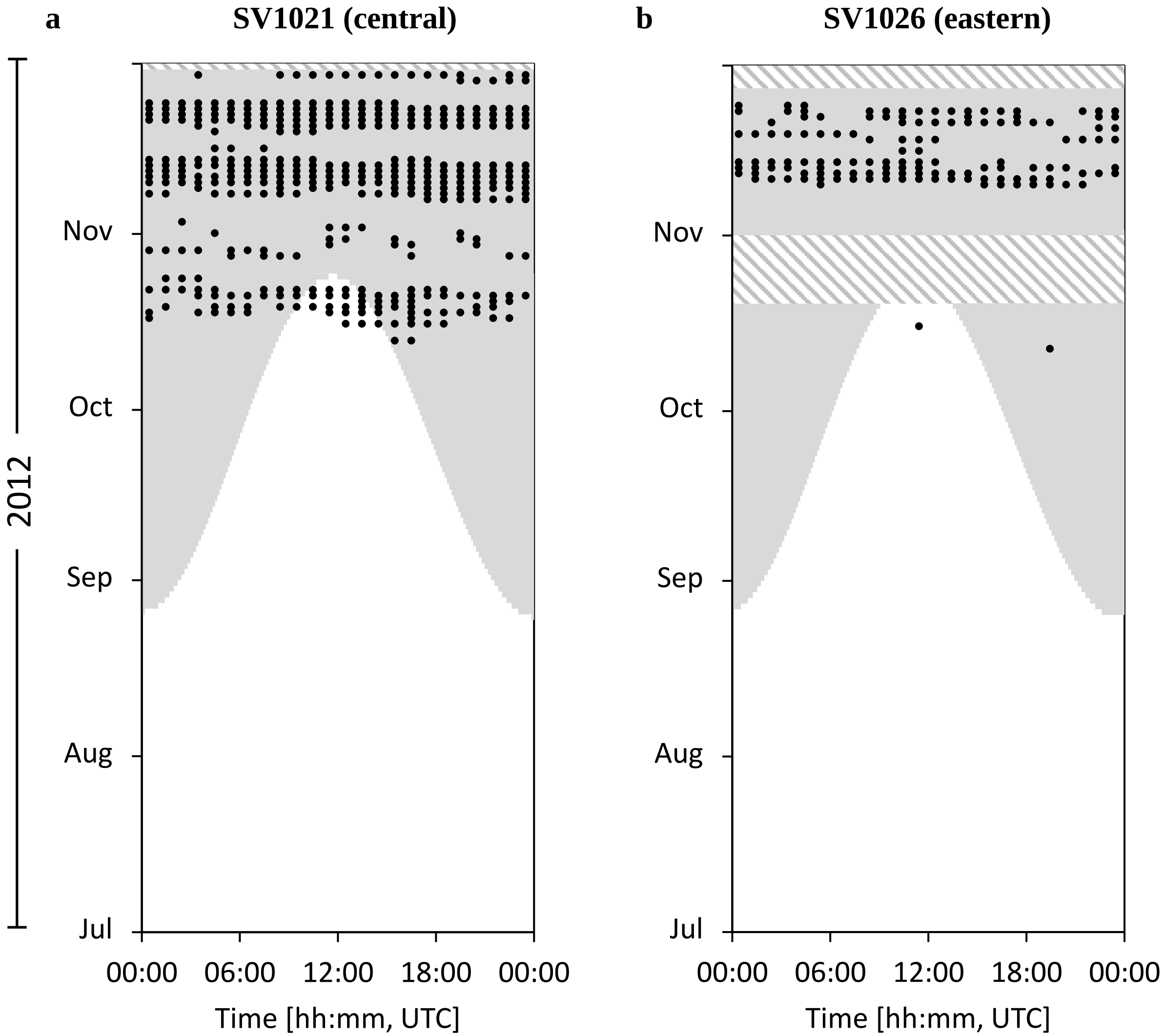
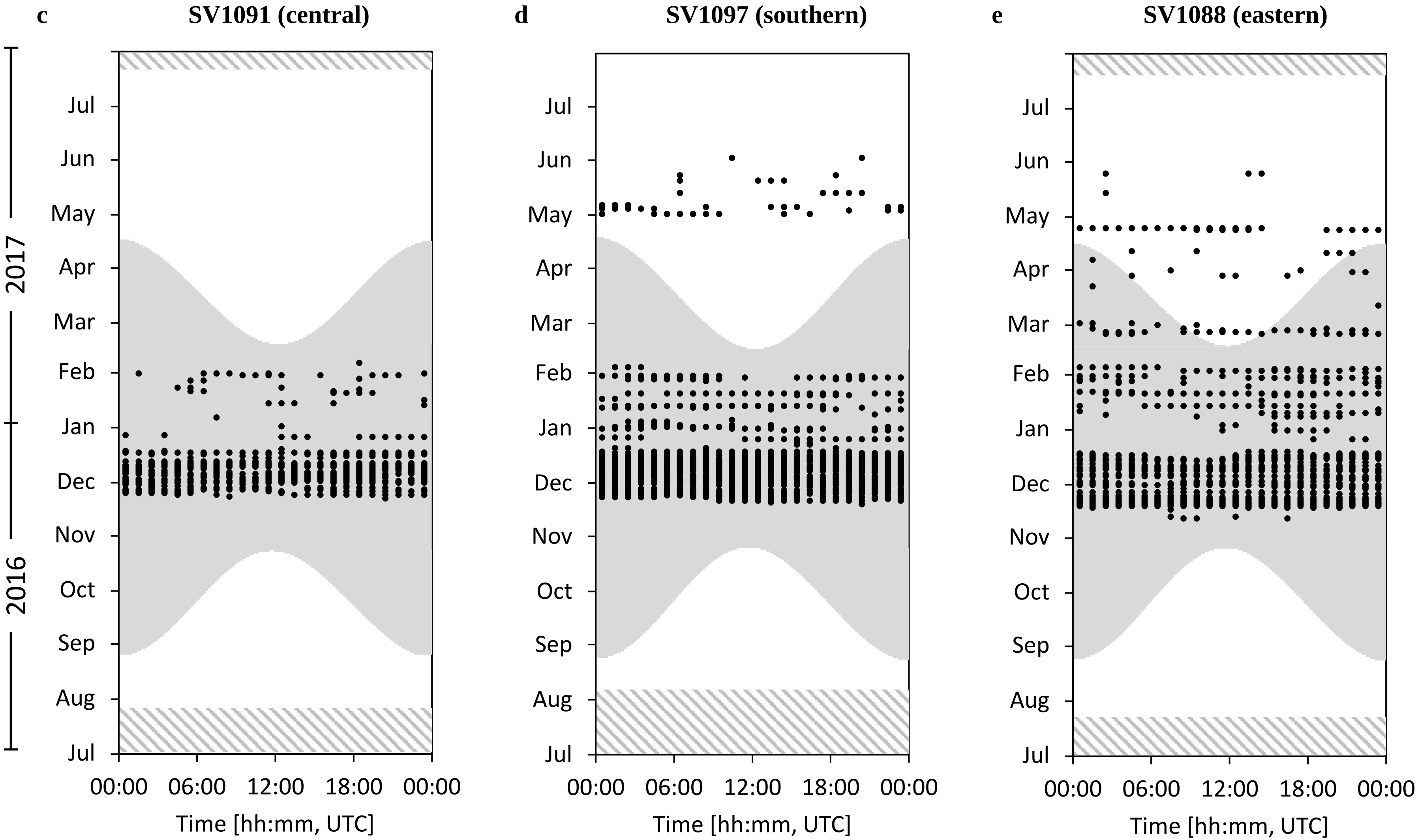


Figure 6. Seasonal and diel distribution of bowhead whale acoustic presence in Fram Strait in 2012 (a-b) and 2016/17 (c-e). Grey shading illustrates times between sunset and sunrise in Coordinated Universal Time (UTC), the local time at the recoding locations. Black dots indicate hours with acoustic presence of bowhead whales. Hatched areas illustrate periods without recordings.



(Continuation of Figure 6)

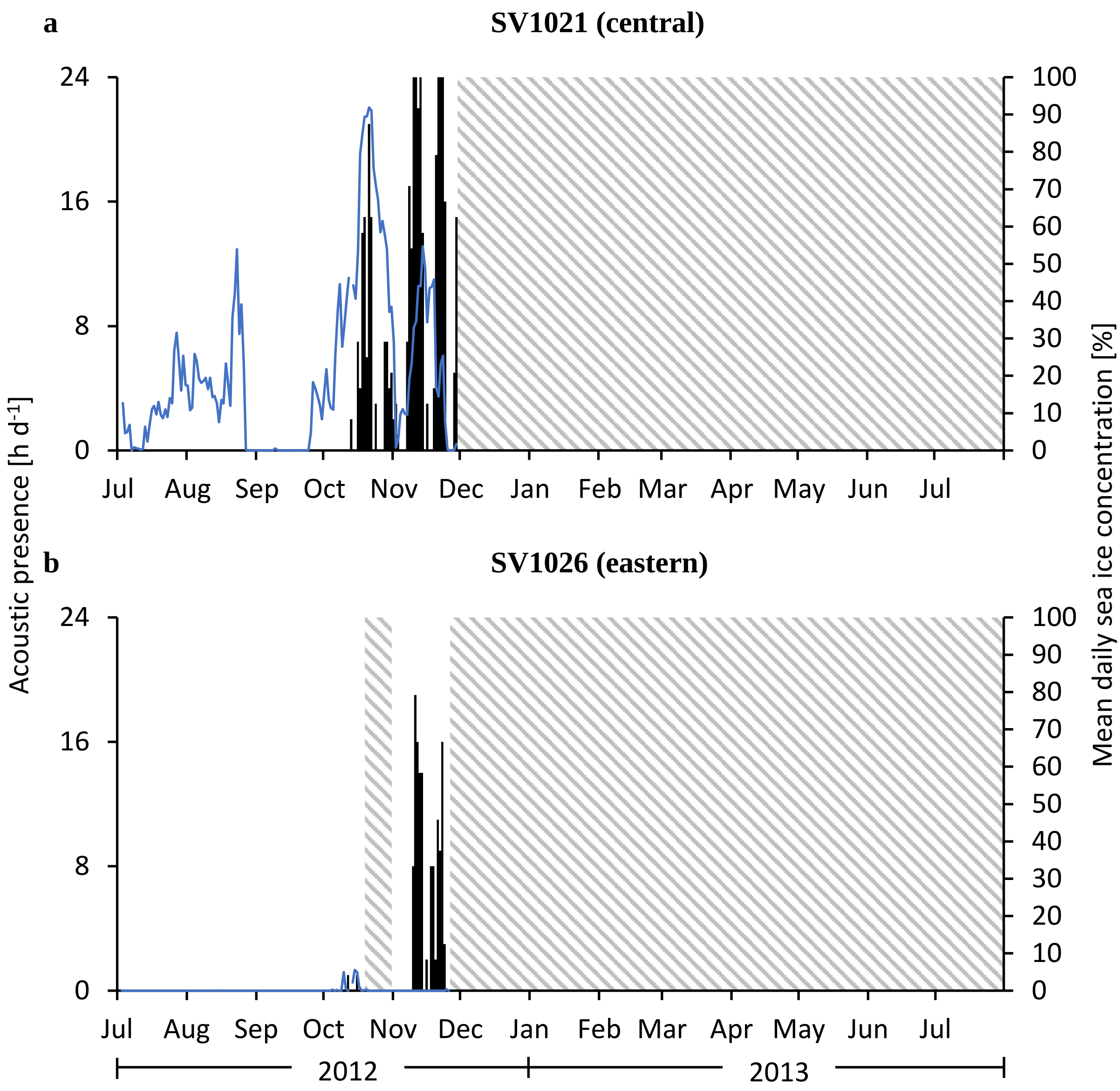
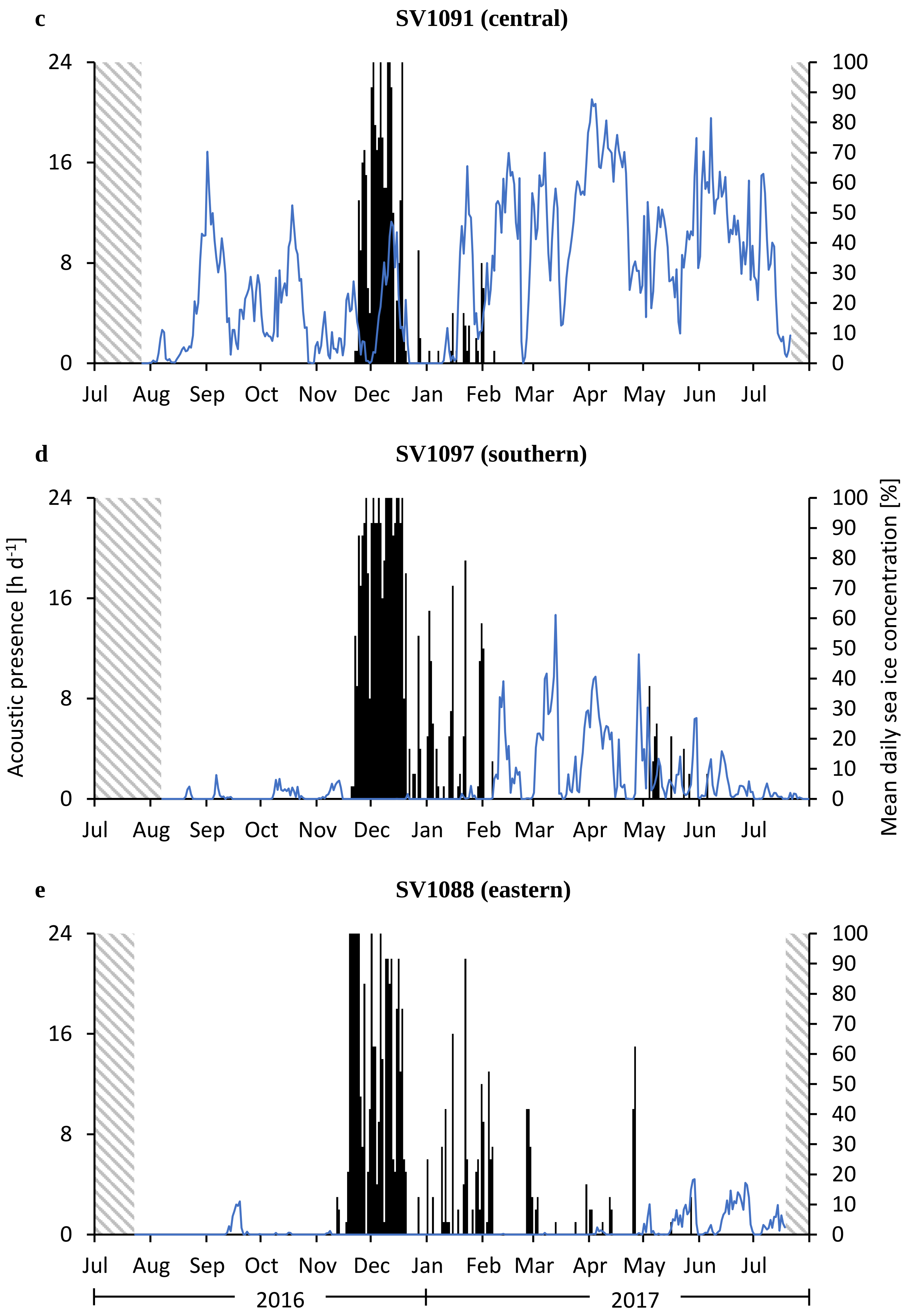


Figure 7. Acoustic presence of bowhead whales in Fram Strait in 2012 (a-b) and 2016/17 (c-e). Number of hours per day [h d^{-1}] with acoustic presence of bowhead whales (left x-axis, black bars) and mean of daily sea ice concertation [%] within a 35 km radius around each recording location (right x-axis, blue lines). Hatched areas illustrate periods without recordings.



(Continuation of Figure 7)

3.3 Acoustic Repertoire of Bowhead Whales

During the period between November 2016 and May 2017 when bowhead whales were vocally present in eastern Fram Strait, eight bowhead whale song types were identified. 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 repeating pattern, thus were not included in the analysis. 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 8, Figure A4). Some song types displayed up to six different variants. No complex songs, according to the definition of Stafford et al. (2012), were found.

3.3.1 Song Description

In the following, the song types recorded in this study are described in more detail.

Type 1 – The first simple song showed two variants. It started with an up-down-swept signal (unit 1, 350-600 Hz) immediately followed by a single downsweeping moan (unit 2, 300-250 Hz) (Figure 8a). The short upsweeping part in the first unit was not evident in all recordings of song 1.1 and did not occur in variant 1.2 (Figure 8b). In variant 1.2, unit 2 was repeated 2-3 times.

Type 2 – Type 2 was the most prominent song type with six different variants. All variants of type 2 were sequences of repeated, simple downsweeping calls. They generally occurred in bouts of 2-15 similar calls in the frequency range between 250-600 Hz. During peak season in early winter, bouts were often repeated for more than 24 h and by multiple individuals, indicated by overlapping calls. A call regularly started with a short upsweeping phase inflecting into a downsweep. This inflection was sometimes more rounded as in variant 2.1, 2.2 and 2.3 (Figure 8c, d, e), or sharper like in variant 2.4 (Figure 8f). The short upsweeping phase was completely missing in variant 2.5 and 2.6 (Figure 8g, h). In variant 2.2, the downsweeping component additionally ended in a louder, slightly upsweeping inflection (Figure 8d).

Type 3 – Simple songs included in type 3 showed a gradual decline in the start frequency from one phrase compared to the following phrase during a song. Variant 3.1 and 3.3 were made up of 2-3 phrases, which themselves consisted of 2-3 repetitions of the same unit (Figure 8i, k). In contrast, variant 3.2 did not show repetitions of units and only comprised three units subsequently decreasing in start frequency (Figure 8j). All units were downsweeps, commonly started by an upsweeping part. This upsweeping part was not present in the units of variant 3.2 (Figure 8j).

Type 4 – Song type 4 was a call sequence that comprised five repetitions showing a gradual trend in decreasing frequency of a single, slightly curved downsweeping unit (Figure 8l). The decrease in frequency with every call was sometimes more, sometimes less pronounced.

Type 5 – Song type 5 was covering a larger frequency range than every other song type (Figure 8m). It was composed of two repeating units. The first unit was an up-down-up call (unit 1, 600-700 Hz), with the end frequency being less than the start frequency, followed by a relatively broadband downsweep (unit 2, 300-775 Hz).

Type 6 – This song was a simple song with two variations. Variant 6.1 started with a short and narrowband up-down-up call (unit 1, ~600 Hz) with the end frequency being lower than the start frequency. The first unit was followed without a break by an up-downsweeping unit (unit 2, 450-650 Hz) with a pronounced downsweeping phase occasionally ending in a slight upsweep (Figure 8n). Both units were followed by 2-9 repetitions of unit 3, a steep downsweep (250-500 Hz). Variant 6.2 (Figure 8o) started with two up-downsweeps that occurred simultaneously (unit 1) also followed by ~15 repetitions of an up-downsweeping call (unit 2) like in variant 6.1. This downsweeping unit, however, differed to that from variant 6.1 in a lower frequency range and the upsweeping part which was not present in variant 6.1.

Type 7 – Songs of type 7 commonly started with two repetitions of unit 1, an up-down call at around 375 Hz, followed by 1-2 repetitions of a down-up call (unit 2, ~250 Hz) (Figure 8p). Calls of unit 2 were lower in frequency than unit 1. The upsweeping part of unit 2 was not present in all detections, resulting in a call more similar to a short downsweeping moan.

Type 8 – The call sequence was composed of a simple upsweeping unit occurring in bouts of 3-5 repetitions in the 200-350 Hz frequency range (Figure 8q).

3.3.2 Temporal Changes in the Acoustic Repertoire

Songs were recorded on 58 out of 76 days (76 %) with acoustic presence. On the other 18 days, bowhead whales were acoustically present, but either only produced individual calls without any repeating pattern or the SNR of the recorded signals did not allow for classification. The number of different song types and their variants was greatest when acoustic presence peaked at the beginning of the season in early winter (November, December; Figure 9). Fewer song types were recorded between March and May (Figure 9). Song type 2 occurred most frequently and persisted throughout the whole season except for May. In contrast, other types appeared for a shorter time period and then disappeared over time. Even though several song types coexisted at the same time and overlapped in their occurrence, there was an overall trend that song types occurred in succession over the season (Figure 9).

Song type 1 was only recorded at the very first days of bowhead whale acoustic presence in mid-November. Variant 1.1 was replaced after being observed for three days by variant 1.2, which then was recorded for the next four days until the song disappeared completely. Song type 2 was almost omnipresent over the entire season. Variant 3.1 and 3.3 of song type 3 predominantly were observed in November, and on three other occasions in December and February, whereas variant 3.2 was only recorded on 22 November 2016. Type 4 was occasionally recorded in mid-December and 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 for the first time and continued to be recorded throughout the days with acoustic presence in February in the form of variant 6.1. Variant 6.2 replaced the first variant on the last day in February and was then only recorded again on one day at the beginning of March. Song type 7 was only observed on 25 and 26 April, and type 8 was only detected at the end of the season during two days in May (Figure 9).

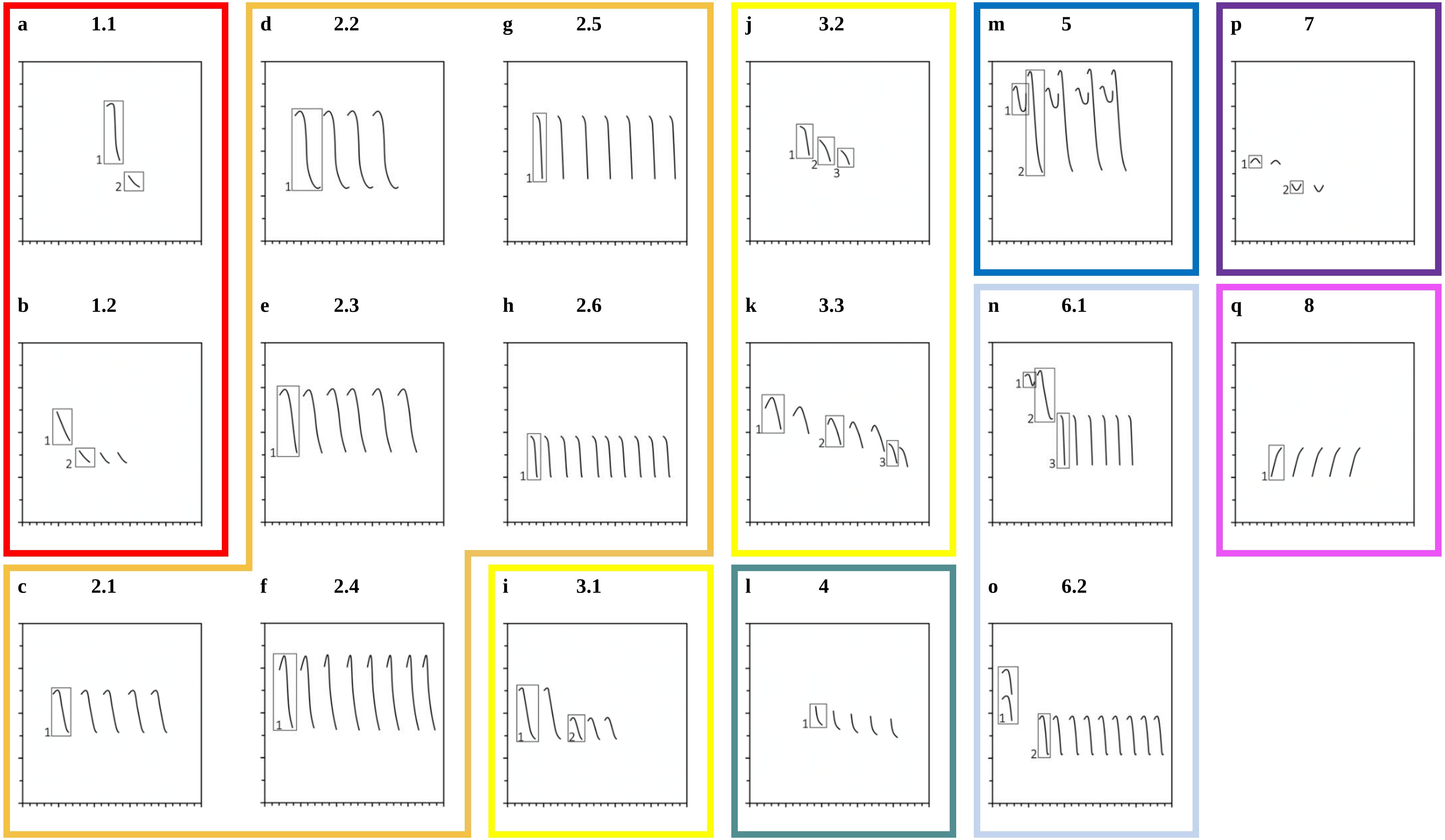


Figure 8. Idealized representations of the song types of bowhead whales recorded by SV1088 in eastern Fram Strait (79° 00.02’ N, 5° 40.12’ E) between November and May 2016/17. The x-axis comprises a time interval of 25 s and the y-axis a bandwidth of 0-800 Hz for every song type. Different song units are encompassed by a box. For spectrographic examples of the song types see Figure A4.

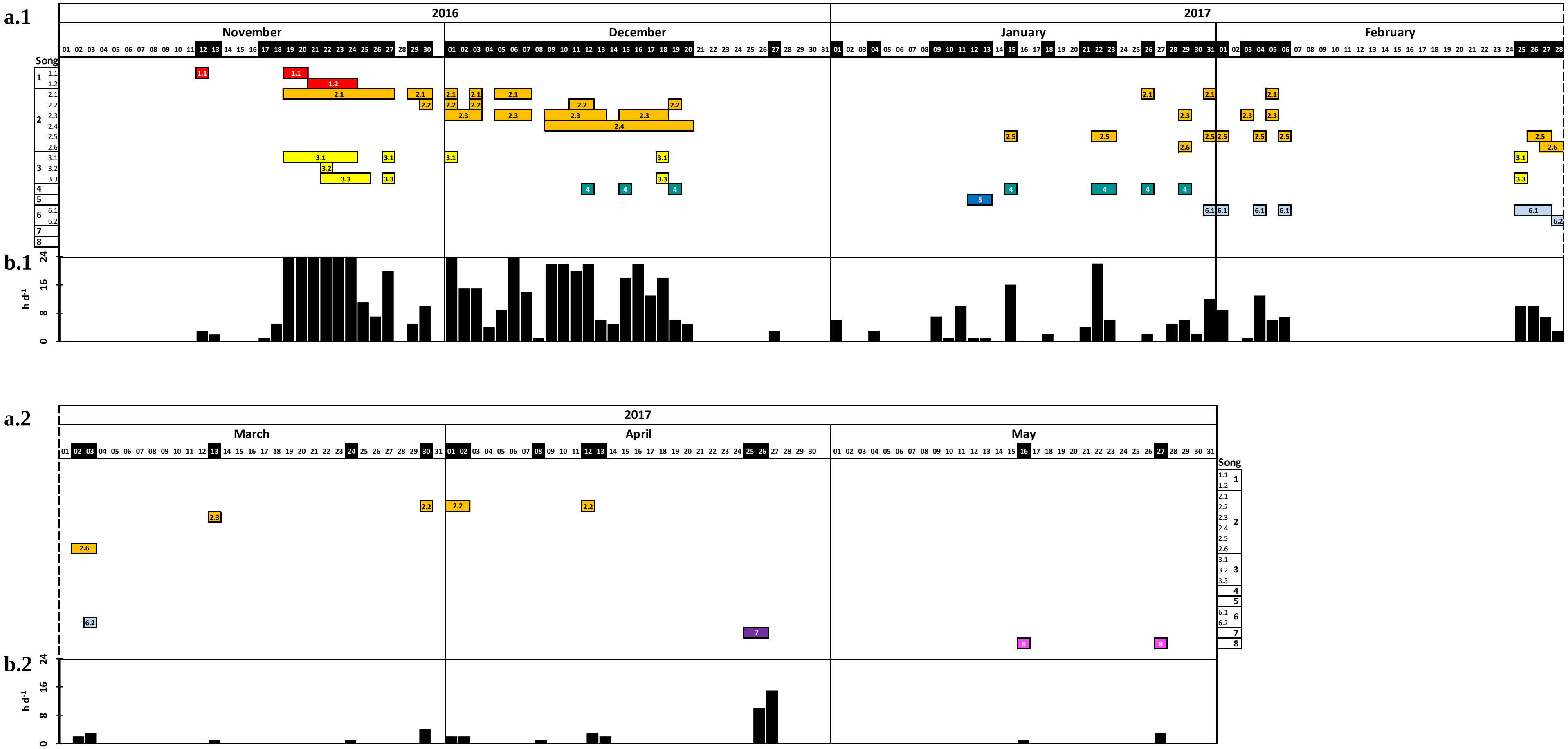


Figure 9. Temporal patterns in the occurrence of bowhead whale song types in eastern Fram Strait (79° 00.02’ N, 5° 40.12’ E) between November 2016 and May 2017. Calendar days on which distinct song types of bowhead whales were recorded in eastern Fram Strait by SV1088 from November 2016 until February 2017(**a.1**), and March until May 2017 (**a.2**). Black bars indicate the number of hours per day [h d^{-1}] with acoustic presence of bowhead whales from November 2016 until February 2017 (**b.1**), and March until May 2017 (**b.2**).

4 DISCUSSION

4.1 Data Reliability & Errors

– How reliable are the results of this study? –

The validity of the results is limited by the way acoustic data were obtained and analysed. To consider the weaknesses of data acquisition, however, is vital for the correct use and interpretation of the results (Širović 2016).

Passive acoustic monitoring (PAM) critically depends on the vocalisations of the target species, and hence can only provide "presence-only" data when assessing the occurrence of a species. While the detection of a sound indicates the physical presence of a species within the detection range of the recording device, the absence of sounds not necessarily implies its absence. In consequence, PAM only allows to make statements on the *acoustic* presence of a species. Even though the present data indicate a seasonal difference in the bowhead whale presence, with a peak in acoustic occurrence during winter and absence in summer, it cannot be excluded that bowhead whales remained silent and thus undetected in summer.

Apart from constraints related to the use of PAM techniques, the detector performance most likely had the biggest impact on the extent to which the data represent reality. The performance of the automated detector LFDCS was evaluated by determining hourly acoustic presence of bowhead whales compared to a manually annotated reference data set (ground truth). Overrepresentation of bowhead whale acoustic presence was not an issue here since all false detections were eliminated during post-processing of the LFDCS detector output. The estimated recall was relatively low, with only 32.6 % of the hours with manually annotated acoustic presence also found by LFDCS. Consequently, LFDCS missed 67.4 % of the hours with acoustic presence. This implies that bowhead whale acoustic presence is strongly underrepresented by the LFDCS approach. However, there are reasons to believe that the estimated performance level does not represent the true detector performance. In a previous study on the performance of LFDCS in determining bowhead whale acoustic presence, LFDCS exhibited a relatively high performance as it was able to correctly recall 85 % of the hours detected by a human analyst (Hiemer 2018). The poor performance of LFDCS quantified in this study is suspected to be caused by a combination of the characteristics of the test data set and the LFDCS detector settings. LFDCS was set to only detect calls above the SNR threshold of 8.0 dB. However, the bowhead whale calls contained in the test data set were comparatively silent, thus faint to detect. In fact, the mean SNR of the bowhead whale calls contained in the test data set was estimated to be 3.0 dB (± 1.6, n=87). (Note: The way the SNRs were calculated differs to that used by the LFDCS algorithm. The SNR values therefore might be higher if calculated by LFDCS). Hence, LFDCS is likely to have missed a large proportion of the bowhead whale calls contained in the manually annotated data set because they did not meet the SNR requirements for detection. Compared to automated detection approaches, human analysts are much better at detecting faint calls within a spectrogram as they are able adapt their sensitivity to the prevailing acoustic conditions (Leroy et al. 2018). In case of low SNRs, human analysts are able to lower their intrinsic threshold enabling them to detect calls that would not have been detected by them in high SNR conditions (Leroy et al. 2018). Since the rest of the acoustic recordings exhibited higher SNRs, not as many of the bowhead whale acoustic presence might have been missed as indicated by the detector evaluation, although a certain level of underrepresentation cannot be excluded.

The manual review of all automated detections revealed that LFDCS performed with only 58.6 % precision, implying that 41.4 % of all hours were false positive. False detections were eliminated during the manual review of the LFDCS detector output, resulting in an improved precision. In this context, many of the false positive hours were noticed to contain detections assigned to call type 4 of the LFDCS call library (Figure A5). Further in-depth analysis is needed to fully confirm this empirical statement but call type 4 alone appears to be too unreliable to be used for determining bowhead whale presence. Future studies working with this call library, therefore, should consider either to revise or delete this call type.

Vocalisations produced by bowhead whales and other marine mammal species – such as humpback whales *Megaptera novaeangliae* and bearded seals *Erignathus barbatus* – significantly overlap in their frequency range. Thus, the acoustic distinction between those species may be difficult. Both bowhead whales (e.g., Ljungblad et al. 1982; Würsig and Clark 1993) and humpback whales (e.g., Payne and McVay 1971) are known to produce elaborate songs and their geographic distribution within Fram Strait partly overlaps, although humpback whales appear to avoid areas with sea ice (Storrie et al. 2018). However, in comparison to the songs of humpback whales, the songs of bowhead whales are shorter and appear less complex due to a lower number of different units per song (Tyack and Clark 2000). Even if these differences in song production between both species were considered during manual inspection, the possibility of misclassifying humpback whale sounds as bowhead whale sounds could not be excluded completely. Detections that remained uncertain (e.g., Figure A6) were excluded from further analysis. Conversely, despite their overlap in frequency range, misclassification of bearded seals as bowhead whales is rather unlikely since the acoustic repertoire of bearded seals substantially differs from that of bowhead whales (Risch et al. 2007). Additionally, bearded seals occurring around Svalbard have been observed to only vocalise during a discrete period from early April to mid-July (Van Parijs et al. 2001) when bowhead whale acoustic activity had already declined considerably. Hence, it is assumed that the misidentification of bearded seal sounds as bowhead whales did not have a major effect – if any – on the results of this study.

Besides interfering sounds of biological origin, the recordings contained a non-quantifiable amount of ice sounds. Sounds of breaking ice (ice tremors) are highly variable and unpredictable in their spectrographic structure (Figure A7), thus challenging to distinguish from other sounds. It was accounted for the risk of misclassifying sounds of breaking ice as bowhead whales by adding exemplary ice sounds into the LFDCS call library. Even though automated detections were confirmed by manual inspection, it still is likely that some of the ice sounds were falsely classified as bowhead whales. The abundance of ice sounds was particularly problematic between mid-February and April in the 2016/17 sampling period. During that period, sounds of breaking ice were masking large parts of the spectrogram, especially in the frequency range in which bowhead whale sounds most commonly occur, i.e. below 1 kHz. In consequence, bowhead whale vocalisations could not always be verified with certainty, potentially resulting in an underrepresentation of bowhead whale acoustic presence between mid-February and April (Figure 7c-e).

For analysing the bowhead whale acoustic repertoire, one major challenge in classifying songs was to decide whether two similar songs should be considered the same type or not, i.e. how different songs should be to be assigned to different types. The approach applied here during the classification of the acoustic repertoire of bowhead whales aimed for a robust classification system by considering song types still the same type if the number of repetitions of units differed between songs but the unit structure, arrangement of units and frequency range remained similar. However, song classification still is subjective and may – amongst other factors – depend considerably on the personality and level of experience of the human analyst. In general, two opposing approaches, either "splitting" and "lumping", can apply when assigning elements into defined categories (Simpson 1945). While a "splitter" would assign songs to a new type, even if the differences are minor, a „lumper" would group everything similar together. Hence, the classification scheme for the detected bowhead whale songs could look completely different if done by a different human analyst.

4.2 Temporal Patterns in the Acoustic Presence of Bowhead Whales

– Is Fram Strait an important habitat for bowhead whales? –

Vocalisations 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, while no conclusions on bowhead whale presence are possible for the 2012 sampling period since the recording devices stopped to record already in November. No bowhead whale sounds were detected during the summer months from mid-June to September in both recording periods. This seasonal pattern is in accordance with previous acoustic studies on bowhead whale presence in Fram Strait (Moore et al. 2012; Ahonen et al. 2017; De Vreese et al. 2018; Stafford et al. 2012).

According to historic whaling records, Fram Strait constantly has been an important habitat for bowhead whales (Moore and Reeves 1993). Before 1818, whaling concentrated in Fram Strait between 76°N and 80°N. The "best" 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. While whaling records indicated that Fram Strait was a summering area for bowhead whales that had overwintered in the southwestern Greenland Sea near Iceland (Ross 1993), the present data and those from previous studies suggest that Fram Strait is a wintering area for the Spitsbergen bowhead whale population (e.g., Stafford et al. 2012, this study). If Fram Strait still serves as a summering area for the population remains unclear. On the one hand, it is possible that bowhead whales still occupy this area in summer but are vocally inactive, thus being left undetected through acoustic monitoring. On the other hand, seasonal and regional occurrences within the population may have been changed over time in response to long-term climatic changes and due to centuries of whaling pressure in the region between spring and autumn (Ross 1993).

Acoustic presence persisted from November until spring and was most intense during winter when vocalisations of bowhead whales were detected almost daily, often persisting over the entire day, for several weeks. The acoustic behaviour during winter has been described recently for bowhead whales in Disko Bay, western Greenland (Tervo et al. 2009). They observed multiple individuals singing simultaneously, with the songs being more frequent in winter than in spring. Stafford et al. (2012) made similar findings for the western part of Fram Strait where songs of bowhead whales were recorded almost constantly from November until 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 mating period of bowhead whales, presumed to be in late winter and spring (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 seasonally occupy Fram Strait also for feeding. Bowhead whales commonly occur in “oceanographically complex” areas (Lowry 1993) where bathymetric and oceanographic features cause favourable feeding conditions (Falk-Petersen et al. 2015; Finley 2001). 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 et al. 1999; Rudels and Quadfasel 1991). 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 1995). Large amounts of zooplankton of Atlantic origin, such as *Calanus finmarchicus*, are transported with the Atlantic inflow into Fram Strait in the east (Blachowiak-Samolyk et al. 2007; Smith 1988). In the west, the Transpolar Drift transports Arctic zooplankton, such as *C. hyperboreus* and *C. glacialis*, from the Arctic Ocean into Fram Strait. In between these two water masses, a frontal boundary, known as the Polar Front, is formed, which tends to coincide with the ice-edge (Joiris and Falck 2011). Along the ice-edge, melting sea ice and increasing solar radiation thrive phytoplankton growth in spring by increasing the water column stability (Smith et al. 1987), thus providing an abundant food source for zooplankton (Wiig et al. 2007). Bowhead whales filter-feed on zooplankton including calanoid copepods (mainly *Calanus* spp.) and euphausiids (e.g., *Thysanoessa* spp.) with their baleen plates (Lowry et al. 2004; Lowry 1993). 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). Whereas in autumn, bowhead whales migrate into shelf habitats off east Greenland where shallow waters may provide better opportunities to encounter copepods, which descent 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 provide optimal feeding conditions for bowhead whales in Fram Strait during spring. In another baleen whale species, the blue whale *Balaenoptera musculus*, singing and feeding activities have been considered to be mutually exclusive (Oleson et al. 2007b). Thus, the observed decline in acoustic presence in spring may relate to a shift in behaviour from mating to feeding (see also Tervo et al. 2009).

The observed acoustic absence in summer may represent the migration of bowhead whales from Fram Strait to summering areas. What is currently known about the seasonal migration of bowhead whales from the Spitsbergen population stems from a single observation of a satellite-tracked bowhead whale. This whale was presumed to overwinter in Fram Strait at about 78-80°N and moved towards south to 70°N along the Greenland shelf break during summer and returned north to 80°N in December. The tracked movement pattern from north to south in summer is reverse to what has been described for other bowhead whale populations (Lydersen et al. 2012). 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 (Heide-Jørgensen et al. 2006; Reeves et al. 1983; Quakenbush et al. 2010). Even though the conclusions about the seasonal movement of Spitsbergen's bowhead whales stem from a single observation, they are in accordance with historic records from whaling operations centuries ago (Lydersen et al. 2012; Moore and Reeves 1993). Whalers described to start hunting in Arctic waters northwest of Svalbard at 80°N, referred to as the "Northern Whaling Ground", between April and May. By the end of spring, some bowhead whales historically have been observed moving north from Svalbard into the receding pack ice, while others moved southwest with the East Greenland Current. Following the presumed migration of bowhead whales, whalers moved farther south along Greenland's east coast to the "Southern Whaling Ground" (71-74°N) where bowhead whales were caught between June and August (Moore and Reeves 1993). According to two recent aerial surveys, bowhead whales occur in both areas mentioned in the whaling records in summer (Vacquié-Garcia et al. 2017). Bowhead whales were found close to the marginal ice zone north of Svalbard (Vacquié-Garcia et al. 2017) and within the "Southern Whaling Ground" off the east Greenland coast during summer (Gilg and Born 2005; Boertmann et al. 2009). Additionally, Boertmann et al. (2015) reported a considerably high number of bowhead whales within the Northeast Water Polynya in northeast Greenland in August. 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 had left eastern Fram Strait for summer. However, it cannot be excluded that bowhead whales were present in eastern Fram Strait during summer but vocally inactive since bowhead whales have been sighted approximately 150 km to the north (Wiig et al. 2010; Wiig et al. 2007) and approximately 300 km to the southwest (de Boer et al. 2019) of this study's central recording sites during summer in past years.

Differences in the acoustic behaviour of bowhead whales between the western and eastern part of Fram Strait seem to reflect regional differences in habitat suitability. Compared to the extensive and loud singing of bowhead whales in western Fram Strait (Stafford et al. 2012), the acoustic signals of bowhead whales in the eastern part of Fram Strait (this study) were considerably less frequent and loud. Such latitudinal differences between east and west 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°W). Even though the recording sites in western, central and eastern Fram Strait were only a few hundreds of kilometres apart, the western part of Fram Strait seems to be preferred by bowhead whales over the central and eastern part. One reason may be the contrast 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, even though animals have been observed in the open water far off the marginal ice edge in the past (e.g. Lydersen et al. 2012; de Boer et al. 2019). Based on 27 satellite-tracked individuals from the Eastern Canada-West Greenland population, Ferguson et al. (2010) found the sea ice habitat selection of bowhead whales to vary with season. Bowhead whales preferred high sea ice concentrations (> 65 %) during summer and lower sea ice concentrations (35-65 %) during winter while remaining within the sea ice margin. Bowhead whales in the Bering Sea were found in areas with even higher sea ice concentrations (90-100 %) during winter (Citta et al. 2012). However, according to the present data, bowhead whale sounds were detected most often when sea ice was absent. During the sampling periods, sea ice concentrations were highly variable around the recording sites in eastern Fram Strait and most of the year well below 65 %. Sea ice is thought to provide shelter from killer whale *Orcinus orca* predation, 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 activity, thus undisturbed for most parts of the year (Ahonen et al. 2017). Considering the affinity of bowhead whales for sea ice habitats, they might have spent less time in eastern Fram Strait because sea ice concentrations were unfavourably low. Irrespective of probably low habitat suitability, bowhead whales were detected for several months around the recording sites in eastern Fram Strait. Therefore, eastern Fram Strait is suspected to be the easterly distribution range boundary of the bowhead whale overwintering area.

4.3 Temporal Patterns in the Acoustic Behaviour of Bowhead Whales

– Does the acoustic repertoire of bowhead whales change within season? –

This part of the study provides the first description of the acoustic repertoire of bowhead whales in eastern Fram Strait. During a one-year period, eight distinct bowhead whale song types were identified. No complex songs were found in the recordings from eastern Fram Strait. Instead, the acoustic repertoire exclusively consisted of single calls (not analysed), simple songs and call sequences with the latter being recorded most commonly. This is in marked contrast to western part of Fram Strait where over 60 distinct complex songs were recorded over a single overwintering period (Stafford et al. 2012), and 184 different songs types over a 3-year period (Stafford et al. 2018). However, Stafford et al. (2012) also noted considerable differences in sound complexity between different recording sites in the western and central part of Fram Strait. While they overserved extensive singing activity in the west, most of their bowhead whale sounds recorded further to the east were simple calls and call sequences, which is in accordance with the acoustic repertoire described here.

The songs described here were not stereotypic in their appearance, i.e. songs within a song type displayed some variability. For the variability of songs was accounted by considering them as a variant of the assigned song type. On the one hand, the variability may simply be intra-song variation. On the other hand, variability could also be the consequence of the song being produced by different individuals or due to different distances between sound source and recording device, with the result that silent parts of the song were not recorded.

The production of multiple songs within a season has previously been observed for the Eastern Canada-West Greenland population (Tervo et al. 2011; Stafford et al. 2008), and the Bering-Chukchi-Beaufort population (Delarue et al. 2009; Johnson et al. 2015). Additionally, a study in western Fram Strait revealed an extremely high diversity in the songs of bowhead whales from the Spitsbergen population (Stafford et al. 2008). 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 Johnson et al. 2015; Tervo et al. 2009). However, there is evidence for song sharing among bowhead whales (Johnson et al. 2015; Stafford et al. 2008; Tervo et al. 2011). The temporal overlap of songs recorded in Disko Bay have shown that several individuals in the area sang the same song at the same time (Stafford et al. 2008).

The large variety of songs produced by bowhead whales seems so be exceptional among other singing baleen whales including humpback whales (e.g., Payne and McVay 1971), fin whales *Balaenoptera physalus* (e.g., Watkins et al. 1987) and blue whales (e.g., Cummings and Thompson 1971). Although humpback whales are well known for their long and complex songs, their annual vocal repertoire is restricted to a single song produced by all animals in a geographic area (Payne and McVay 1971; Winn and Winn 1978). It is also worth noting that the vocalisations produced by right whales *Eubalaena* spp., the closest relative of bowhead whales, are not as elaborate and remarkably varied (Clark 1982). Apparently, there seems to be an advantage for bowhead whales to produce various song types. On the other hand, selection pressure on song stereotypy for interspecific identification might be reduced in bowhead whales since they are the only baleen whale resident in the Arctic, hence allowing for greater diversity in song types as hypothesised by Stafford et al. (2018).

Besides the presence of multiple distinct song types, there was also a succession of the song types observed with the progressing season. Even though more than one song type was recorded at a given time, song types appeared and eventually disappeared after being recorded for a certain time period. Similarly, Stafford et al. (2018) also mentioned the song types in the repertoire of bowhead whales recorded in western Fram Strait to seasonally change, but did not further address this phenomenon. Likewise, a seasonal progression of song types had been observed for bowhead whales from 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). Multiple possible explanations exist to interpret the observed seasonal succession of song types. First, new songs types may emerge during a season as observed in humpback whales (Noad et al. 2000). The humpback whale song is produced by all males in a population and it constantly, but gradually evolves over time as new song components are introduced. However, "revolution" of the bowhead whale song does not seem to have occurred here as one would expect to see gradual changes from one song type to another. If indeed the song types identified in this study gradually changed into one another, these changes might have gone undetected due to the relatively low amplitude of the bowhead whale sounds and the small sample size. Secondly, 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 though 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, it still is possible that whales overwintering elsewhere in the Fram Strait area were temporarily moving into or passing the detection range of the recording device, hence causing the temporary occurrence of a song type. Another possible explanation for the seasonal succession of song types is that different song types are used for different communication purposes or in different behavioural contexts. Thus, certain song types may only be produced during certain time periods hereby explaining the temporal pattern in the vocal behaviour of bowhead whales. The vocal behaviour of bowhead whales probably serves various social functions such as mating, competition, defence or maintenance of contact and cohesion between whales. Vocalisations may also be non-social, enabling the whale to sense its environment for navigation, or to herd together prey like it has been observed for Norwegian herring-eating killer whales (Simon et al. 2006). Ellison et al. (1987), for instance, suggested that bowhead whales may be able to sense ice conditions acoustically. The production of songs is speculated to be related to a mating context. Here, only simple songs were recorded and those occurred throughout the season from November until April. The mating season of bowhead whales is believed to be in late winter and spring (Koski et al. 1993) which corresponds well with the period in which songs were recorded.

Song type 2 formed an exception among every other call type because it was recorded throughout almost the entire season, with only minor variations in the song unit structure. Each variant of type 2 was a call sequence made up of 2-15 repetitions of a single downsweeping call. Considering that song type 2 was frequently recorded over half a year, this song type may 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, but the production of this song type might be related to feeding behaviour or reflect social interactions between individuals. Apart from bowhead whales, simple frequency-modulated downsweep sounds are also known to be produced by several other baleen whale species such as blue whales (e.g., McDonald et al. 2001), fin whales (e.g., Thompson et al. 1992), Antarctic minke whales *Balaenoptera bonaerensis* (Dominello and Širović 2016), sei whales *B. borealis* (Calderan et al. 2014), and humpback whales (Darling 2015). For instance, blue whales produce bouts of repeated, downswept sounds in the 80-40 Hz frequency range referred to as D-calls (McDonald et al. 2001). Although blue whale D-calls and bowhead whale song type 2 differ in their respective frequency range, they still might serve similar functions. The production of D-calls in blue whales is common to both female and male, and is generally associated with group feeding behaviour (Oleson et al. 2007a). However, D-calls also were observed in other behavioural contexts than feeding, for instance in the context of escorting behaviour involving two males and a female (Schall et al. 2019). The behavioural function of call sequences has also been discussed for long-finned pilot whales *Globicephala melas*, whose repeated call sequences make up a large portion of their vocal repertoire. The study results indicated that call sequences 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. Given the fact that the production of song type 2 was not restricted to a specific time period, combined with the different behavioural contexts in which calls sequences of other cetacean species have been recorded, indicates a basic, thus diverse function of song type 2.

The here recorded song types differ from those previously described for other bowhead whale populations. A comparison between the songs recorded in Disko Bay, western Greenland and the Chukchi Sea indicated that songs of bowhead whales are unique to the area in which they were recorded (Delarue et al. 2009). In fact, the songs reported here even are different to the songs described for the Spitsbergen population recorded only a few hundreds of kilometres to the west (Stafford et al. 2012). Despite some resemblance in the unit structure, the songs recorded in western Fram Strait were more complex and contained units above 1 kHz. However, the possibility cannot be excluded that the song types recorded in eastern Fram Strait are similar to those recorded in the west but were missing the more silent or high-frequency parts, given the relatively low amplitude of the bowhead whale calls recorded in this study.

The acoustic repertoire of bowhead whales appears to not only vary geographically, but also annually. According to published literature, the songs of bowhead whales within a population seem to completely change from one year to another (e.g. Tervo et al. 2011; Würsig and Clark 1993). Bowhead whale songs recorded during the spring migration in the Chukchi Sea off Point Barrow in 1980, 1985, 1986 and 1988 were completely different from each other (Würsig and Clark 1993). How the acoustic repertoire of bowhead whales overwintering in Fram Strait changes with year is, however, a subject for future studies. The acoustic repertoire described here was recorded within a single sampling year and does not allow for interannual comparisons. Nevertheless, a first empirical impression may indicate the extent to which the songs from bowhead whales of the Spitsbergen population differ between the 2012 and the 2016/17 sampling period (this study). Two different bowhead whale song types were recorded at the central recording site (SV1021) in the 2012 sampling period (Neumann 2017). The two songs were named "downsweep song" and "upsweep song" based on the spectrographic structure of the predominant unit. While no upsweep song was detected in the recordings from 2016/17, song type 3 described in this study was found to noticeably resemble the downsweep song recorded in 2012. Both the downsweep song and song type 3 consist of 2-3 phrases of downswept units that gradually decline in the start frequency from one phrase compared to the following phrase (Neumann 2017). Even though this conclusion is based on a single observation, it may already indicate that at least some song types are preserved to some degree and carried from one year to another, while others disappear, and new ones appear.

5 OUTLOOK – BOWHEAD WHALES IN A CHANGING ARCTIC ECOSYSTEM

The present study highlights the importance of Fram Strait as an overwintering area, and potentially also a suitable mating and feeding habitat, for the endangered Spitsbergen bowhead whale population. However, Fram Strait, like the rest of the Arctic region, is undergoing physical and biological changes in response to climate change. Since the beginning of the satellite record in 1979, the Arctic sea ice has been decreasing markedly in extent and thickness (e.g., Comiso 2012; Stroeve et al. 2008). If greenhouse gases continue to be emitted at their current rate, the Arctic is projected to be nearly ice-free in summer by the year 2037 (e.g., Wang and Overland 2009).

Bowhead whales are, among narwhals *Monodon monoceros* and belugas *Delphinapterus leucas*, the only cetacean species that inhabits Arctic waters year-round. As such, they are well adapted to live in ice-covered waters and are able to easily move through areas of heavy sea ice cover (George et al. 1989). The sea ice habitat is believed to provide feeding opportunities for bowhead whales and shelter from killer whale predation (Ferguson et al. 2010).

The rapid decline in sea ice cover does not only affect the ice-associated bowhead whales directly as they are progressively losing their habitat, but also indirectly, e.g. by altering the food web structure and increasing noise pollution from anthropogenic activity, risk of predation and competition for prey (Moore and Reeves 2018; Reeves et al. 2014).

Temporal shifts in the annual pattern of ice recession in spring and ice formation in autumn are expected to impact marine trophic cascades, indirectly affecting the quantity and quality of zooplanktonic prey available to bowhead whales (Laidre et al. 2008). Bowhead whales are specialised to feed on herbivorous zooplankton (Lowry et al. 2004). In spring, melting sea ice exposes the nutrient-rich water to sunlight, hereby creating favourable conditions for phytoplankton growth (Smith et al. 1987). The phytoplankton bloom, in turn, provides an abundant food source for zooplankton which ascent from deeper waters at specific times of the year (Bluhm and Gradinger 2008). Although sea ice retreat is proposed to regionally result in increased phytoplankton blooms in the Arctic (e.g., Arrigo and van Dijken 2015), zooplankton communities can only benefit from that if their grazing periods coincide with phytoplankton blooms (George et al. 2015). In fact, reduced sea ice cover will allow an earlier bloom, thereby disrupting the temporal coupling between phytoplankton and copepod grazers. This will potentially affect the seasonal feeding opportunities for bowhead whales (Laidre et al. 2008; Reeves et al. 2014).

Moreover, the ongoing reduction in sea ice will cause previously ice-covered Arctic regions to become accessible for anthropogenic activities. Underwater noise from ship traffic, drilling and seismic surveys is of major concern for marine mammals as they heavily rely on sound for communication and navigation (Reeves et al. 2014). Bowhead whales are believed to be particularly affected by low-frequency noise (< 1 kHz) from large vessels and seismic surveys because such anthropogenic sounds significantly overlap with the frequencies that bowhead whales emit and perceive (Ahonen et al. 2017). Further, the low frequencies of airgun signals allow them to be transmitted over large distances to areas remote from industrial activities and shipping lanes (Nieukirk et al. 2012; Thode et al. 2012). In Fram Strait, airgun signals were recorded throughout the year (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 stop vocalising if airgun pulses were too loud (Blackwell et al. 2015). However, the long-term effects of increased anthropogenic noise on bowhead whales are unknown (Parks et al. 2007). Besides noise pollution, the increase in human activities in the Arctic region puts bowhead whales at risk of ship strikes, entanglement in fishing gear and exposure to leaked or spilled oil and other harmful contaminants (Reeves et al. 2014).

Additionally, the reduction in sea ice will allow subarctic species to expand their distribution northwards, resulting in increased competition for food and increased predation pressure on Arctic endemic species, including the bowhead whale (Laidre et al. 2008; Moore and Reeves 2018). One of the reasons bowhead whales live in association with sea ice is likely to seek protection from killer whales (Finley 2001), their only known natural predator (Philo et al. 1993). Killer whales usually avoid areas with heavy sea ice cover, presumably because ice can harm their large dorsal fin and due to the risk of ice entrapment (Ferguson et al. 2010). However, killer whale sightings within the distribution range of bowhead whales have increased recently in the Canadian Arctic as a result of declining sea ice (Ferguson 2009; Higdon and Ferguson 2009). With reductions in sea ice, the risk of killer whale predation is possibly increasing for bowhead whales (Kovacs et al. 2011). In addition, subarctic species that seasonally move into the Arctic region to feed, such as humpback, blue and fin whales, may arrive earlier and stay longer, thus increasing the competition for prey with those species living in the Arctic region year-round (Laidre et al. 2008; Moore and Reeves 2018).

The resilience of bowhead whales to the changes in the Arctic ecosystem related to climate change is difficult to predict, but those changes most likely add additional pressure on the already vulnerable Spitsbergen population (Moore and Reeves 2018). First responses to the fast reduction of their sea ice habitat will presumably involve shifts in geographic distribution (Gilg et al. 2012; Tynan and DeMaster 1997). In this context, this study provides baseline data on the seasonal occurrence and distribution of bowhead whales and helps to identify their current key habitats. However, long-term monitoring efforts are necessary to track the effects of sea ice loss related to climate change on the bowhead whale population (Kovacs et al. 2011; Laidre et al. 2008).

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APPENDIX

Table A1. Parameter file with the set of parameters that have been applied to process the acoustic recordings of this study by the Low-Frequency Detection and Classification System (LFDCS). The parameter file is a single text file and its parametric values can be varied simply via a text editor program. When processing recordings, the parameter file is read and the given parameters then control the behaviour of LFDCS in, e.g. creating the spectrogram, noise reduction, call detection (pitch tracking) and classification (Baumgartner 2019).

```
             Experiment:  FRAM
                  Indir:
                 Outdir:
              StartDate:  MM/DD/YY hh:mm:ss
           PlatformType:  Mooring
             PlatformID:  ARKXXX-XX
         InstrumentType:  Sonovault
           FileDateSpec:  YYYYMMDD-hhmmss
          FileExtension:  wav
             FileFormat:  WAV
           InstrumentID:  SVXXXX
             Originator:  Karolin Thomisch
               Location:  XX°N XX°E
           FileDuration:  300 or 600
                  Frame:  1024
           ResampleRate   5333
                Overlap:  0.8
                 Smooth:  1

        CallLibraryFile:
      CallLibraryFileBB:

  DetectionFileDuration:  5.0                    ; how many days worth of autodetections to put in each detection file

                  Scale:  0.0030                 ; conversion parameters for spectrogram (dB -> unsigned short int)
                 Offset:  -100.0

    SpectrogramDuration:  30.0                   ; duration of the spectrogram window to be processed (seconds); choose based on how
                                                 ; long longest call is expected to be

    PitchTrackingWindow:  25.0                   ; duration of the window where pitch tracking will occur (seconds)
                                                 ; make a few seconds shorter than SpectrogramDuration because that time is used to
                                                 ; identify and remove transient and persistent broadband signals before a spectrum
                                                 ; can be moved into the spectrogram

   NoiseReductionWindow:  10.0                   ; duration of the window over which spectrogram equalization will take place (seconds)
                                                 ; equalization occurs by subtracting an exponentially-weighted running mean from each
                                                 ; frequency band in the spectrogram; results are deviations in amplitude from the
                                                 ; background noise

     AvgFFTLowThreshold:  -999.0                 ; minimum level for how quiet the average FFT value can be relative to background to be
                                                 ; included in the exponentially-weighted running means; helps keep very quiet periods out
                                                 ; of the running mean used for spectrogram normalization (really specific to DMON
                                                 ; hydrophone shut-off)

    AvgFFTHighThreshold:  999.0                  ; maximum level for how loud the average FFT value can be relative to background to be
                                                 ; included in the exponentially-weighted running means; helps keep very loud broadband
                                                 ; noise out of the running mean used for spectrogram equalization

    AvgFFTDurationLimit:  300.0                  ; indicates how long to tolerate running mean *not* being updated; after this period,
                                                 ; running mean is forced to reset

        BBP_InThreshold:  7.0                    ; minimum level in spectrogram to indicate a persistent broadband sound - defines "loud"
                                                 ; broadband sound (dB)

         BBP_InDuration:  3                      ; minimum duration of loud sound before ending pitch tracking (seconds)
       BBP_OutThreshold:  5.0                    ; maximum level of spectrogram to indicate quiet after a persistent broadband sound (dB)
        BBP_OutDuration:  0.5                    ; minimum duration of quiet period after a persistent broad sound to resume pitch
                                                 ; tracking (seconds)

        BBP_MaxDuration:  30.0                   ; maximum duration of a persistent broadband sound - after this duration, the running mean
                                                 ; is reset and the persistent sound is considered part of the background
  BB_DetectionThreshold:  9.6                    ; minimum level in spectrogram to trigger transient broadband detection (dB)
      BB_MinSegmentSpan:  75.0                   ; minimum frequency range of a transient broadband segment (Hz)
        BB_MinTotalSpan:  200.0                  ; minimum accumulated frequency range of all transient broadband segments of a broadband
                                                 ; signal (Hz)
BB_MinBroadbandDuration:  0.5                    ; minimum duration of a transient broadband signal (seconds); min and max frequency of each
                                                 ; broadband segment is saved, then lowest min and the highest max are used to box out entire
                                                 ; transient broadband sound

     DetectionThreshold:  8.0                    ; minimum amplitude in a spectrogram to trigger the DCS/pitchtracking (dB)
                                                 ; pitch track forward to locate the end of the call and pitch track backwards to identify
                                                 ; the start of the call (backward pitch track is final pitch track)
                                                 ; do it this way because the call will likely start earlier in time than when it is first
                                                 ; detected with the amplitude threshold (call ramps up at beginning and ramps down at end)

  CostGradientThreshold:  10.0                   ; used to decide when to stop pitch tracking (i.e., to identify the start or end of the
                                                 ; end of a call (dB)

      DistanceWeighting:  20.0                   ; weight associated with "jumping" an octave in frequency in successive time slices (dB)

        MinCallDuration:  0.25                   ; minimum duration of a pitch track to be kept as a legitimate call (seconds)
        MinAvgAmplitude:  8.0                    ; minimum average amplitude of the pitch track to be kept as a legitimate call (dB)
           BlankingTime:  0.25                   ; time before and after a time slice in the pitch track to be blanked or set to zero (seconds)
           BlankingFreq:  4.0                    ; frequency above and below a time slice in the pitch track to be blanked or set to zero (Hz)
```

Table A2. Hourly acoustic presence determined (a) manually by a human analyst and (b) automatically by the Low-Frequency Detection and Classification System (LFDCS) with a signal-to-noise ratio (SNR) threshold of 8 dB and a Mahalanobis distance less than or equal to 1.5. Acoustic presence is indicated by a 1 and acoustic absence by a 0.

a **Ground truth data set (human analyst)**

Date \ Time	00:00-00:59	01:00-01:59	02:00-02:59	03:00-03:59	04:00-04:59	05:00-05:59	06:00-06:59	07:00-07:59	08:00-08:59	09:00-09:59	10:00-10:59	11:00-11:59	12:00-12:59	13:00-13:59	14:00-14:59	15:00-15:59	16:00-16:59	17:00-17:59	18:00-18:59	19:00-19:59	20:00-20:59	21:00-21:59	22:00-22:59	23:00-23:59
01.10.2016	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.10.2016	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
01.11.2016	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.11.2016	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
01.12.2016	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
15.12.2016	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
01.01.2017	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
15.01.2017	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
01.02.2017	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
15.02.2017	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
01.03.2017	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.03.2017	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

b **Automated detector (LFDCS)**

Date \ Time	00:00-00:59	01:00-01:59	02:00-02:59	03:00-03:59	04:00-04:59	05:00-05:59	06:00-06:59	07:00-07:59	08:00-08:59	09:00-09:59	10:00-10:59	11:00-11:59	12:00-12:59	13:00-13:59	14:00-14:59	15:00-15:59	16:00-16:59	17:00-17:59	18:00-18:59	19:00-19:59	20:00-20:59	21:00-21:59	22:00-22:59	23:00-23:59
01.10.2016	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.10.2016	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
01.11.2016	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.11.2016	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
01.12.2016	1	0	1	0	1	0	0	1	0	1	0	1	1	0	0	0	1	1	1	1	1	1	1	0
15.12.2016	0	1	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0
01.01.2017	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.01.2017	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0
01.02.2017	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
15.02.2017	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
01.03.2017	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15.03.2017	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

True positives False positives True negatives False negatives

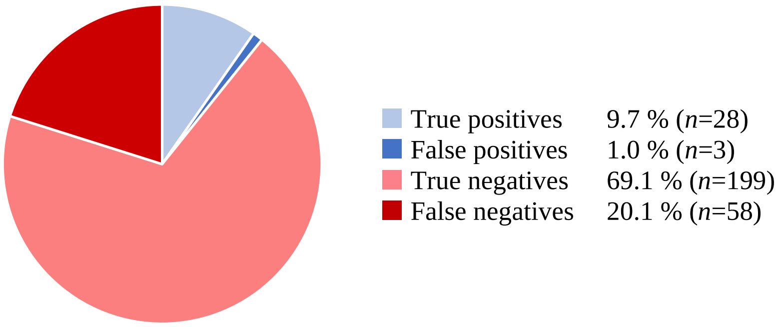
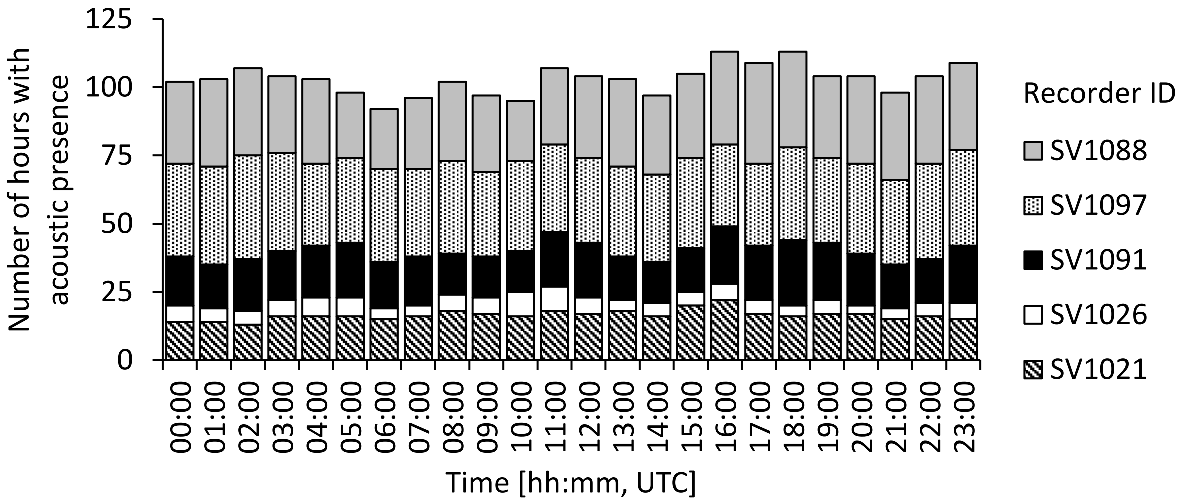


Figure A1. Proportion of true positives and true negatives as well as false positives and false negatives among all hours processed by LFDCS (i.e. 288 h) compared with the ground truth data set. Of all LFDCS-processed hours, 9.7 % were correctly determined as containing bowhead whale presence (true positives). LFDCS correctly did no detect any acoustic presence (true negatives) in 69.1 % of the hours. Accordingly, in 20.1 % of all processed hours, acoustic presence was missed (false negatives). Only 1.0 % of all processed hours were falsely determined by LFDCS to be with acoustic presence (false positives).

a



b

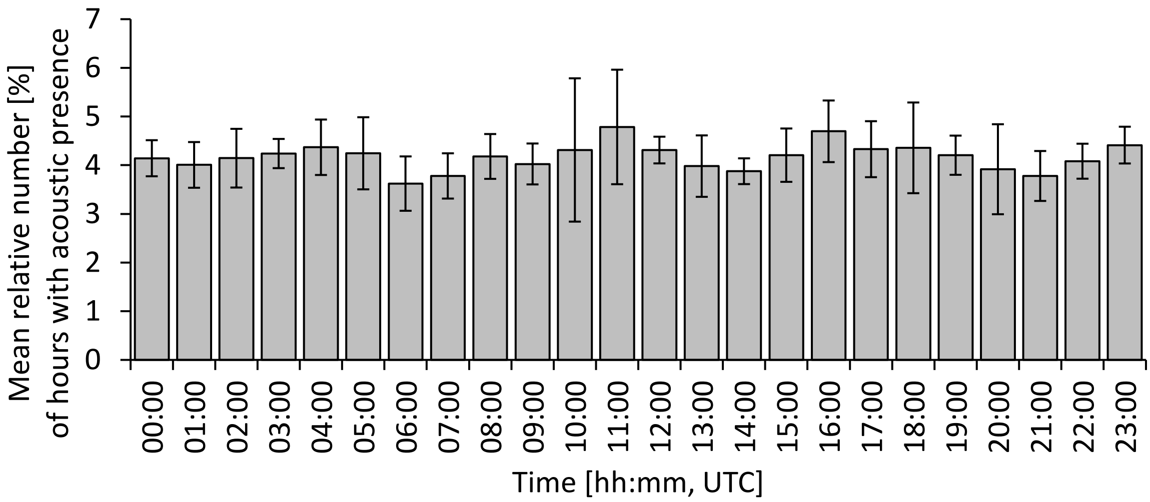


Figure A2. Distribution of hours with acoustic presence of bowhead whales across daytimes in Coordinated Universal Time [hh:mm, UTC]. (a) Absolute number of hours with acoustic presence per daytime for each recording location (*n*=5). **(b)** Mean ± SD (*n*=5) number of hours with acoustic presence per daytime in relation to all hours with acoustic presence.

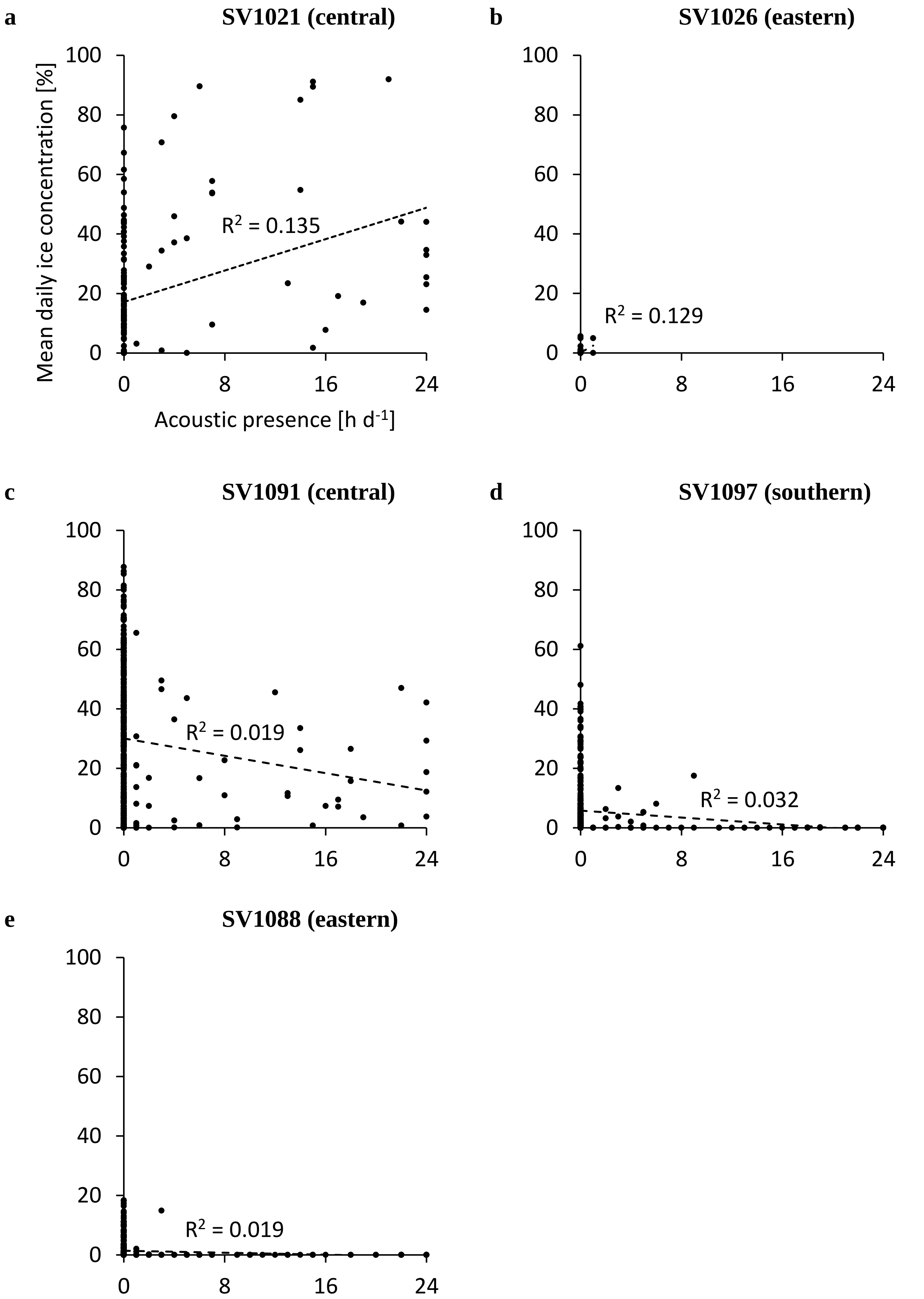


Figure A3. Relationship between acoustic presence [h d^{-1}] and mean of daily sea ice concertation [%] within a 35 km radius around each recording location, expressed by the coefficient of determination R^2.

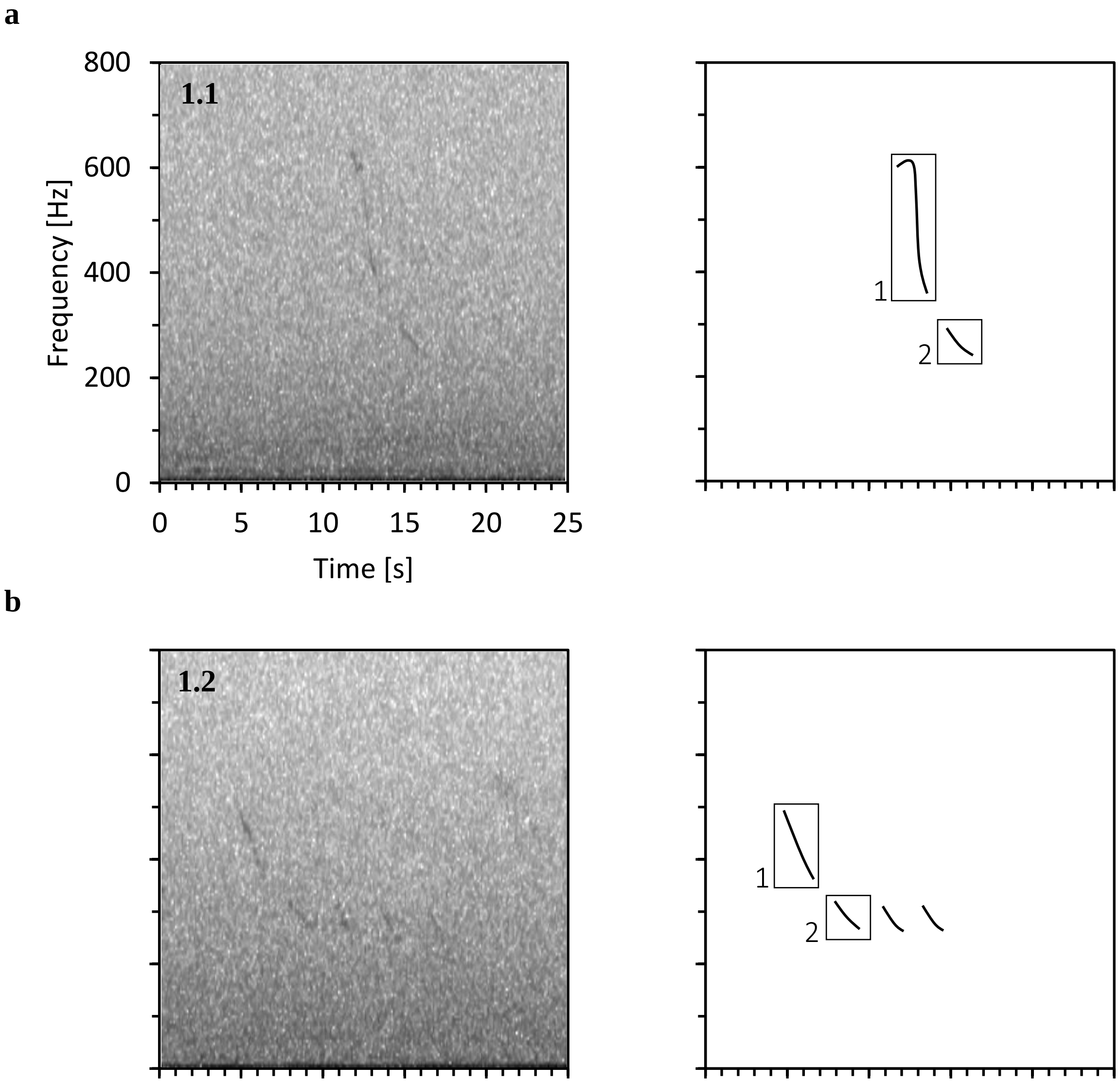
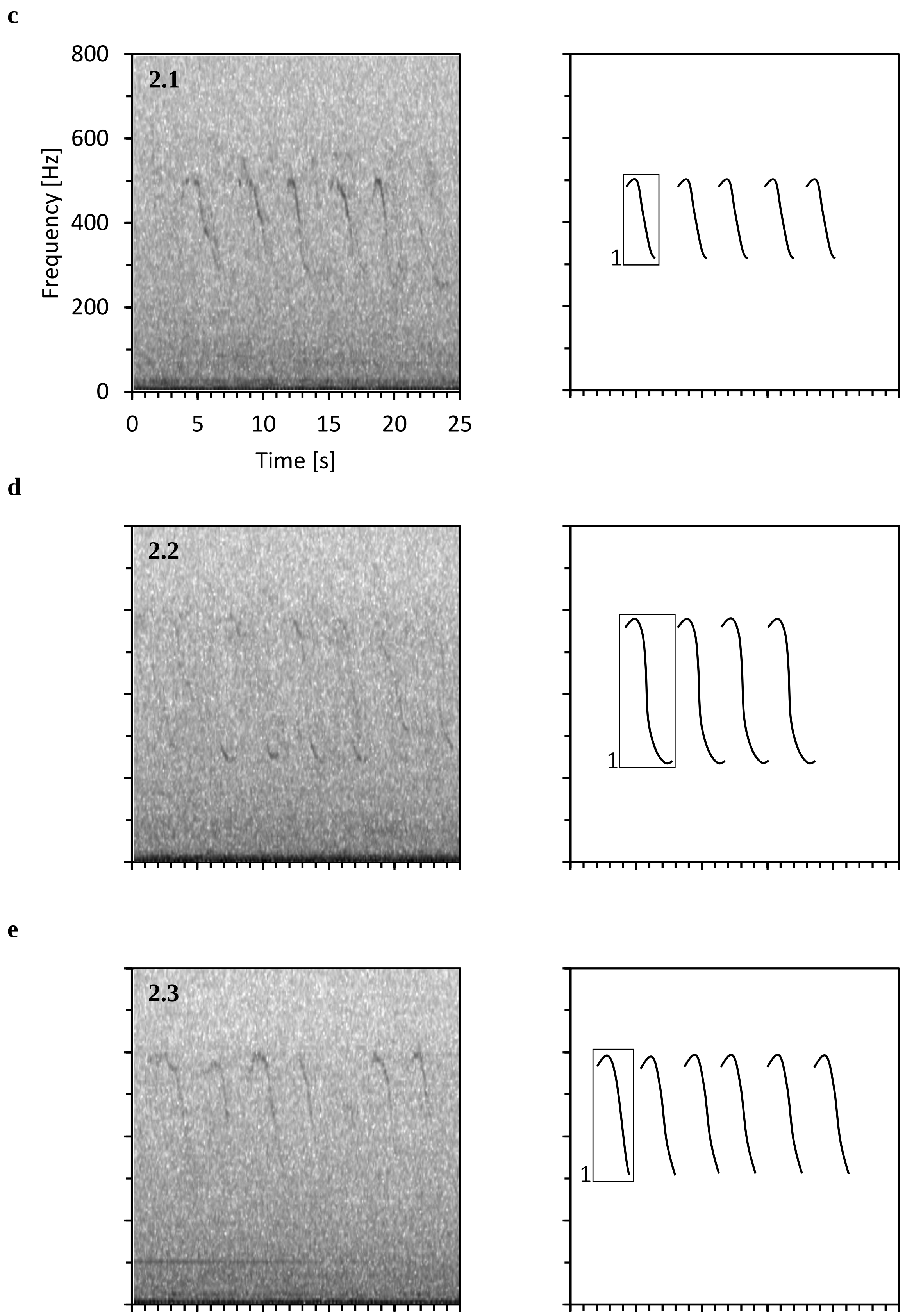
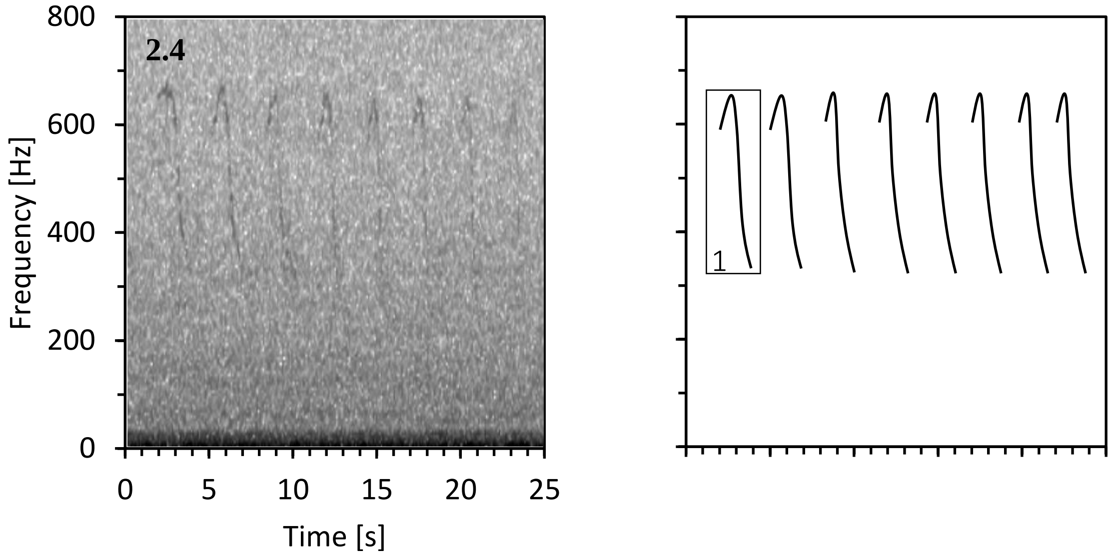


Figure A4. Song types of bowhead whales recorded by SV1088 in eastern Fram Strait (79° 00.02’ N, 5° 40.12’ E) between November and May 2016/17. Each spectrographic example (left panels, spectrogram settings: FFT 1,024, overlap 90 %, contrast 55, Hann window) is supplemented by an idealized representation (right panels) of the corresponding song type. The x-axis comprises a time interval of 25 s and the y-axis a bandwidth of 0-800 Hz for every song type. Different song units are encompassed by a box.

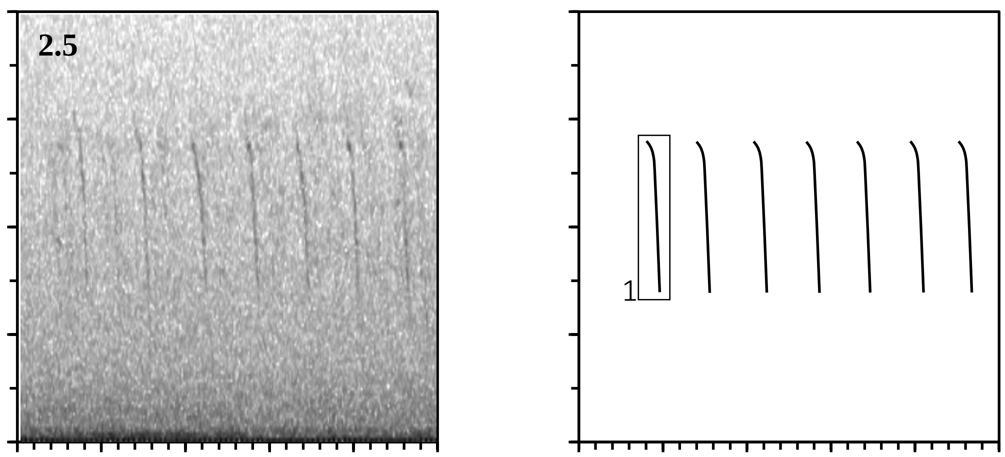


(Continuation of Figure A4)

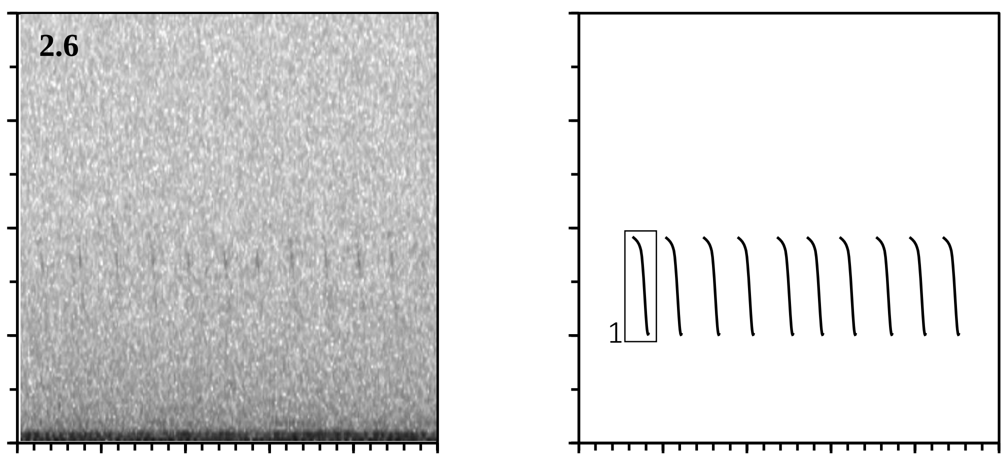
f



g

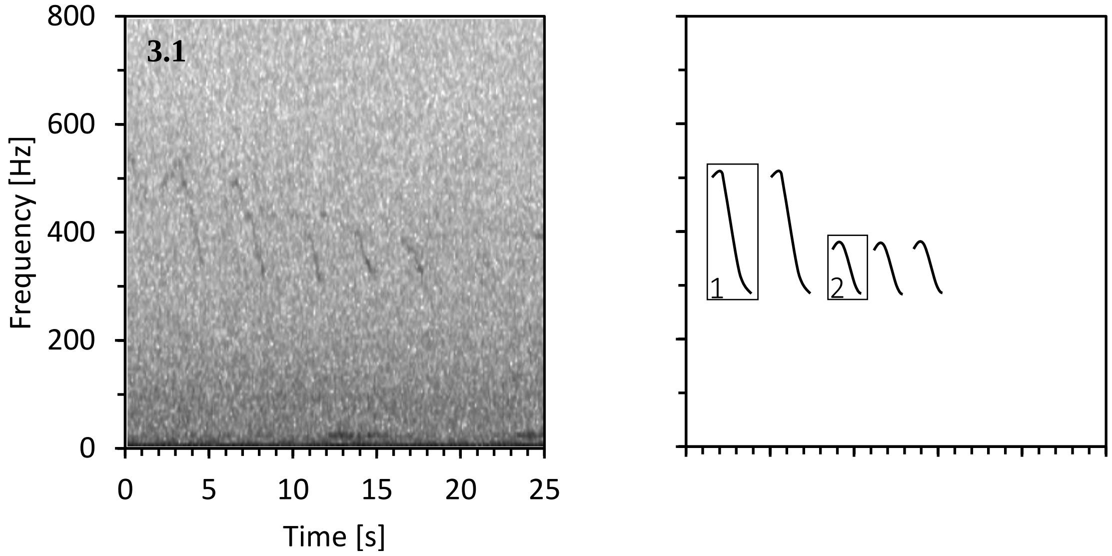


h



(Continuation of Figure A4)

i



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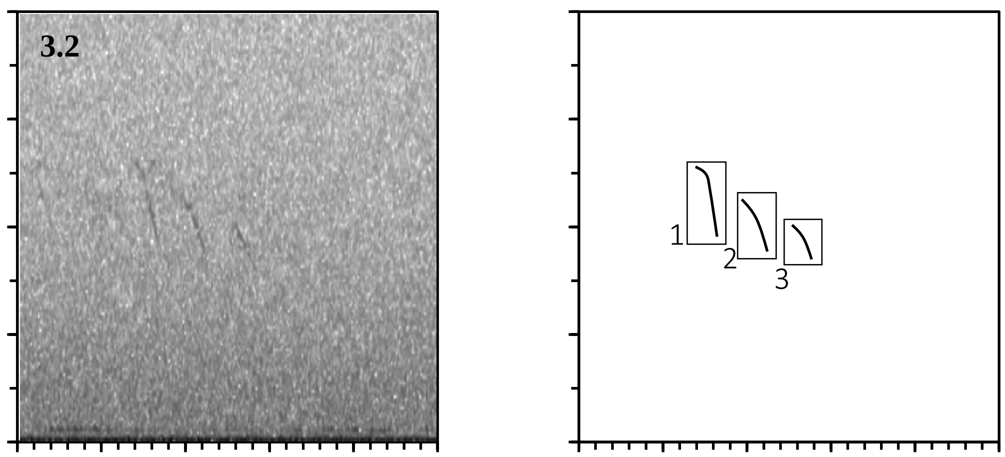
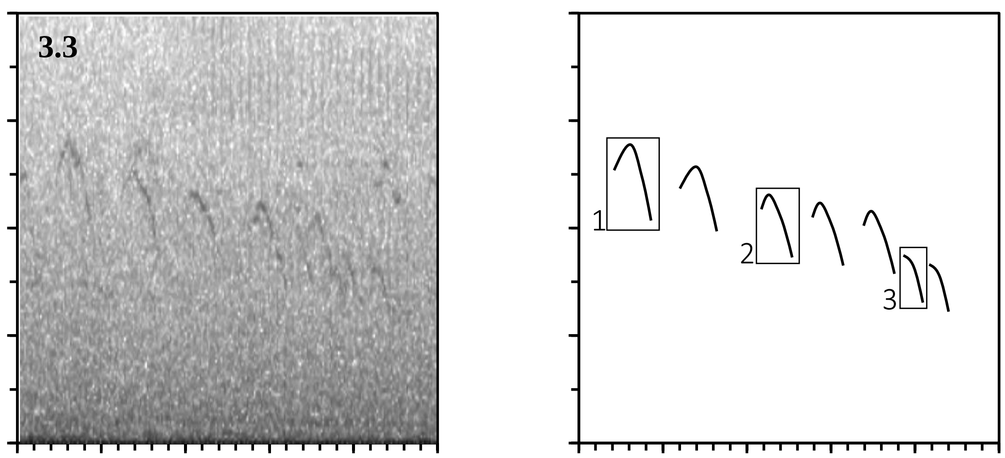
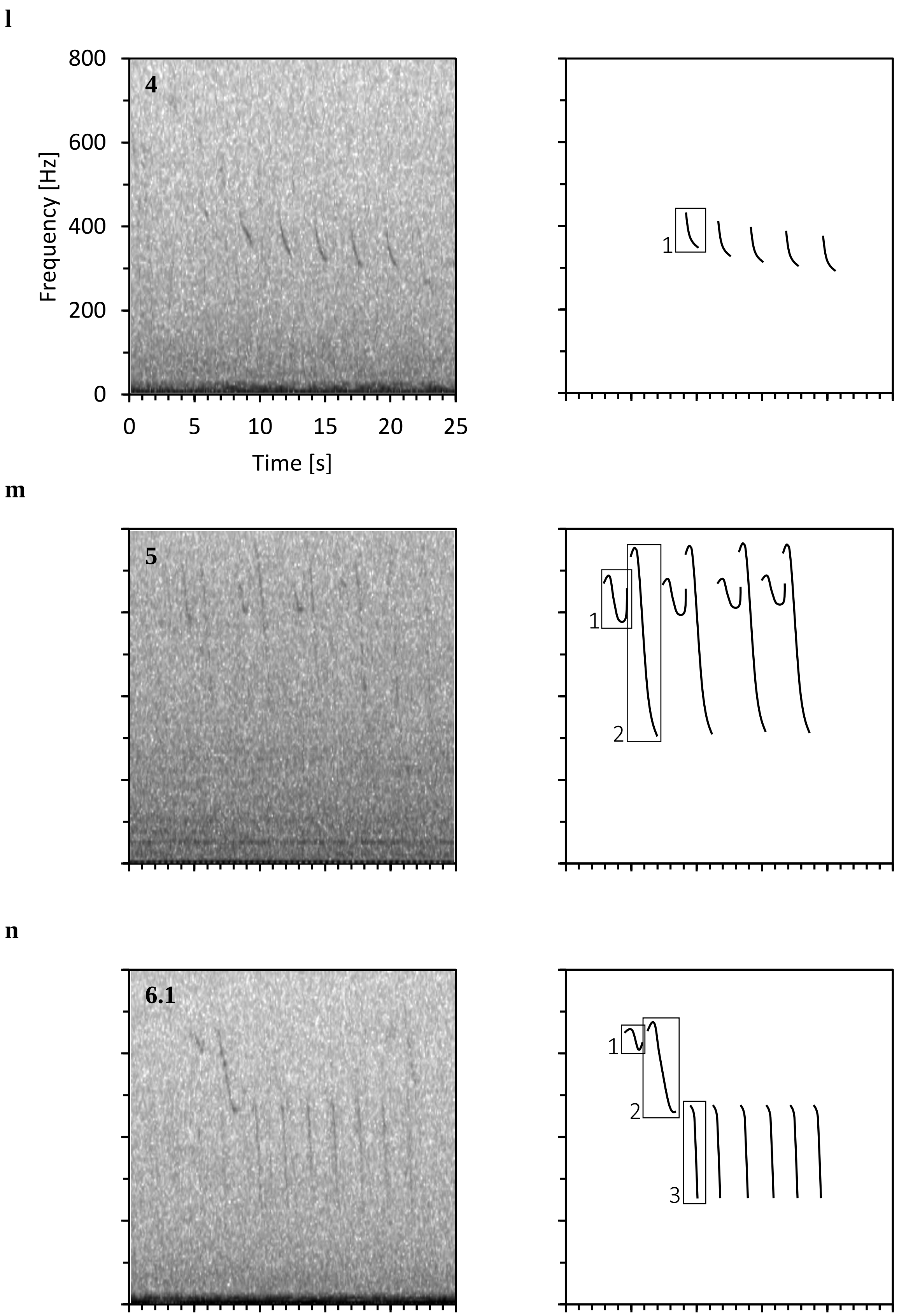


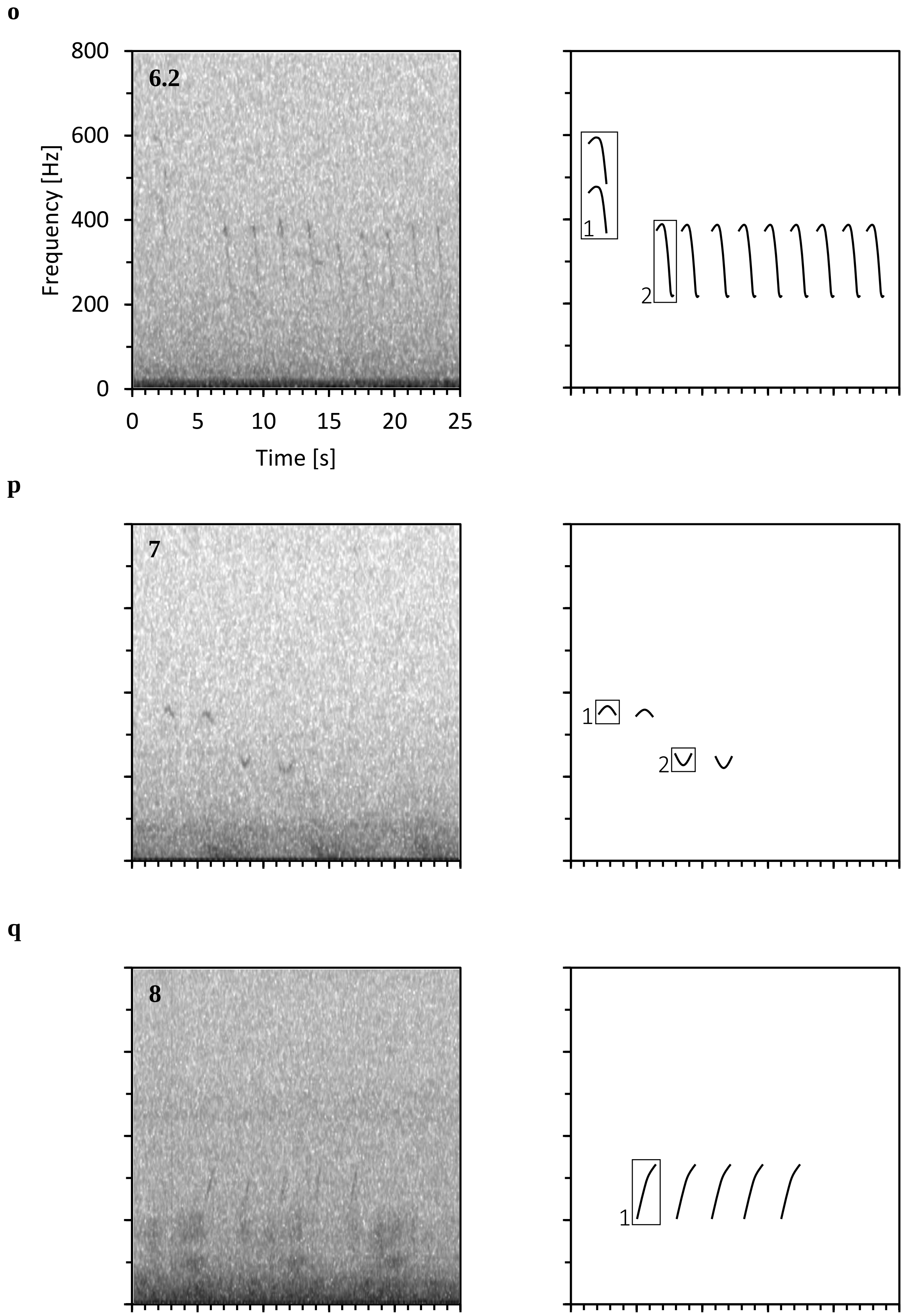
k



(Continuation of Figure A4)



(Continuation of Figure A4)



(Continuation of Figure A4)

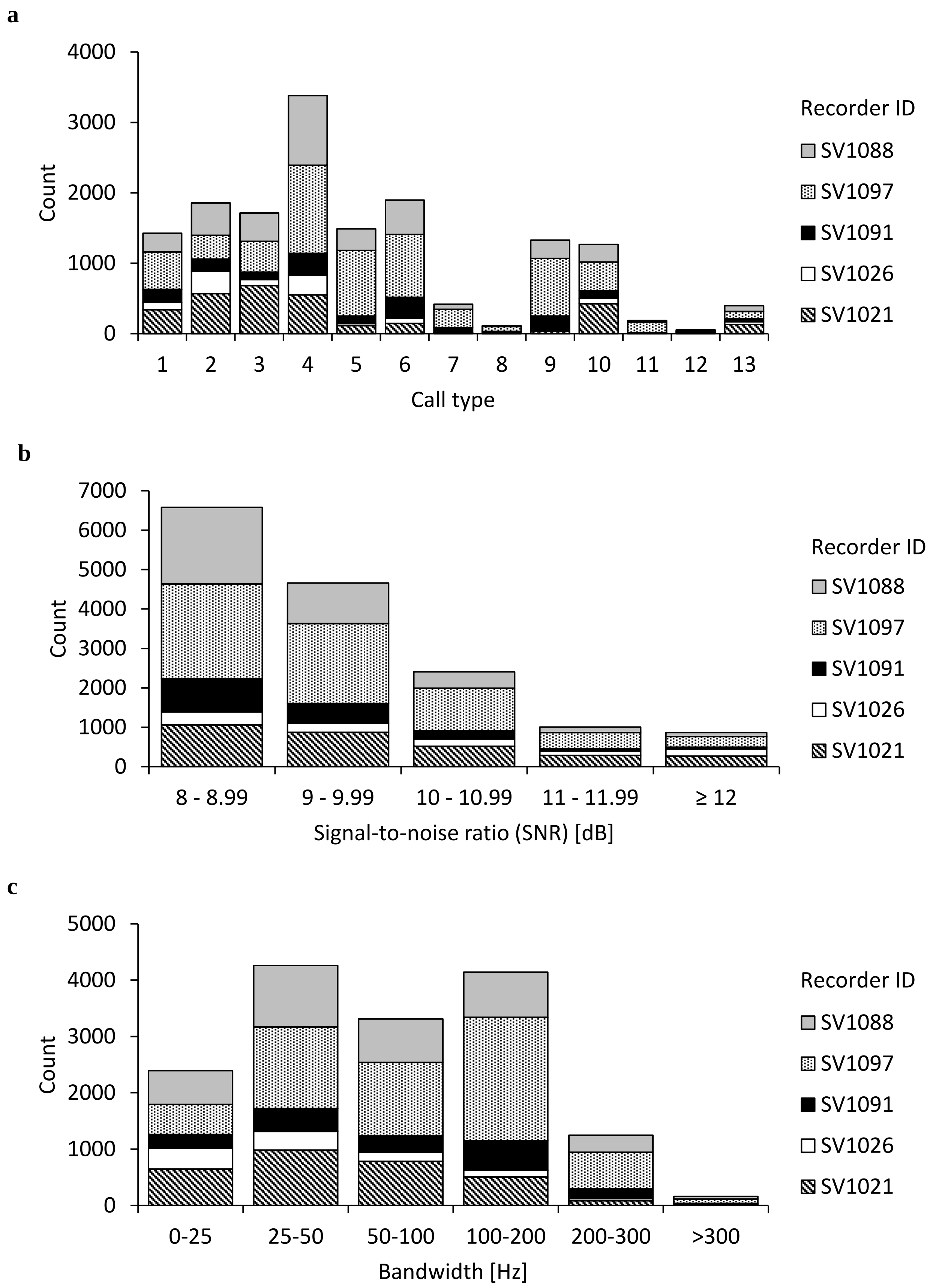
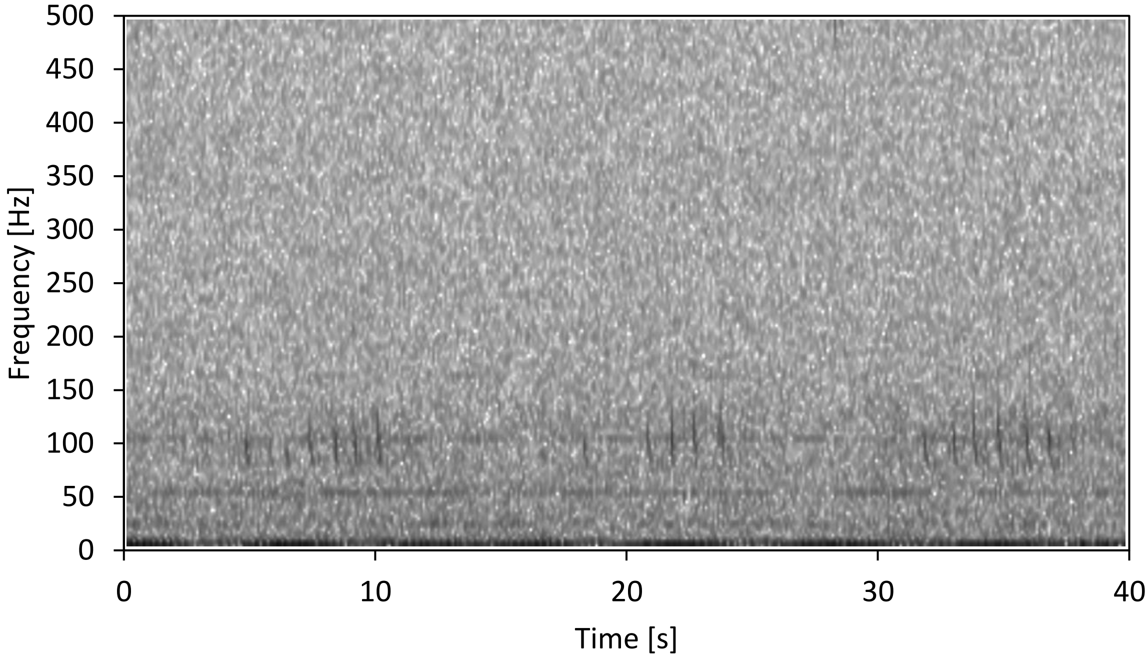


Figure A5. Frequency distribution of automated detection properties. (a) Frequency distribution of all bowhead whale call types assigned by the Low-Frequency Detection and Classification System (LFDCS) for all recorders. **(b)** Frequency distribution of signal-to-noise ratios (SNRs) [dB] and **(c)** bandwidths [Hz] of bowhead whale calls detected by LFDCS for all recorders.

a



b

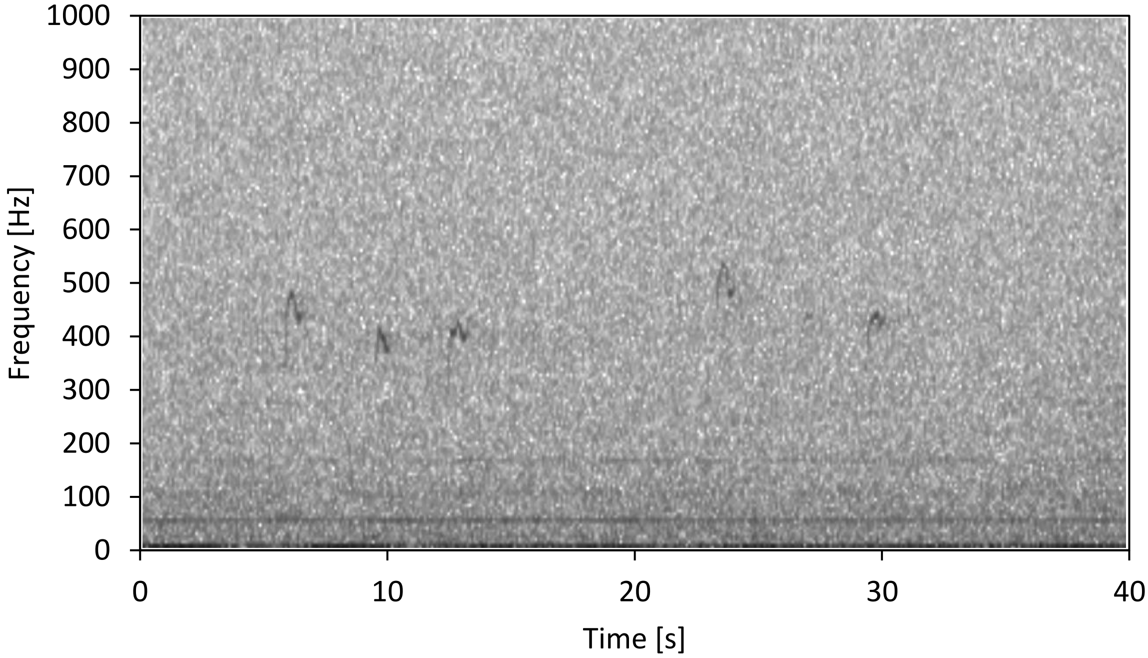


Figure A6. Spectrogram of signals of unknown, biological origin recorded by SV1088 in eastern Fram Strait (79° 00.02' N 5° 40.12' E) in January 2017. Spectrogram settings: FFT 1,024, Overlap 90 %, Brightness 55, Contrast 55, Hann window. (**a**) Series of tonal downsweep signals of unknown origin in the 75-130 Hz frequency band. (**b**) Series of inflected calls of unknown origin.

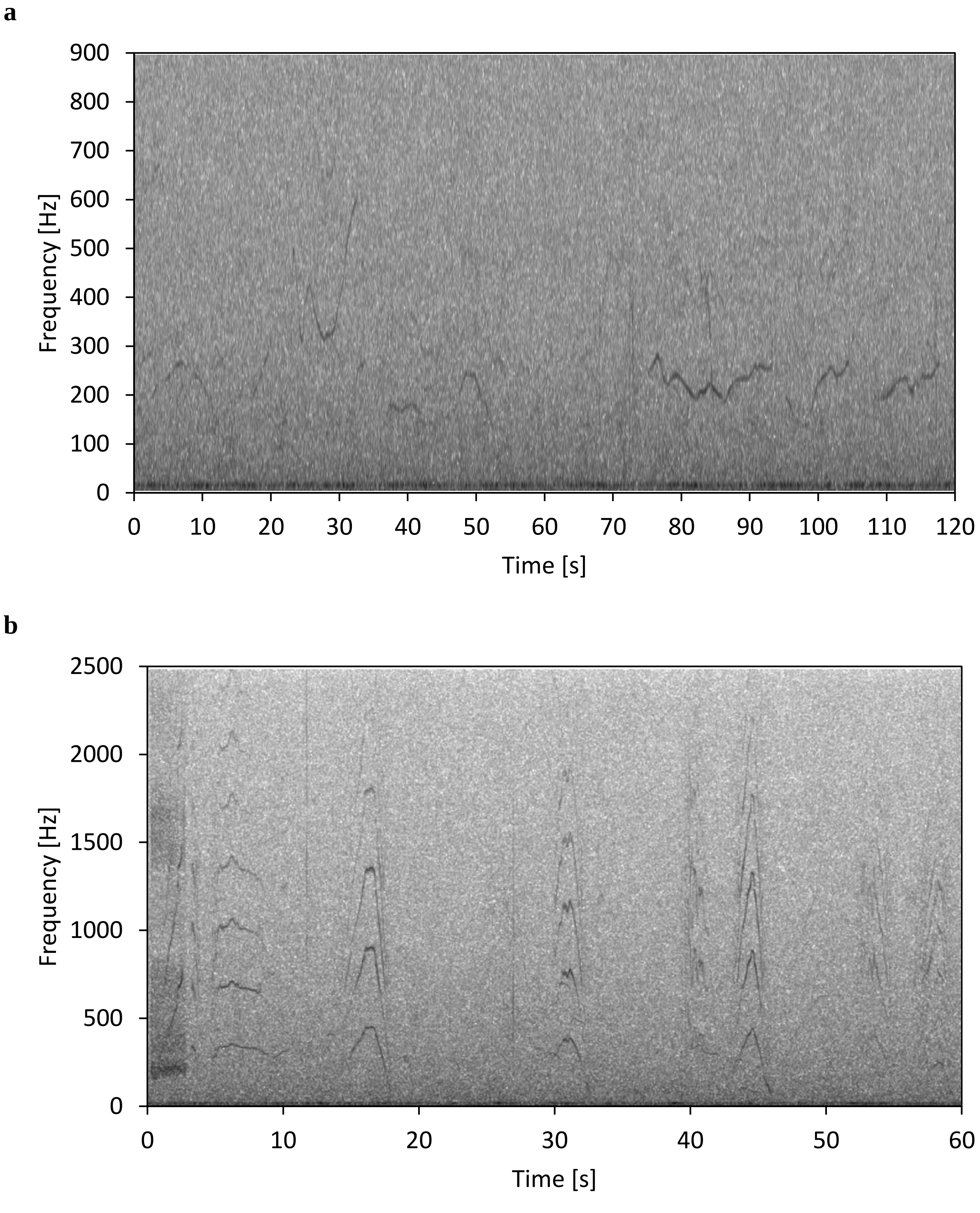


Figure A7. Spectrograms of ice tremors. Recorded by SV1021 on 24 October 2012 in central Fram Strait (78° 49.76' N, 0° 25.77' E). Spectrogram settings: FFT 1,024, Overlap 90 %, Brightness 50, Contrast 55, Hann window.