Vocal behaviour of bowhead whales (*Balaena mysticetus*) in eastern Fram Strait

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ABSTRACT

Bowhead whales (*Balaena mysticetus*) of the East Greenland-Svalbard-Barents Sea (Spitsbergen) population have been depleted close to the point of extinction by commercial whaling and are still considered as endangered. Due to their low abundance and the remoteness of their 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) as part of the Ocean Observing System FRAM (**Fr**ontiers in **A**rctic **M**arine **M**onitoring). Data recorded in 2012 and 2016/2017 were analysed for the acoustic occurrence of bowhead whales at an hourly resolution using an automated detector.

Bowhead whales were acoustically present from autumn throughout the winter months (October-February) and occasionally in spring (March-June), supporting hypotheses that Fram Strait is an important overwintering area. Acoustic presence peaked between mid-November and mid-December when bowhead whales were recorded almost daily, often hourly for several days in a row. The observed peak in acoustic presence coincided with the presumed mating period of bowhead whales, starting in late winter, indicating that Fram Strait may also serve as a mating area. Detailed analyses of recordings of a single year and location revealed eight distinct bowhead whale song types comprising simple songs and call sequences. No bowhead whales were recorded in summer (July-September), indicating that they either were vocally inactive or had migrated to summering areas.

Compared to previous studies in western Fram Strait, bowhead whale detections in our recordings were less frequent and less complex. The observed regional differences in bowhead whale acoustic behaviour across Fram Strait suggest that our mooring locations in eastern Fram Strait may represent the eastern distribution boundary of the bowhead whale overwintering area.

Keywords: Acoustics, Vocalisation, Arctic, Habitat, Seasonality

INTRODUCTION

Beginning in 1611, centuries of commercial whaling greatly reduced the global bowhead whale population with the East Greenland-Svalbard-Barents Sea population (henceforth referred to as Spitsbergen population) being depleted to near extinction (Jonsgård, 1981; Reeves, 1980; Shelden *et al.*, 1995; Woodby *et al.*, 1993). Despite becoming protected in the early 1930s, the Spitsbergen population does not show signs of recovery and is still considered as being 'endangered' by the IUCN Red List of Threatened Species (Cooke *et al.*, 2018). The population size prior to commercial whaling has been estimated at 52,500 individuals (Allen *et al.*, 2006), while today it is believed to number in the range of 50-250 individuals (Cooke *et al.*, 2018). 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.

Historic whaling records suggest that Fram Strait, located between Greenland and Svalbard, was a key area for this population (Woodby *et al.*, 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., Fahrbach *et al.*, 2001). The dynamic hydrological conditions within Fram Strait create large productive areas with high zooplankton abundance (Blachowiak-Samolyk *et al.*, 2007). 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 *et al.*, 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). 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), detailed information about the maximum extent of their distribution is still lacking.

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 hotspot area for bowhead whales and other cetacean species (Kovacs *et al.,* 2006; Storrie *et al.,* 2018) 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 activities – in particular noise from ship traffic, drilling and seismic surveys – 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 *et al.,* 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).

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.

MATERIAL & METHODS

Data Collection

Passive acoustic data were collected by five recorders (Sono.Vault, 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, respectively; 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 (**Fr**ontiers in **A**rctic **M**arine **M**onitoring, Soltwedel *et al.,* 2013; Fig. 1, Table 1). The recorders were moored at depths around 800 m and scheduled to record continuously 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. 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 for the 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.

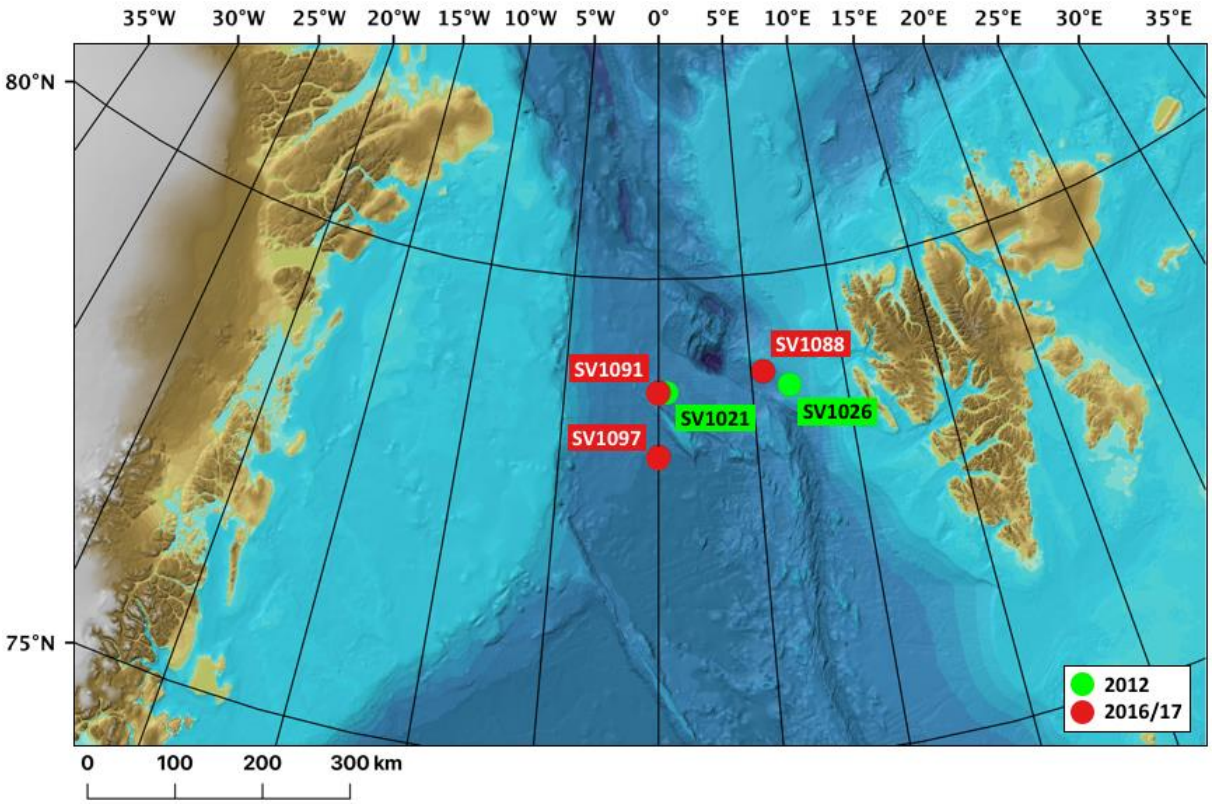

Fig. 1. Deployment locations of the five recorders in Fram Strait between Greenland and Svalbard. Recorder SV1021 and SV1026 were recording in 2012 (green dots), while SV1091, SV1097 and SV1088 were recording year-round in 2016/17 (red dots). SV1021 and SV1091 belong to the central recording site, SV1097 to the southern and SV1026 and SV1088 to the eastern recording site.

Table 1. Locations and recording parameters of passive acoustic recorders deployed in Fram Strait between 2012 and 2018. Deployment and recording period are given in the format 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

Acoustic Analysis

Bowhead whale vocalisations were automatically detected and classified based on a user-developed call library in the Low-Frequency Detection and Classification System (LFDCS) (Baumgartner *et al.*, 2011; for details on call detection please refer to Hiemer, 2019). To eliminate false positive hours, all automated detection events of bowhead whales were manually reviewed on an hourly basis in terms of a false-positive control (for details on detector performance please refer to Hiemer, 2019). 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 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, USA) for the presence of at least one bowhead whale call validated by a trained analyst.

The acoustic repertoire of bowhead whales within a one-year period was assessed from acoustic data recorded by SV1088 in eastern Fram Strait. Spectrograms were visually checked for the presence of bowhead whale songs. In this study, the term 'song' comprised both call sequences and *true* songs, thereby following the differentiation of

Stafford *et al.* (2012). By definition, true songs are made up by different calls, named 'units' (or 'notes'), combined into phrases (Würsig *et al.*, 1993). Call sequences, in contrast, are a series of repeated similar calls (Blackwell *et al.*, 2007). 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.

Sea Ice Data

Sea ice coverage in the study area was derived from satellite data (Spreen *et al.*, 2008). Daily sea ice concentration data with a 6.25 × 6.25 km^2 resolution were downloaded from a database provided by the University of Bremen (available at: https://seaice.uni-bremen.de/data/amsr2/asi_daygrid_swath/n6250/). Mean daily sea ice concentrations were calculated from all data points within a 35 km radius around each recording location. As bowhead whale vocalisations are estimated to propagate over 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.

RESULTS

Bowhead whale sounds were detected at all recording sites and during both sampling periods in 2012 and 2016/17. 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; Fig. 2). In both sampling periods, bowhead whales started to be acoustically present in autumn. While bowhead whales in 2012 started to call already in mid-October, first detections of bowhead whales occurred not until mid-November in the recordings of 2016/17 (Fig. 2).

In 2012, acoustic presence occurred in distinct blocks, each lasting around a week, from mid-October until the end of November when recordings stopped (Fig. 2a-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 and 2017, bowhead whales were recorded at all recording sites from late autumn throughout winter (November-February) and occasionally during spring (March-May) at the southern and eastern recording sites (SV1097, SV1088; Fig. 2d-e). No bowhead whales were detected from July to November 2016 and in July 2017 at all recording sites (Fig. 2c-e). Acoustic presence peaked between mid-November and mid-December when bowhead whales were recorded almost daily, often hourly for several days in a row (Fig. 2c-e). During this period, 68 % 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 (Fig. 2c-e). Due to prevailing noise of breaking ice, no bowhead whales were acoustically detected at the central (SV1091) and southern recording sites from mid-February throughout April (Fig. 2c-d). While bowhead whales were sporadically recorded again at the southern recording site in May and June, no further acoustic detections occurred at the central recording site during these months. At the eastern recording site, acoustic presence of bowhead whales continued in patches, each lasting 2-4 d, until the end of May (Fig. 2e).

Within a one-year period, eight distinct bowhead whale song types were identified, providing the first description of the acoustic repertoire of bowhead whales in eastern Fram Strait (for detailed descriptions of the song types please refer to Hiemer, 2019). The song types were divided into five *true*, but simple songs and three call sequences. No complex songs, according to the definition of Stafford *et al.* (2012), were found. The number of different song types was greatest when acoustic presence peaked at the beginning of the season in early winter (November-December; Fig. 3). Fewer song types were recorded between March and May (Fig. 3). Song type 2 occurred most frequently and persisted throughout the whole season except for May. There was an overall trend that song types occurred in succession over the season (Fig. 3).

Sea ice concentrations were highly variable among the recording sites, with sea ice concentrations being highest at the central, and lowest at the eastern recording sites throughout the sampling period (Fig. 2). The relationship between sea ice concentrations and bowhead whale acoustic presence was inconclusive using Poisson regression.

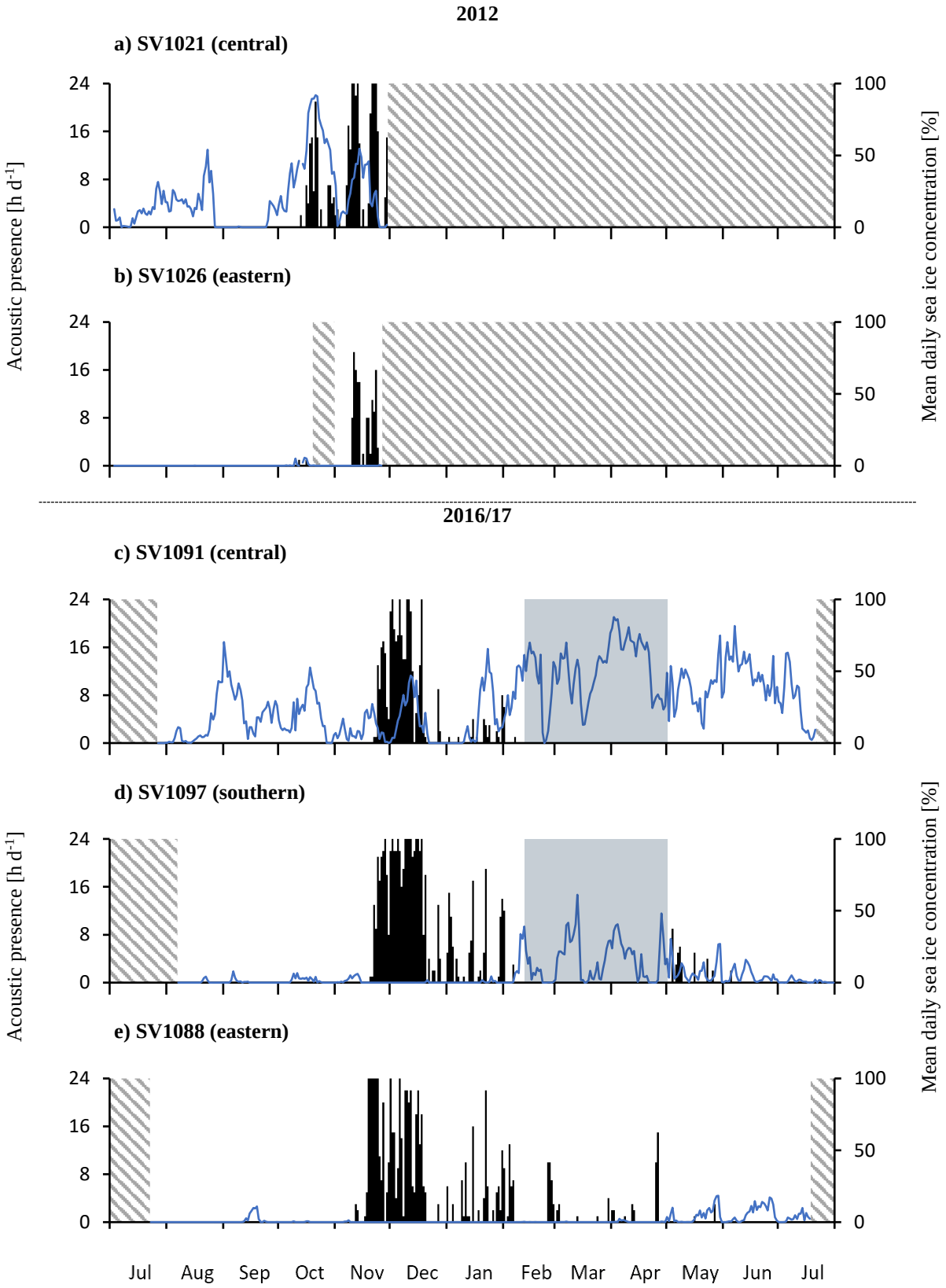

Fig. 2. Acoustic presence of bowhead whales in Fram Strait in 2012 (a-b) and 2016/17 (c-e). Number of hours per day [h d^{-1}] with acoustic presence of bowhead whales (left y-axis, black bars) and mean daily sea ice concertation [%] within a 35 km radius around each recording location (right y-axis, blue lines). Hatched areas illustrate periods without recording data. Blue areas indicate the time period between mid-February and April 2017 when sounds of breaking ice were masking large parts of the spectrogram at the central and southern recording sites.

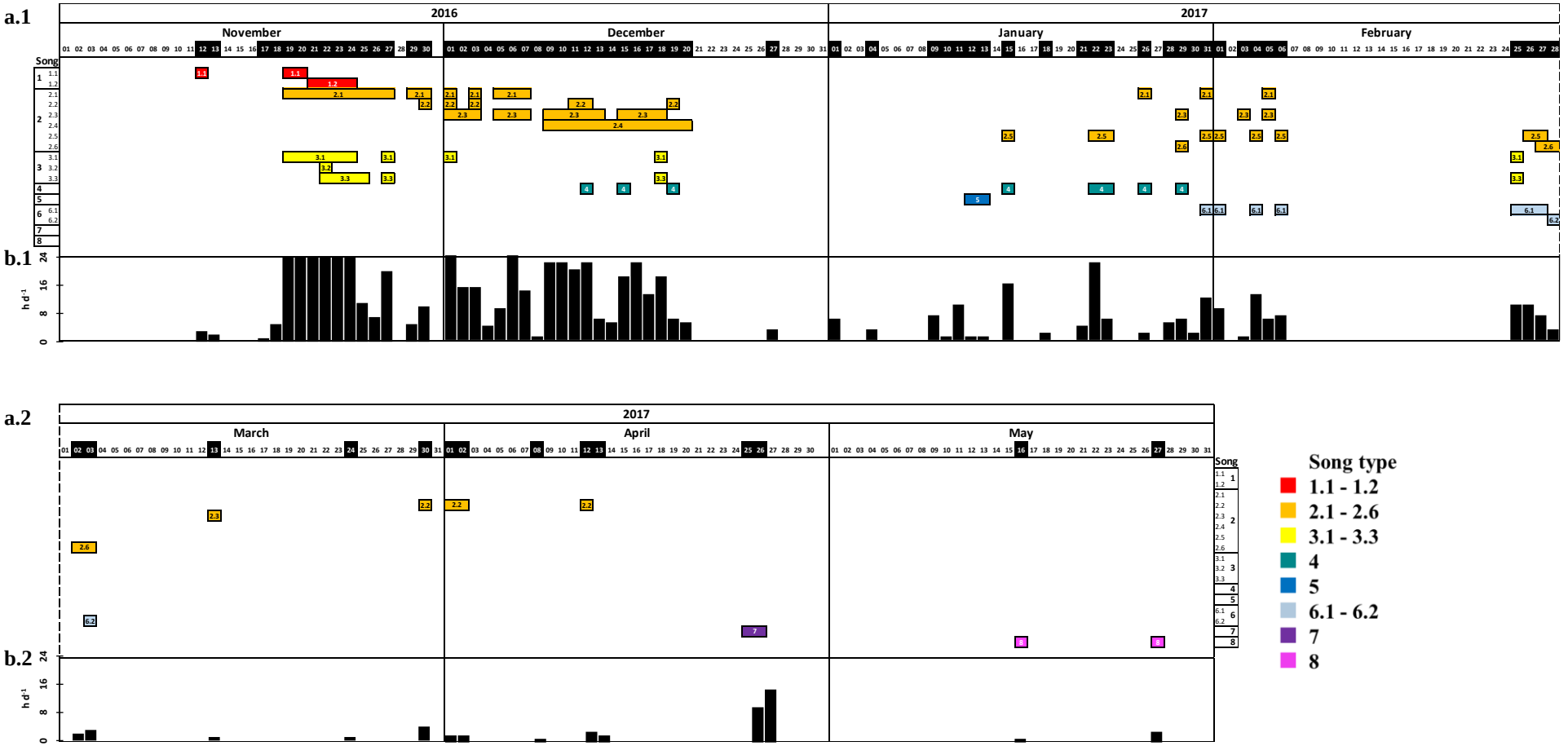

Fig. 3. Temporal patterns in the occurrence of bowhead whale song types in eastern Fram Strait (79° 00.02' N, 5° 40.12' E) between November 2016 and May 2017. Calendar days on which distinct song types of bowhead whales were recorded in eastern Fram Strait by SV1088 from November 2016 until February 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). Variants of the song types are assigned a sub-number.

DISCUSSION

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

According to historic whaling records, Fram Strait has consistently been an important habitat for bowhead whales (Moore *et al.,* 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 *et al.,* 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 shifted 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 continued from autumn 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 recently been described for bowhead whales in Disko Bay, western Greenland (Tervo *et al.,* 2009). They observed multiple individuals singing simultaneously, with songs being more frequent in winter than in spring. Stafford *et al.* (2012) showed similar results for the western part of Fram Strait where songs of bowhead whales were recorded almost constantly between November and April. Singing is assumed to be a form of sexual display performed by males to attract females (Würsig *et al.,* 1993). As intense singing coincided with the presumed mating period of bowhead whales, starting in late winter (Koski *et al.,* 1993), Stafford *et al.* (2012) concluded that Fram Strait might be a mating area for the Spitsbergen bowhead whale population.

Apart from being an overwintering and potential mating area, bowhead whales may also seasonally occupy Fram Strait for feeding. Bowhead whales commonly occur in 'oceanographically complex' areas (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 *et al.,* 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 are transported with the Atlantic inflow into Fram Strait in the east (Blachowiak-Samolyk *et al.,* 2007; Smith, 1988). Bowhead whales filter-feed on zooplankton including calanoid copepods and euphausiids (Lowry, 1993; Lowry *et al.,* 2004). During spring and early summer, bowhead whales have been reported to preferentially stay in productive areas above bottom slopes (de Boer *et al.,* 2019; Lydersen *et al.,* 2012; Moore, 2000; Moore *et al.,* 2000). 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 cater for 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.,* 2007). Thus, the observed decline in acoustic presence in spring may relate to a shift in behaviour from mating to feeding (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 satellite-tracked bowhead whale (Lydersen *et al.,* 2012). This whale presumably overwintered in Fram Strait at about 78-80°N. From there it moved south towards 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. 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; Quakenbush *et al.,* 2010; Reeves *et al.,* 1983). 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 *et al.*, 1993). Considering what is known about the summer migration of bowhead whales combined with the decrease in acoustic activity from early spring onwards, bowhead whales might have left eastern Fram Strait for summer. However, it cannot be excluded that bowhead whales were present in eastern Fram Strait during summer but vocally inactive or outside of the recording area since bowhead whales have been sighted approximately 150 km to the north (Wiig *et al.,* 2007; Wiig *et al.,* 2010) and approximately 300 km to the southwest (de Boer *et al.,* 2019) of this study's central recording sites during summer in past years.

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 possible reason for this may be the difference in sea ice cover between western and eastern Fram Strait. While the eastern part of Fram Strait is a region with low sea ice concentrations, the western part of Fram Strait is ice-covered almost year-round (Nöthig *et al.,* 2015). Bowhead whales are known to live in close association with sea ice, even though animals have been observed in the open water far off the marginal ice edge in the past (de Boer *et al.,* 2019; Lydersen *et al.,* 2012). Sea ice is thought to provide shelter from killer whale (*Orcinus orca*) predation, offer feeding opportunities (Ferguson *et al.,* 2010) and may be beneficial for the transmission and reception of acoustic signals (Stafford *et al.,* 2012). Additionally, the presence of sea ice leaves western Fram Strait inaccessible for anthropogenic activities, thus undisturbed for most parts of the year (Ahonen *et al.,* 2017). Considering that sea ice concentrations were unfavourably low in eastern Fram Strait, bowhead whales may have spent less time in the region or were less vocally active because of the potential risk of killer whale predation as suggested by Stafford *et al.* (2012). Irrespective of probably low habitat suitability, bowhead whales were detected for several months around the recording sites in eastern Fram Strait. Therefore, our mooring locations in eastern Fram Strait may represent the eastern distribution boundary of the bowhead whale overwintering area.

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