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Interannual variability in acoustic detection of blue and fin whale calls in the Northeast Atlantic High Arctic between 2008 and 2018

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ABSTRACT: Northern Hemisphere blue and fin whales are regular summer migrants to Arctic waters. Given the profound changes the Arctic is currently undergoing due to global warming, changes in habitat use and distribution of these migratory species are predicted. In this study, 3 passive acoustic recorders, 2 in Fram Strait about 95 km apart and 1 north of the Svalbard Archipelago (Atwain), were used to investigate the spatial and temporal vocal occurrence of these species in the Northeast Atlantic High Arctic. Acoustic data were available for 7 years for western Fram Strait (WFS), 2.5 years for central Fram Strait (CFS) and 3 years for Atwain. At both Fram Strait locations, most blue whale call detections occurred from August through October, though recently (2015–2018) in WFS a clear increase in blue whale call rates was detected in June/July, suggesting an expansion of the seasonal occurrence of blue whales. In WFS, fin whale calls were detected intermittently, at low levels, almost year-round. In CFS, fin whale calls were more frequent but occurred mainly from July through December. At Atwain, blue whale detections commenced in July, both species were recorded in September/October and fin whale calls extended into November. Results from this study provide novel long-term baseline information about the occurrence of blue and fin whales at extreme northerly locations, where traditional ship-based survey methods are seasonally limited. Continued sampling will support investigation of how environmental change influences cetacean distribution and habitat use.

KEY WORDS: *Balaenoptera musculus musculus* · *Balaenoptera physalus* · Passive acoustic monitoring · Seasonal occurrence · Temporal expansion

1. INTRODUCTION

Blue whales *Balaenoptera musculus* and fin whales *B. physalus* have worldwide distributions ranging from tropical to polar regions (Cooke 2018a,b). These fast-swimming rorqual whales became the focus of commercial exploitation in the 1900s, due to the development of faster vessels and highly effective harpoons. During the modern whaling era, blue whales were hunted to the brink of extinction and fin whales were greatly reduced over their entire range. At present, Northern Hemisphere blue whale *B. musculus musculus* abundance estimates are still quite low in the North Atlantic region, apart from around Iceland and the Azores (Pike et al. 2009, Silva et al. 2013, Moore et al. 2019). A recent assessment of blue whales in the central North Atlantic estimated an abundance of 3000 (CV = 0.40) whales, suggesting an increasing trend in this area (Pike et al. 2019). Nevertheless, in the Northeast Atlantic, particularly

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around Svalbard and along the coast of northern Norway, blue whales continue to be rare and there has been no assessment of their numbers in this region since 1996 (Pike et al. 2009). Sightings of fin whales are more common in the North Atlantic and recent abundance estimates show clear evidence of recovery (e.g. Vikingsson et al. 2015, Pike et al. 2019). The North Atlantic population of fin whales is now likely close to, or larger than, the population was prior to the onset of modern whaling, with a total estimate of ~79 000 individuals (CV = 0.13) in the North Atlantic (Cooke 2018b). While blue whales are protected, fin whales are harvested commercially at very low levels by Iceland (NAMMCO 2019a). Abundance estimates and distribution surveys for both species have focused on the region around the southeastern coast of Greenland and north of Iceland, with relatively little survey effort further north. However, there has been a notable increase in the number of reported sightings of migratory species, such as blue and fin whales, in the Svalbard area over recent decades (Storrie et al. 2018).

Both blue and fin whales are generally thought to be seasonal visitors to the Northeast Atlantic sector of the Arctic and are mainly observed during the open water season in summer/early autumn. Habitat use is not well known for either species in this area, but in general, these species are thought to arrive at feeding grounds at high latitudes (defined here as latitudes above the Arctic Circle, >66° 33′ N) in late spring/early summer and depart in autumn to spend the winters in more temperate areas (Moore et al. 2019). However, recent data from passive acoustic recorders suggest that some fin whales might overwinter at high latitudes (Simon et al. 2010, Klinck et al. 2012, Ahonen et al. 2017). Sea ice is likely one of the main factors limiting the distribution of blue and fin whales, due to either physical obstruction of normal movement and breathing or secondary oceanographic effects on prey availability (Širović et al. 2004, 2009, Simon et al. 2010). However, as the Arctic is rapidly changing and the region is undergoing profound physical and biological changes associated with increasing air and water temperatures and decreasing sea ice extent, it is likely that habitat use and movement behaviour of the migratory whale species that frequent the Arctic seasonally will be affected.

Studying the geographic range and habitat use of a species is fundamental to understanding its ecology and predicting how it will respond to environmental changes (Gaston & Fuller 2009). However, this undertaking is especially challenging for highly mobile, pelagic species like blue and fin whales. In addition, vessel and aerial-based visual surveys in the Arctic are limited due to extreme seasonal variation in light conditions and inclement weather outside the narrow summer period. Visual surveys face challenges even in good light and weather conditions due to possible misidentification of species and responsive movement of animals towards or away from approaching vessels/aircraft (Pike et al. 2019). Tracking studies have been used at temperate latitudes to investigate distribution and habitat use in these wide-ranging cetaceans (e.g. Silva et al. 2013, Irvine et al. 2014, Jiménez López et al. 2019, Palacios et al. 2019). However, the retention time of tags in these fast-swimming whales is relatively short, so animals tagged in temperate areas often do not retain tags long enough to reveal where they go when they come to the Arctic (e.g. Silva et al. 2013, Pérez-Jorge et al. 2020).

During recent years passive acoustic monitoring (PAM) has been used successfully to study the behaviour and distribution of many cetacean species in the Arctic (e.g. Moore et al. 2012, Hannay et al. 2013, Clark et al. 2015, Ahonen et al. 2017, 2019, Hauser et al. 2017, Stafford et al. 2018). PAM allows for relatively low-cost, long-term monitoring throughout the year, under ice and in all weather conditions. PAM does have limitations, as call detection is influenced by the vocal behaviour of animals, and masking from natural and anthropogenic sounds influences what is detected (Stafford et al. 2007, Hannay et al. 2013). Nevertheless, PAM provides the ability to collect year-round data on multiple species in otherwise inaccessible, remote locations (e.g. Stafford et al. 2007, Moore et al. 2012, Hannay et al. 2013).

Over the past 2 decades, an increasing number of long-term PAM studies have been used to investigate distribution and migration patterns of blue and fin whales in various locations around the world, including polar regions (e.g. Širović et al. 2004, Simon et al. 2010, Delarue et al. 2013, Thomisch et al. 2016, Shabangu et al. 2019, Escajeda et al. 2020). Both blue and fin whales are good candidates for PAM because they produce readily identifiable stereotyped sounds. North Atlantic blue whales produce long (~20 s), low-frequency (16–18 Hz), frequency-modulated moans that can occur as repetitive 'songs' (Edds 1982, Mellinger & Clark 2003). Additionally, they produce higher frequency, shorter and more variable arch or D calls (Mellinger & Clark 2003). Blue whales vocalise regularly throughout the year, with peaks from midsummer into winter months (Stafford et al. 2001, Širović et al. 2004). Fin whales also produce low-frequency signals, but these are short (~1 s), frequency-modulated downsweeps that decrease in frequency from ~25 to 18 Hz and are often referred to in the literature as 20 Hz pulses (Watkins et al. 1987). These 20 Hz pulses can be produced either randomly or as repetitive bouts (singing) that can last hours to days (Watkins et al. 1987). Although fin whale vocalisations are detected year-round in some locations (Stafford et al. 2010, Morano et al. 2012, Nieukirk et al. 2012), in the northwest Atlantic, fin whale singing has been recorded from June through March, peaking in October through December (Simon et al. 2010, Davis et al. 2020). The peak coincides with the fin whales' presumed reproductive season (Watkins et al. 1987, 2000).

The purpose of this study was to investigate the acoustic presence of blue and fin whales in the Northeast Atlantic High Arctic using 2 PAM stations in the Fram Strait and 1 north of the Svalbard Archipelago (Atwain). Data from western Fram Strait (WFS) span a 10 yr period, allowing for investigation of possible temporal shifts in seasonal migration patterns for these 2 species. This novel long-term baseline data on occurrence of blue and fin whales in the High Arctic will be valuable for investigating how environmental changes are affecting the phenology of seasonally resident cetaceans.

2. MATERIALS AND METHODS

2.1. Instrument type and deployment locations

Three Autonomous Underwater Recorders for Acoustic Listening (AURAL M2, Multi-Électronique Inc.; receiving sensitivity of −164 ± 1 dB re1 V μPa^{-1} with a 16 dB system gain and flat response from 5 Hz to 32.8 kHz, Kinda et al. 2013) were deployed on oceanographic moorings located in the Northeast Atlantic High Arctic (Fig. 1). Two of these moorings were situated in Fram Strait, 95 km apart. The westernmost mooring (hereafter referred to as WFS) is maintained annually by the Norwegian Polar Institute. It is situated at circa 78° 50′ N and 5° W, on the slope of the continental shelf (water column depth of ca. 1015 m). The AURAL was installed at a depth of 70–85 m (the exact depth changed slightly among years; Table 1). The central Fram Strait mooring (CFS) was maintained by the Alfred Wegener Institute and was situated at 78° 50′ N, 0° 46′ W (water column depth of ca. 2611 m). This AURAL was installed at a depth of 58 m on the mooring line. The third mooring was situated north of the Svalbard Archipelago at 81° 30′ N and 30° 5′ E (hereafter referred to as Atwain; water column depth of ca. 850 m). During the 2015–2016 data collection period, this mooring was moved to shallower water (ca. 200 m, approximately 20 km away from original deployment location; see Table 1 for exact locations). This mooring is part of an instrumentation platform that provides data for the A-TWAIN project (https://www.npolar.no/en/projects/a-twain/), whose aim is studying long-term variability and trends in the Atlantic water inflow to the Arctic Ocean north of Svalbard. This AURAL was installed at a depth of 55–60 m on the mooring line (see Table 1 for exact depths for each location and year).

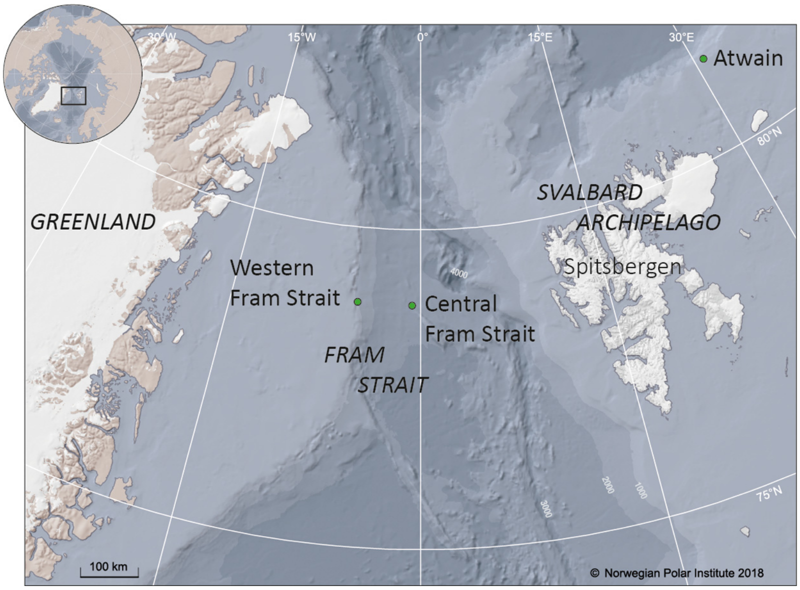

Fig. 1. Study area and locations of the 3 oceanographic moorings with AURALs (green dots)

2.2. Acoustic data and detections

Acoustic data were available for 7 years for WFS (between 2008 and 2018), 2.5 years for CFS (between 2008 and 2012) and 3 years for Atwain (between 2012 and 2016). Data from WFS for 2008–09 were previously presented in Moore et al. (2012) but are reanalysed herein (i.e. the raw data were processed in a uniform way with the newer data) for comparative purposes. Sampling rate, duty cycle (number of minutes recorded at the start of each hour), and recording time varied among years and locations; full deployment details for each recorder are presented in Table 1. Because battery life is a limiting factor for these instruments, the longer duty cycle used during

Table 1. Summary information for passive acoustic monitoring (PAM) deployment locations. Longer duty cycles resulted in shorter data collection period in 2012–13 and 2013–14

Location	Year	Data collection period	Coordinates	Hydrophone depth (m)	Water depth (m)	Sampling rate (Hz)	Duty cycle	Total recordings (h)
Western Fram Strait	2008–09	20.09.2008–10.09.2009	78° 49.885′ N, 4° 59.074′ W	82	1021	8192	9 min 30 min^{-1}	2563.2
	2010–11	25.09.2010–25.08.2011	78° 50.191′ N, 5° 00.692′ W	75	1017	16384	14 min h^{-1}	1876
	2012–13	03.09.2012–10.04.2013	78° 47.972′ N, 4° 59.2′ W	75	1014	32768	17 min h^{-1}	1496
	2013–14	09.09.2013–26.04.2014	78° 50.038′ N, 4° 59.591′ W	76	1015	32768	17 min h^{-1}	1564
	2015–16	08.09.2015–29.08.2016	78° 50.164′ N, 65° 00.086′ W	74	1010	32768	12 min h^{-1}	1713.6
	2016–17	10.09.2016–26.08.2017	78° 50.283′ N, 4° 59.191′ W	84	1018	32768	12 min h^{-1}	1684.8
	2017–18	11.09.2017–27.08 2018	78° 50.324′ N, 5° 00.146′ W	71	1022	32768	12 min h^{-1}	1684.8
Central Fram Strait	2008–09	10.08.2008–14.07.2009	78° 50.2′ N, 0° 46.9′ W	58	2600	8192	9 min 30 min^{-1}	2440.8
	2010–12	01.08.2010–15.03.2012	78° 50.2′ N, 0° 46.9′ W	58	2600	8192	12 min h^{-1}	2846.4
Atwain	2012–13	19.09.2012–03.05.2013	81° 32.59′ N, 30° 51.40′ E	55	850	32768	17 min h^{-1}	1543.6
	2013–14	23.09.2013–01.05.2014	81° 32.675′ N, 30° 51.207′ E	59	850	32768	17 min h^{-1}	1502.8
	2015–16	20.09.2015–04.12.2016	81° 24.255′ N, 31° 13.533′ E	57	200	32768	12 min h^{-1}	2121.6

2012–2013 and 2013–2014 for both WFS and Atwain recorders resulted in shorter data collection periods (7–8 mo instead of close to a full year). Consequently, 2013 and 2014 late spring/summer data were not available for analysis at either location.

The spectrogram correlation modality in the program Ishmael (Mellinger & Clark 2000) was used as a pre-processing tool to detect times with low frequency signals for both blue and fin whales. Prior to analysis, all data collected with sampling rates greater than 8192 Hz were downsampled to 8192 Hz, and a low-pass filter (100 Hz) was applied. Additionally, a spectrogram equalization of 30 s was applied to reduce low-frequency noise from strumming and distant shipping. For blue whales, the spectrogram correlation parameters consisted of a 10 s long frequency modulated (FM) down-sweep from 18 to 16 Hz. The detection contour width was 3 Hz and a 1 s fast Fourier transform with 75% overlap was used. For fin whales, a 2 s long FM down-sweep from 30 to 19 Hz was used, with a contour width of 7 Hz. The resulting files with detections were then manually checked because all recording locations had some periods with low frequency noise. The data were corrected by removing all false positives and adding false negatives into the final dataset of blue and fin whale signals. Because the duty cycle varied among sites and years (Table 1), all blue whale detections were normalized to call counts per hour for each day (standardised number of calls per day) by dividing the number of calls per day by total recording time (min) per day and extrapolating to the number of calls per hour (e.g. total calls per day/total minutes recording per day × 60). For fin whales, determining individual call counts was more difficult (individual calls were not as clear throughout the recording periods) so daily presence is reported as number of hours per day (0–24) with at least one clear fin whale call. For WFS and Atwain, the first 12 min of recording were used to count daily presence of fin whale calls (except for WFS 2008–09 which recorded 9 min each half hour and thus only the first 9 min period was used). For CFS, daily presence was assessed for the full recording time: 18 min for 2008–2009 and 14 min for 2010–2012. To ensure that no bias was introduced due to differences in the number of minutes used for each location, 25% of data from each year was reanalysed. Fin whale detection results remained the same — at most only a few hours with detections each year were missed when sampling intervals were shorter. Based on these results, this is not considered to be a substantial issue. From the detection results described above, weekly averages were produced for both species at each location.

2.3. Temporal shifts in acoustic presence: model approach

For WFS, acoustic data were available for 7 years within a 10 yr period (from 2008 to 2018) allowing for investigation of possible temporal shifts in seasonal acoustic presence. Generalised additive models (GAMs) were fitted using the mgcv package (Wood 2011) in R (version 3.3.2; R Core Team 2016) to determine whether there were differences in call rates (calls per hour per day) between years. GAMs were selected as the best method to explore these data because they allow nonlinear relationships between predictor variables (in this case day, year, or period). Recordings started in September each year and lasted until the following August, except for 2012–13 and 2013–14 when recordings lasted only until April and in 2008–09 when recording continued until September 2009 (see Table 1). Temporal autocorrelation was examined using a first order autoregressive model (corAR1) structure in the model. As temporal autocorrelation was low (phi < 0.2), this term was not included in the final model selection.

Possible temporal shifts in acoustic presence were investigated by dividing the available data into 2 periods: early (data from 2008–2014) and more recent (data from 2015–2018). This division was considered to be the best way to split the 7 years of available data into 2 approximately equal data sets (4 data collection years in the early period and 3 in the latter period). A GAM was fitted with the response variable calls per hour (raw count, not standardised) and the predictor variables day and period. The variable day was included as a thin-plate spline smooth term and period as a 'by' factor variable within the smooth term to create separate smooth curves of day for each period (see Wood 2021 for more detail). Because the duty cycle varied between years (see Table 1), an offset term with variable time was included in the model. The distribution family used for this model was Tweedie (Tweedie 1984). Tweedie is a flexible distribution that can be used for different types of count data and is suitable for zero-inflated data (Wood et al. 2016). Tweedie behaves like a Poisson distribution if the P parameter equals 1, or can adopt a Gamma distribution when P equals 2. When using Tweedie in GAMs, the parameter P is automatically estimated by the model. The function predict.gam in the mgcv package was used to predict and compare call detections between the early and more recent periods.

To examine intra-annual patterns in acoustic presence, data for each year from WFS were divided into 2 periods: September to December (autumn/early winter) and April to August (September for 2009; spring/summer). This division made it possible to exclude months with no detections (zeros in data set) given that instrument turn-around (changing batteries and redeploying the unit) usually occurred during September each year. A GAM with the response variable calls per hour (raw count, non-standardised) and the predictor variables day and year was fitted separately for these 2 time periods. The variable day was included as a thin-plate spline smooth term and year as a 'by' variable within the smooth term, so that a separate smooth term was made for each year. An offset term with variable time was again included in the model. The distribution family used for these models was Tweedie. After fitting the models, the function predict.gam was used to compare the call rates among years.

2.4. Distance to ice edge calculations

Because the presence of sea ice has been suggested as an environmental feature that excludes subarctic whales from the Arctic during seasons with heavy ice cover, daily sea ice extent images (Sea Ice Index data) were downloaded from NSIDC (Fetterer et al. 2017) and used to calculate minimum distance (km) from the mooring location to the ice edge (defined by the minimum 15% concentration contour, NSIDC). Daily GeoTIFF files for the Northern Hemisphere were downloaded for each recording period and processed in R using the rgdal and raster packages (Bivand et al. 2020 and Hijmans 2020, respectively). Positive distances to the ice edge indicate the mooring was ice covered, whereas negative distances indicate the mooring was in open water.

2.5. Detection distance estimation

To obtain estimates of the range of distances over which blue and fin whale calls could be detected, the parabolic equation range-dependent acoustic model (Collins 1993) was used in Matlab R2012b (MathWorks Inc.) to model transmission loss in September. This month was selected as it was the month with the most consistent detections for both blue and fin whales. The purpose of this exercise was to provide maximum detection distances over which individually distinct calls could be detected, not conduct an in-depth study of propagation loss in the study area. For blue whales, a frequency of 16 Hz and a source level of 179 dB re 1 µPa (Samaran et al. 2010)[1] was used. For fin whales a frequency of 20 Hz and a source level (SL) of 171 dB re 1 µPa (Charif et al. 2002) was used. It was assumed that both species vocalized at 30 m depth (Lewis et al. 2018). Minimum estimates of noise levels (NL) for each location were obtained: WFS 77 dB at 16 Hz and 79 dB at 20 Hz (Ahonen et al. 2017, this study), CFS 77 dB at 16 Hz and 78 at 20 Hz (Klinck et al. 2012) and Atwain 76 dB at 16Hz and 74 dB at 20 Hz (this study). Because these values were all within 5 dB of each other, NLs of 77 dB at 16 Hz and 78 dB at 20 Hz were used. Sediment composition and sound speeds were obtained for Fram Strait from Hebbeln & Berner (1993). Critical (CR) values of 6 dB for blue whales and 10 dB for fin whales were set to achieve minimum signal-to-noise ratio for detectable calls. These CR values were estimated by selecting 15 blue and 15 fin whale calls from the data set that were just above the detection threshold and calculating signal-to-noise ratios for these calls. Transmission loss (TL) plots from September were examined to determine the maximum distance over which calls could be detected based on noise levels at each location. For blue whales, the cutoff level was the distance at which propagation loss was less than 96 dB (SL – (NL + CR) = 179 – 83) and for fin whales this was 83 dB (171 – 88). For a blue whale calling at 30 m depth, the maximum detection distance was ~100 km in deep water in mid-Fram Strait, but only 60 km near the shelf. For fin whales, these distances were 55 and 30 km, respectively.

3. RESULTS

3.1. Seasonal occurrence of blue whale calls

Across the study period, blue whale calls were detected in all sampling locations during the months of July, August, September and October (Fig. 2). Call detections varied across years in each location. Acoustic signals occurred in bouts that lasted hours to days. However, only at CFS (in 2010 and 2011) were blue whales vocal continuously over extended periods, i.e. nearly every day, from August through September (Fig. 3).

3.1.1. Western and central Fram Strait

Across all years, most blue whale call detections occurred from August through October at both Fram Strait locations (Figs. 2A,B & 3). Blue whale call detections were absent between November and May in CFS. In WFS, calls were absent between January and March and rare in November, December, April and May. In WFS, there was no clear pattern in weekly averages (Fig. 2A). Overall, 2010 and 2011 had the fewest detections (Fig. 2A). In 2016 and 2018, blue whale calls were detected more frequently as early as June, whereas in the earlier years for which summer data were available, frequent detections were mainly from August onwards (Figs. 2A & 3). In 2017, blue whale calls were detected until early November (Figs. 2A & 3). In CFS, 2010 and 2011 had considerably more detections than 2008 (Figs. 2B & 3). Blue whale detections were sparse during June and July at CFS. There were only 3 days with detections in June 2009 and no detections in July 2009 or June 2011. In July 2011, there were 15 days with blue whale call detections, but with weekly averages of fewer than 2 calls per hour (Figs. 2B & 3). Unfortunately, temporal overlap in sampling at the WFS and CFS sites during months with blue whale detections was limited, restricting comparison between these locations (Figs. 2A,B & 3). However, in general, the highest weekly averages in CFS were concentrated over a shorter season (August through September) than those in WFS (August through October). The year and site with the greatest occurrence of blue whale calls was CFS in 2010 and 2011, whereas WFS had the lowest number of blue whale call detections in 2010 and 2011.

3.1.2. Atwain

At Atwain, blue whale calls were recorded intermittently from July to October, with detections on 10 or fewer days each month (Fig. 3). Summer data (from June through August) were only available for 2016, whereas autumn data (from Septem-

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[1] The source level for Antarctic blue whales was used in the absence of source levels for North Atlantic blue whales based on the characteristics of the signal and the relative size of the animals. We are assuming that similarly sized species might have similar sound production mechanisms. More importantly, both Atlantic and Antarctic blue whales make calls with similar characteristics – frequency modulated with songs composed of variations of a single note

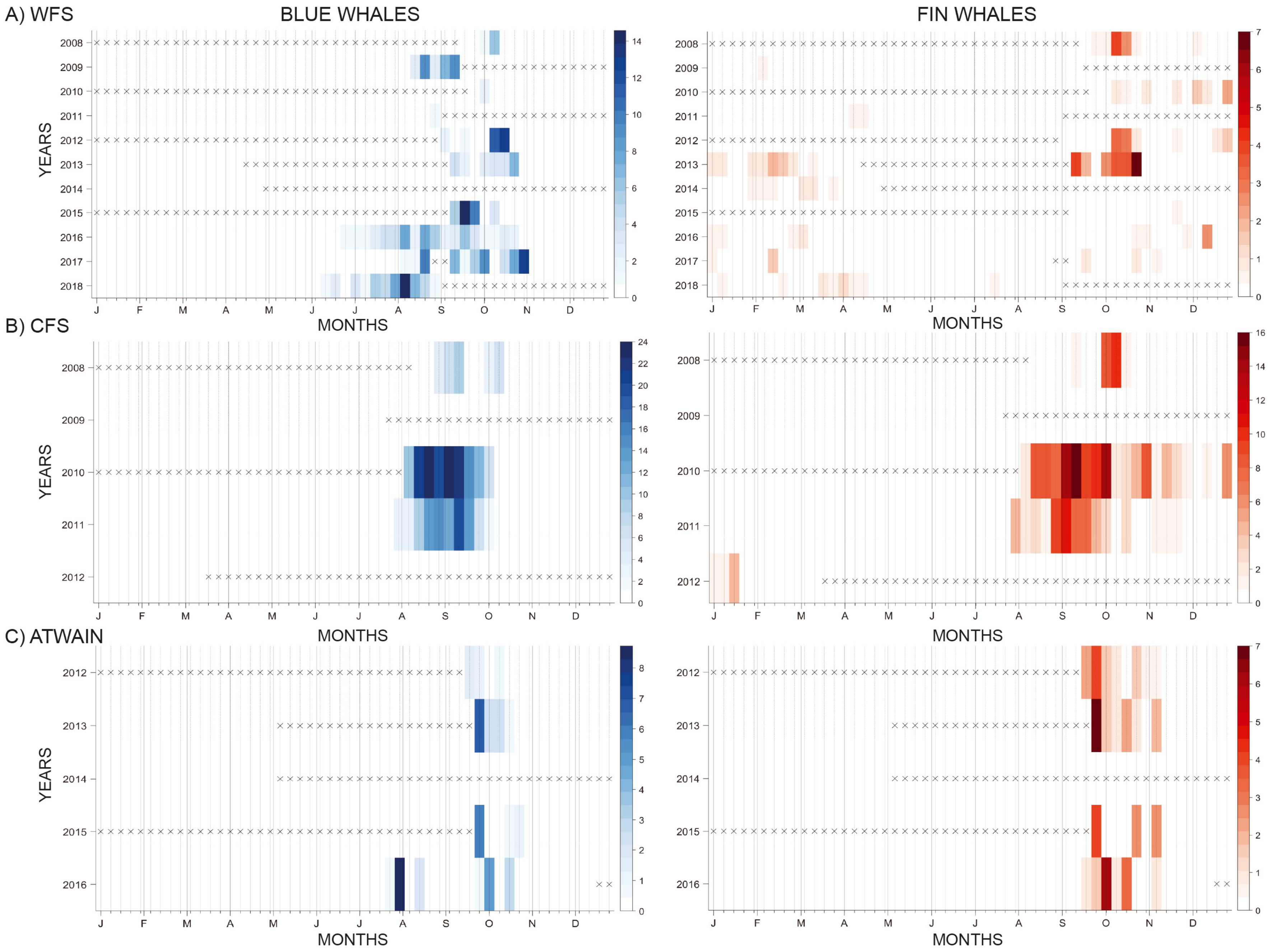

Fig. 2. Weekly mean call rates by location and year for blue whales and fin whales at (A) western Fram Strait (WFS), (B) central Fram Strait (CFS) and (C) Atwain. Vertical lines indicate divisions between months (major ticks) and weeks (minor ticks). Crosses indicate time periods with no available data. Colour intensity indicates the average number of calls detected per week. Note that colour scale differs between locations and species. Only years where data was collected are presented, resulting in different *y*-axis scales between locations

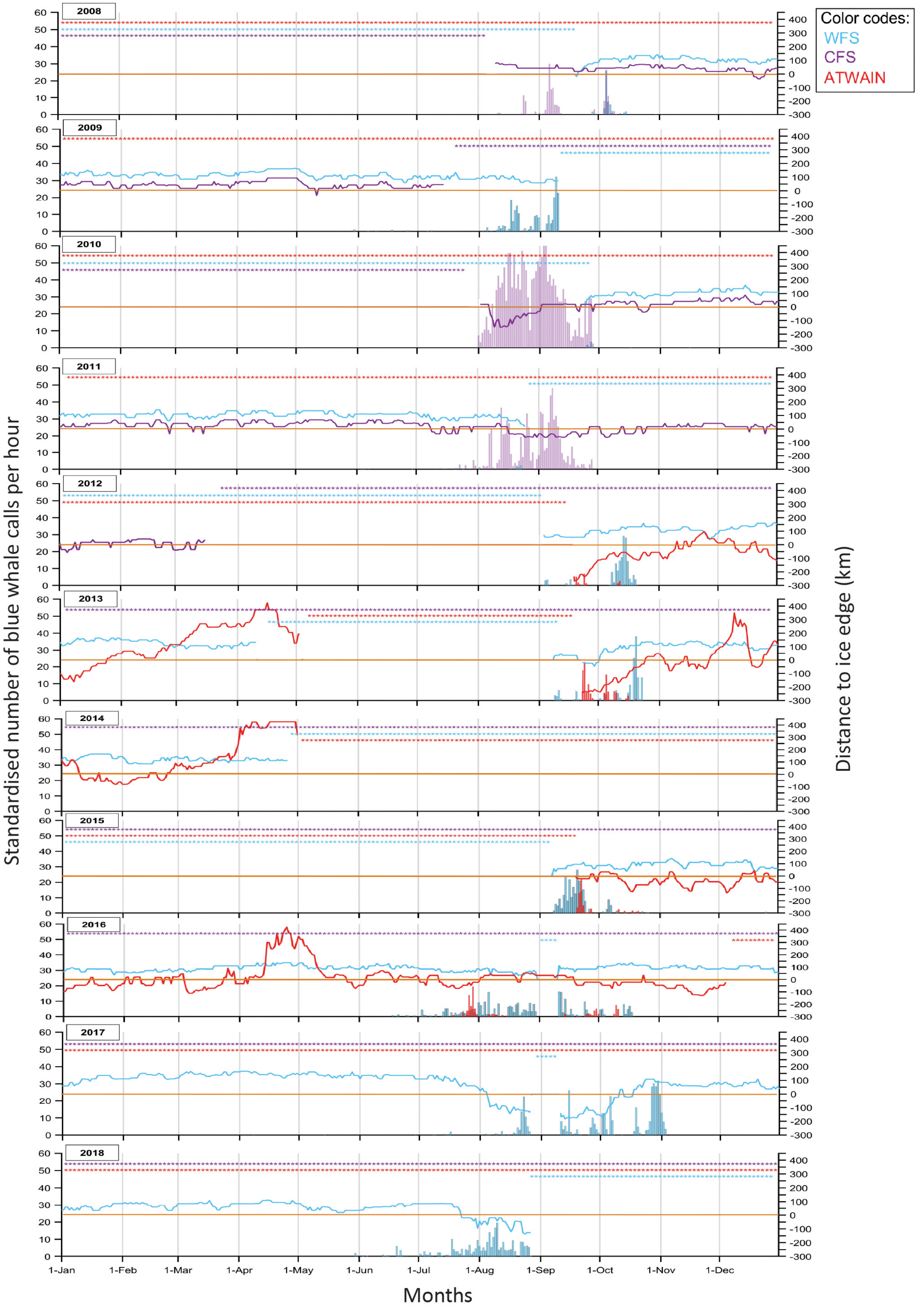

Fig. 3. Daily blue whale call detections (bars) and distance to ice edge (km; lines) for western Fram Strait (WFS; blue), central Fram Strait (CFS; purple) and for Atwain (red) for 2008–2018. Negative distance to ice edge indicates the mooring was in open water and positive distance indicates the mooring was ice-covered. Stars indicate data were not available

ber through November) were available for 4 years. Autumn 2012 had the fewest blue whale detections. Weekly averages did not reveal any obvious pattern over the different years (Fig. 2C). Peak detections during autumn varied from mid-September to the beginning of October and during the year with summer data, the peak detection rate occurred in August.

3.2. Temporal shift in blue whale call occurrence in WFS

Seven years of data over a period of 10 yr from WFS allowed for examination of potential temporal changes in blue whale call detections over a decade. There was a clear shift in blue whale call detections over time, with an increasing number of calls in more recent years (2015–2018) than in earlier years (2008–2014), a seasonal shift toward calling earlier in the summer and a somewhat less prominent extension later into the autumn (Fig. 4 shows GAM results for the 2 periods; see also Fig. 3 for finer scale, monthly and annual patterns).

For the period September to December (autumn/early winter) in 2008, the peak in call detection occurred towards the end of the first week and start of the second week of October (Fig. 5A). In 2012 and 2013, the timing of this peak was similar to 2008, but call rates were clearly higher than in 2008 and calling extended later into October. In autumn 2015 and 2016, call rate was higher in September than in October. In contrast, in autumn 2017, the peak in call rate occurred in mid-October, with calling extending into November. The number of calls per hour was clearly higher during the late October–early November period in 2017 than in other years.

For the period April to September (spring/summer), there were no data for 2013 or 2014. However, in 2011 this period had clearly fewer call detections than the other 4 years and no clear peak call rate was observed (Fig. 5B). The number of calls per hour increased from the end of July through August and peaked in September in 2009. The call detection pattern in 2017 was fairly similar to that in 2009, but the number of calls was higher in August 2017 than in the same month in 2009. In 2016 and 2018, a very different pattern was observed than in other years, with call detections increasing in the beginning of June and being clearly higher than the other years until mid-August.

3.3. Seasonal occurrence of fin whale 20 Hz calls

Fin whale calls were detected seasonally in CFS and Atwain (summer/autumn), whereas in WFS they were detected intermittently throughout much of the year (Figs. 2 & 6). At all locations, individual loud fin whale signals occurred in bouts that lasted from hours to a few days.

3.3.1. Western and Central Fram Strait

Detections of fin whale 20 Hz calls varied between the 2 Fram Strait locations. At WFS, fin whale calls were detected throughout much of the year, though intermittently (not daily or weekly) and at very low levels (<5 h d^{-1}). No clear seasonal or temporal pattern was detected at this site (Fig. 2A). At CFS, fin whale call detections had a clearer seasonal pattern and there were more hours per day with detections in peak periods (up to 23 h d^{-1}). Most fin whale call detections occurred from July through December, with peak occurrences in August and October (Fig. 2B). However, in January 2012 there were 11 days with detections (Fig. 6). Overall, the 2010–2012 recording period had more detections than 2008–2009. Similar to the situation for blue whales, CFS and WFS are not directly comparable due to different recording dates. However, when both locations had data, CFS had many more fin whale call detections and longer calling bouts than WFS (Figs. 2A,B & 6).

3.3.2. Atwain

At Atwain, fin whale calls were detected from the start of each sampling period (mid-September) through until early November (Fig. 2C). No calls were detected between December and July. Summer data (from June through August) was only available for 2016; however, no detections occurred in June or July and only 2 days in August had fin whale calls (Fig. 6). Weekly averages did not reveal any consistent seasonal pattern over different years and peak detection times varied between years (Fig. 2C).

3.4. Temporal shift in fin whale call occurrence in WFS

Fin whale calls were detected intermittently throughout most sampling periods in all years in

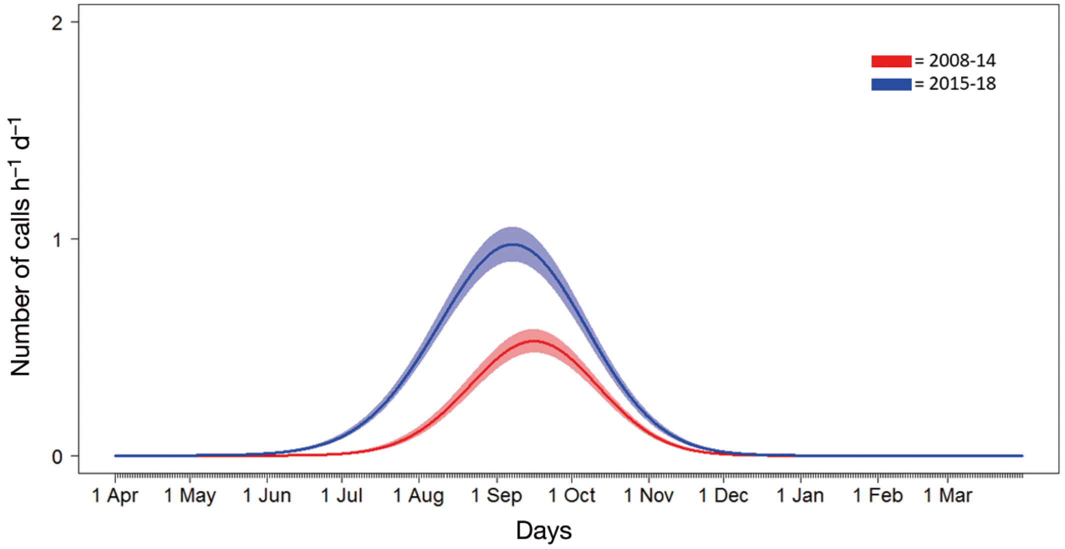

Fig. 4. Generalised additive model results for blue whales at western Fram Strait (WFS), predicting the hourly rate of vocalisations (per day) for early (2008–14) and more recent (2015–18) periods. Shaded area shows 95% confidence interval

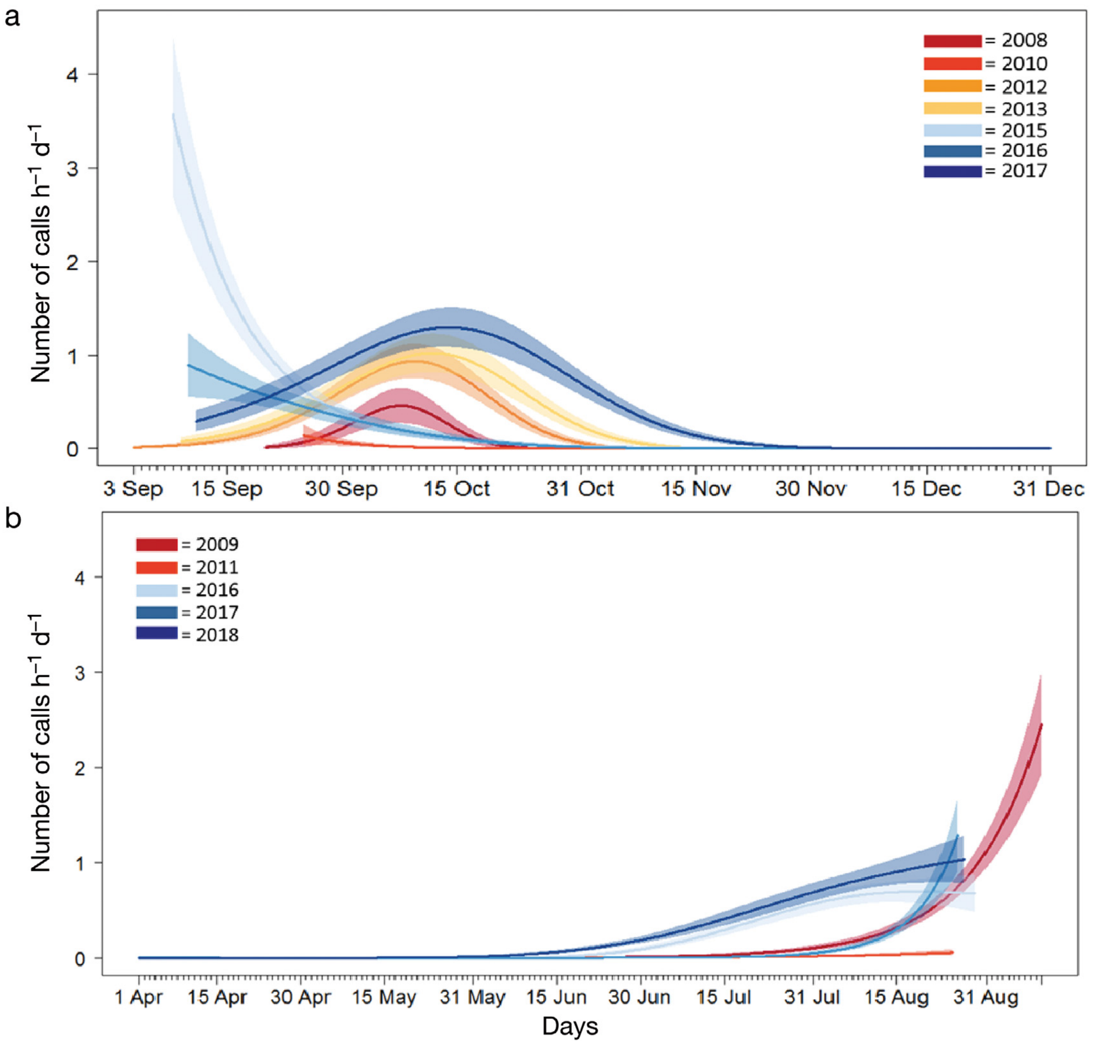

Fig. 5. Generalised additive model results for blue whales at western Fram Strait (WFS) predicting the hourly rate of vocalisations (per day) in each year during (A) September to December and (B) April to September. There were no data for April to September in 2013 or 2014. Shaded area shows 95% confidence interval

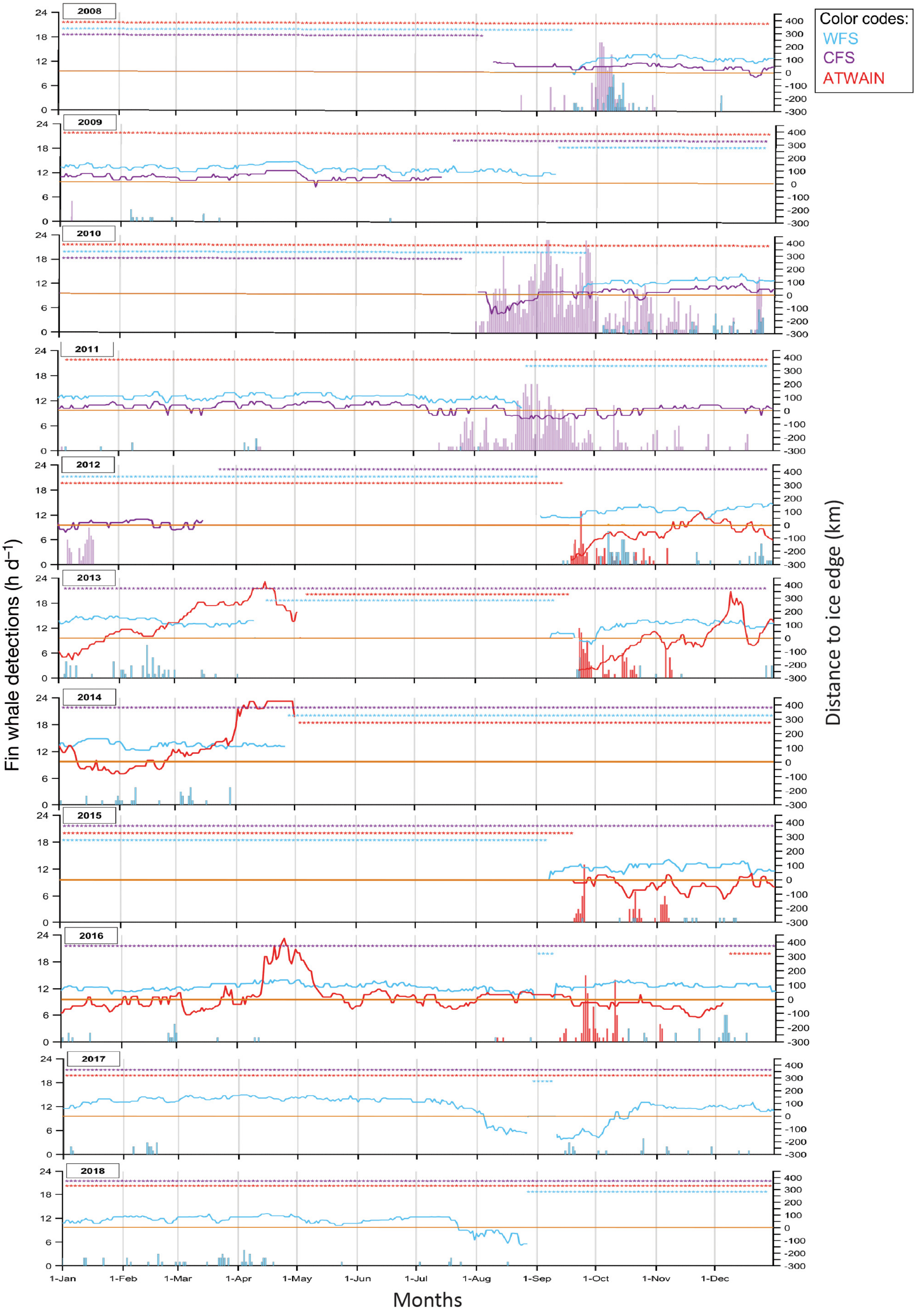

Fig. 6. Number of hours per day with at least one fin whale call (bars) and distance to ice edge (km; lines) for western Fram Strait (WFS; blue), central Fram Strait (CFS; purple) and for Atwain (red) for 2008–2018. Negative distance to ice edge indicates the mooring was in open water and positive distance indicates the mooring was ice-covered. Stars indicate data were not available

WFS. However, no clear seasonal and/or temporal patterns in call detections were found (Fig. 6).

3.5. Distance to ice edge and detection of blue and fin whale calls

No clear patterns were seen regarding distance to the ice edge and occurrence of blue and fin whale call detections at any of the sampling sites (Figs. 3 & 6). However, ice edge plots showed that the ice edge was much closer to the mooring site at CFS than WFS (Fig. 3) and that CFS had more periods when the mooring was in open water (negative distance). Until recently, the WFS site has been ice-covered throughout the year; however, in 2017 between August and the beginning of October and in 2018 between the end of July and the end of August, the mooring was in open water. Distance to the ice edge varied considerably between months and years at Atwain during the data collection period. However overall, April seemed to be the month with the largest distance to ice edge.

4. DISCUSSION

This is the first multi-year study investigating acoustic presence of blue and fin whales in the Northeast Atlantic High Arctic. The PAM devices in this study sampled Fram Strait, the main gateway from the Atlantic Ocean to the Arctic Ocean, and a drift ice environment north of the Svalbard Archipelago above 81° N (Atwain). All 3 recording sites are in areas heavily impacted by global warming (e.g. Lind & Ingvaldsen 2012, Laidre et al. 2015).

Detections of blue whale calls in Fram Strait between June and November have previously been reported (Klinck et al. 2012, Moore et al. 2012, Haver et al. 2017). However, no previous studies included data from multiple years and, until the present effort, no PAM studies have been conducted further north than Fram Strait in the Northeast Atlantic Arctic. Visual surveys have been the only source of distribution and abundance information for these northern areas (Moore et al. 2019). In general, blue whale observations during visual ship-based surveys have been rare in this region (Øien 2009, Pike et al. 2009). However, a recent study that included 13 yr of cetacean sighting data (collected between 2002 and 2014 from various citizen science sources; see Storrie et al. 2018) from around the Svalbard Archipelago suggested an increase in numbers of observations in recent years, although it is important to note that tourist operations also increased in the region during the study period. But visual sightings are limited to months with enough daylight (March through November) and misidentification of species during visual surveys can lead to negative bias in blue whale observations and estimates (Pike et al. 2019). However, since blue whales are known to vocalise throughout the year and the identification of stereotypic low-frequency calls is relatively reliable, detected acoustic presence can be considered a good proxy of overall occurrence for this species. The estimates of the range of distances over which blue whales can be heard placed these animals a maximum of 100 km away (i.e. close to the mooring locations). Blue whales were detected seasonally at all 3 sampling locations, with most detections occurring in late summer/early autumn. Furthermore, acoustic data collected over a 10 yr period from the WFS site revealed an extended temporal presence of blue whales in recent years compared to earlier. GAM models showed that 2015–2018 had clearly higher numbers of blue whale calls per hour and that call rates increased almost a month earlier (mid-June) than 2008–2014. A temporal shift in autumn was not as clear; however, in 2017 calling bouts extended into November. Prior to 2017, blue whale calls were mainly detected only until mid-October and at considerably lower rates (Fig. 5A). Future studies are needed to verify this possible later departure of blue whales from Fram Strait. At all sampling locations, blue whales were absent from late autumn until early summer, so this species remains a seasonal migrant to the Northeast Atlantic High Arctic.

Similar to blue whales, fin whale calling has not been studied extensively in the Northeast Atlantic High Arctic. Fin whale chorusing (overlapping fin whale calls resulting in a continuous noise band) has been documented between September and March in central Fram Strait (Klinck et al. 2012, Haver et al. 2017). These studies relied on a ‘fin index’ (Širović et al. 2004, Nieukirk et al. 2012), which compares energy in the fin whale band to surrounding noise bands. However, this method detects chorus signals that can be hundreds to thousands of km away from the recorder. In addition, this method does not always distinguish between airgun signals and fin whale chorus signals. A previous study of the underwater soundscape in WFS reported fin whale 20 Hz chorusing between September and March (Ahonen et al. 2017). This study relied on the detection of fin whale signals within the 20 Hz energy band (and not individual 20 Hz calls). To be sure that fin whales were actually located close to the PAM sites, only loud, distinct individual calls were explored in the present study. This is likely why there was a lower daily presence and a shorter/different season reported herein than in Klinck et al. (2012) or Ahonen et al. (2017). The choice of method (chorus versus individual calls) is driven by the overall scientific questions being asked in different studies. Certainly, determining chorus is a much quicker, less labour-intensive method than detecting individual 20 Hz signals for fin whales. However, for this study, the interest was in the localized presence of fin whales (tens of km from the mooring versus many hundreds of km); therefore, the detection of individual pulses was selected.

Interestingly, the current study shows very different detection patterns for WFS and CFS. In WFS, individual fin whale calls were detected intermittently at low levels almost year-round, whereas in CFS, detections of fin whale calls were much more seasonal and more abundant (July through December). The WFS mooring was positioned within the East Greenland Current, which transports cold polar water southwards, while the CFS mooring was located in warmer Atlantic waters (Stafford et al. 2012). The western side of Fram Strait is seldom completely free of ice and is often covered with heavy sea ice, whereas ice conditions can vary greatly over short time periods at the CFS site (Stafford et al. 2012). However, ice conditions are generally lighter and distance to the ice edge is much shorter in CFS than in WFS (see for example Fig. 3). It is likely that fin whales prefer the open water conditions and warmer temperatures found in CFS, but this does not explain why fin whales are more seasonal in CFS. What determines their low-level interest year-round at WFS, despite the cold temperatures in this area, remains unknown.

Ship-based visual surveys conducted in Norwegian Arctic waters have shown that fin whales are most often sighted west of Spitsbergen, along Eggakanten (the shelf edge), and are increasing in abundance (NAMMCO 2019b). Storrie et al. (2018) reported that fin whales were sighted around the Svalbard Archipelago and as far north as 81.5° N, but they have not been reported as far east as Atwain previously (Vacquié-Garcia et al. 2017, Storrie et al. 2018; Norwegian Polar Institute's Svalbard Marine Mammal Sighting Database, https://data.npolar.no/sighting/). In the present study, a seasonal pattern in acoustic detections of fin whales was seen at the Atwain site from September until mid-November. Fin whales seem to leave this High Arctic location a few weeks later than blue whales and also arrive later than blue whales. However, only 1 yr of summer data was available for Atwain so further information is needed to verify whether later arrival times are a trend.

Although fin whales were seasonally detected in CFS and Atwain, the fact that individual calls were detected throughout much of the year in WFS confirms that some fin whales are staying at high latitudes throughout the year. This is also supported by results from a recent, novel tracking study in Svalbard, where 40% of tagged animals did not initiate southwesterly migrations during their tracking periods (September–November; Lydersen et al. 2020). In Davis Strait, fin whales are acoustically present until January (Simon et al. 2010) and there was a negative correlation between fin whale calling and sea ice cover, suggesting that they migrated when sea ice formed. In the current study, no clear pattern emerged between distance to ice edge and fin whale call detections, but the increasingly open, drift-ice nature of the ice cover in Fram Strait likely facilitates better conditions for these whales, which are not ice-adapted in the same manner as the Arctic endemic cetaceans.

Sea ice loss in the Arctic is one of the most visible climate-induced changes on the globe (Notz & Stroeve 2016). With the loss of sea ice, there is potential for spatial and temporal increases in habitat for seasonally migrating temperate cetaceans (Moore 2018, Stafford 2019). The Barents/Greenland Sea region is an Arctic 'hot spot', experiencing some of the most rapid declines in the seasonal extent of sea ice in the Arctic, driven in part by higher atmospheric and ocean temperatures (Kelly et al. 2010, Pavlov et al. 2013, Nordli et al. 2014, Onarheim et al. 2014, Laidre et al. 2015). A recent study by Storrie et al. (2018) found signs of northward range expansions in seasonally resident species such as blue and fin whales in Svalbard waters. These findings follow a broader pattern of range expansions of marine animals that has been described as Atlantication or borealization of the North Atlantic/Barents Sea region, associated with increasing water temperatures and decreasing sea ice across the North Atlantic (e.g. MacLeod et al. 2005, MacLeod 2009, Lambert et al. 2014, Fossheim et al. 2015, Vikingsson et al. 2015, Vihtakari et al. 2018, Polyakov et al. 2020). Spatial range expansion could not be investigated with the acoustic data from this study; however, GAM results for WFS suggest a possible temporal/seasonal expansion in blue whale occurrence. The most parsimonious explanation for this is that sea ice loss and warmer waters are making the region more suitable habitat for a longer period in the summer and fall and also causing shifts in prey abundance and availability (Moore et al. 2019). In these times of rapid ecosystem alteration, baleen whales such as blue and fin whales can serve as sentinels of climate change impacts through changes in their phenology, distribution, body condition and abundance (Moore 2018). Passive acoustic sampling is one of the recommended methods to collect data from highly mobile, vocal species such as baleen whales, particularly from remote locations such as High Arctic areas (Moore et al. 2019).

This study provides novel information on acoustic presence of temperate cetaceans in High Arctic waters, information that would be difficult to obtain with traditional survey methods. The Atwain site represents the northernmost acoustic recording of blue and fin whales to date. Additionally, this study shows that blue whales seem to have increased their use of high latitudes by arriving earlier in the year and possibly departing later. Furthermore, this study confirms that at least some fin whales are staying at high latitudes throughout the year, demonstrating the utility of PAM to collect important phenological and distributional information that would otherwise remain unknown.

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LITERATURE CITED

Ahonen H, Stafford KM, de Steur L, Lydersen C, Wiig Ø, Kovacs KM (2017) The underwater soundscape in western Fram Strait: breeding ground of Spitsbergen's endangered bowhead whales. Mar Pollut Bull 123: 97–112

Ahonen H, Stafford KM, Lydersen C, de Steur L, Kovacs KM (2019) A multi-year study of narwhal occurrence in the western Fram Strait — detected via passive acoustic monitoring. Polar Res 38:3468

Bivand R, Keitt T, Rowlingson B (2020) rgdal: bindings for the 'geospatial' data abstraction library. R package version 1.5-16 https://CRAN.R-project.org/package=rgdal

Charif R, Mellinger D, Dunsmore K, Fristrup K, Clark C (2002) Estimated source levels of fin whale (*Balaenoptera physalus*) vocalizations: adjustments for surface interference. Mar Mamm Sci 18:81–98

Clark CW, Berchok CL, Blackwell SB, Hannay DE, Jones J, Ponirakis D, Stafford KM (2015) A year in the acoustic world of bowhead whales in the Bering, Chukchi and Beaufort seas. Prog Oceanogr 136:223–240

Collins MD (1993) A split-step Padé solution for the parabolic equation method. J Acoust Soc Am 93:1736–1742

Cooke JG (2018a) *Balaenoptera musculus* (errata version published in 2019). The IUCN Red List of Threatened Species 2018:e.T2477A156923585. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T2477A156923585.en (accessed 15 Dec 2020)

Cooke JG (2018b) *Balaenoptera physalus*. The IUCN Red List of Threatened Species 2018:e.T2478A50349982. http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T2478A50349982.en (accessed 15 Dec 2020)

Davis GE, Baumgartner MF, Corkeron PJ, Bell J and others (2020) Exploring movement patterns and changing distributions of baleen whales in the western North Atlantic using a decade of passive acoustic data. Glob Change Biol 26:4812–4840

Delarue J, Martin B, Hannay D, Berchok CL (2013) Acoustic occurrence and affiliation of fin whales detected in the northeastern Chukchi Sea, July to October 2007–10. Arctic 66:159–172

Edds P (1982) Vocalizations of the blue whale, *Balaenoptera musculus*, in the St. Lawrence River. J Mammal 63: 345–347

Escajeda E, Stafford KM, Woodgate RA, Laidre KL (2020) Variability in fin whale (*Balaenoptera physalus*) occurrence in the Bering Strait and southern Chukchi Sea in relation to environmental factors. Deep Sea Res II 177: 104782

Fetterer F, Knowles K, Meier W, Savoie M, Windnagel AK (2017) Sea ice index, version 3. National Snow and Ice Data Center, Boulder, CO. http://dx.doi.org/10.7265/N5K072F8 (accessed 15 Jul 2020)

Fossheim M, Primicerio R, Johannesen E, Ingvaldsen RB, Aschan MM, Dolgov AV (2015) Recent warming leads to a rapid borealization of fish communities in the Arctic. Nat Clim Chang 5:673–677

Gaston KJ, Fuller RA (2009) The sizes of species' geographic ranges. J Appl Ecol 46:1–9

Hannay DE, Delarue J, Mouy X, Martin BS, Leary D, Oswald JN, Vallarta J (2013) Marine mammal acoustic detections in the northeastern Chukchi Sea, September 2007–July 2011. Cont Shelf Res 67:127–146

Hauser DD, Laidre KL, Stafford KM, Stern HL, Suydam RS, Richard PR (2017) Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation. Glob Change Biol 23:2206–2217

Haver SM, Klinck H, Nieukirk SL, Matsumoto H, Dziak RP, Miksis-Olds JL (2017) The not-so-silent world: measuring Arctic, Equatorial, and Antarctic soundscapes in the Atlantic Ocean. Deep Sea Res I 122:95–104

Hebbeln D, Berner H (1993) Surface sediment distribution in the Fram Strait. Deep Sea Res I 40:1731–1745

Hijmans RJ (2020) raster: geographic data analysis and modeling. R package version 3.3-13 https://CRAN.R-project.org/package=raster

Irvine LM, Mate BR, Winsor MH, Palacios DM, Bograd SJ, Costa DP, Bailey H (2014) Spatial and temporal occurrence of blue whales off the U.S. west coast, with implications for management. PLOS ONE 9:e102959

Jiménez López MEJ, Palacios DM, Legorreta AJ, Urbán J, Mate R (2019) Fin whale movements in the Gulf of California, Mexico, from satellite telemetry. PLOS ONE 14: e0209324

Kelly B, Bengtson JL, Boveng PL, Cameron MF and others (2010) Status report on ringed seals (*Phoca hispida*). NOAA Technical Memorandum NMFS-AFSC-212. US Dept of Commerce, Springfield, VA

Kinda GB, Simard Y, Gervaise C, Mars JI, Fortier L (2013) Under-ice ambient noise in Eastern Beaufort Sea, Canadian Arctic, and its relation to environmental forcing. J Acoust Soc Am 134:77–87

Klinck H, Nieukirk SL, Mellinger DK, Klinck K, Matsumoto H, Dziak RP (2012) Seasonal presence of cetaceans and ambient noise levels in polar waters of the North Atlantic. J Acoust Soc Am 132:EL176–EL181

Laidre KL, Stern H, Kovacs KM, Lowry L and others (2015) Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conserv Biol 29:724–737

Lambert E, Pierce GJ, Hall K, Brereton T and others (2014) Cetacean range and climate in the eastern North Atlantic: future predictions and implications for conservation. Glob Change Biol 20:1782–1793

Lewis LA, Calambokidis J, Stimpert AK, Fahlbusch J and others (2018) Context-dependent variability in blue whale acoustic behaviour. R Soc Open Sci 5:180241

Lind S, Ingvaldsen RB (2012) Variability and impacts of Atlantic water entering the Barents Sea from the north. Deep Sea Res I 62:70–88

Lydersen C, Vacquiè-Garcia J, Heide-Jørgensen MP, Øien N, Guinet C, Kovacs KM (2020) Autumn movements of fin whales (*Balaenoptera physalus*) from Svalbard, Norway, revealed by satellite tracking. Sci Rep 10:16966

MacLeod CD (2009) Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. Endang Species Res 7:125–136

MacLeod CD, Bannon SM, Pierce GJ, Schweder C, Learmonth JA, Herman JS, Reid RJ (2005) Climate change and the cetacean community of north-west Scotland. Biol Conserv 124:477–483

Mellinger DK, Clark CW (2000) Recognizing transient low-frequency whale sounds by spectrogram correlation. J Acoust Soc Am 107:3518–3529

Mellinger DK, Clark C (2003) Blue whale (*Balaenoptera musculus*) sounds from the North Atlantic. J Acoust Soc Am 114:1108–1119

Moore SE (2018) Climate change. In: Wursing B, Thewissen JGM, Kovacs KM (eds) Encyclopedia of marine mammals, 3rd edn. Academic Press, Cambridge, p 194–197

Moore SE, Stafford KM, Melling H, Berchok C, Wiig Ø, Kovacs KM, Richter-Menge J (2012) Comparing marine mammal acoustic habitats in Atlantic and Pacific sectors of the High Arctic: year-long records from Fram Strait and the Chukchi Plateau. Polar Biol 35:475–480

Moore SE, Haug T, Vikingsson GA, Stenson GB (2019) Baleen whale ecology in arctic and subarctic seas in an era of rapid habitat alteration. Prog Oceanogr 176: 102118

Morano JL, Salisbury DP, Rice AN, Conklin KL, Falk KL, Clark CW (2012) Seasonal and geographical patterns of fin whale song in the western North Atlantic Ocean. J Acoust Soc Am 132:1207–1212

NAMMCO (North Atlantic Marine Mammal Commission) (2019a) Catch database. https://nammco.no/topics/catch-database/ (accessed on 16 March 2020)

NAMMCO (North Atlantic Marine Mammal Commission) (2019b) Report of the Abundance Estimates Working Group, October 2019, Tromsø, Norway. https://nammco.no/topics/abundance_estimates_reports/

Nieukirk SL, Mellinger DK, Moore SE, Klinck K, Dziak RP, Goslin J (2012) Sounds from airguns and fin whales recorded in the mid-Atlantic Ocean, 1999–2009. J Acoust Soc Am 131:1102–1112

Nordli Ø, Przybylak R, Ogilvie AEJ, Isaksen K (2014) Long-term temperature trends and variability on Spitsbergen: the extended Svalbard Airport temperature series, 1898-2012. Polar Res 33:21349

Notz D, Stroeve J (2016) Observed Arctic sea-ice loss directly follows anthropogenic CO2 emission. Science 354:747–750

Øien N (2009) Distribution and abundance of large whales in Norwegian and adjacent waters based on ship surveys 1995-2001. NAMMCO Sci Publ 7:31–47

Onarheim IH, Smedsrud LH, Invaldsen R, Nilsen F (2014) Loss of sea ice during winter north of Svalbard. Tellus, Ser A, Dyn Meterol Oceanogr 66:23933

Palacios DM, Bailey H, Becker EA, Bograd SJ and others (2019) Ecological correlates of blue whale movement behavior and its predictability in the California Current Ecosystem during the summer-fall feeding season. Mov Ecol 7:26

Pavlov AK, Tverberg V, Ivanov BV, Nilsen F, Falk-Petersen S, Granskog MA (2013) Warming of Atlantic Water in two west Spitsbergen fjords over the last century (1912-2009). Polar Res 32:11206

Pérez-Jorge S, Tobeña M, Prieto R, Vandeperre F, Calmettes B, Lehodey P, Silva MA (2020) Environmental drivers of large-scale movements of baleen whales in the mid-North Atlantic Ocean. Divers Distrib 26:683–698

Pike DG, Vikingsson GA, Gunnlaugsson T, Øien N (2009) A note on the distribution and abundance of blue whales (*Balaenoptera musculus*) in the Central and Northeast North Atlantic. NAMMCO Sci Publ 7:19–30

Pike DG, Gunnlaugsson T, Mikkelsen B, Halldórsson SD, Víkingsson GA (2019) Estimates of the abundance of cetaceans in the central North Atlantic based on the NASS Icelandic and Faroese shipboard surveys conducted in 2015. NAMMCO Sci Publ 11, https://doi.org/10.7557/3.4941

Polyakov IV, Alkire MB, Bluhm BA, Brown KA and others (2020) Borealization of the Arctic Ocean in response to anomalous advection from sub-Arctic seas. Front Mar Sci 7:1–32

R Core Team (2016) R: a language and environment for statistical computing. R: Foundation for Statistical Computing, Vienna

Samaran F, Adam O, Guinet C (2010) Detection range modeling of blue whale calls in Southwestern Indian Ocean. Appl Acoust 71:1099–1106

Shabangu FW, Findlay KP, Yemane D, Stafford KM, van den Berg M, Blows B, Andrew RK (2019) Seasonal occurrence and diel calling behaviour of Antarctic blue whales and fin whales in relation to environmental conditions off the west coast of South Africa. J Mar Syst 190:25–39

Silva MA, Prieto R, Jonsen I, Baumgartner MF, Santos RS (2013) North Atlantic blue and fin whales suspend their spring migration to forage in middle latitudes: building up energy reserves for the journey? PLOS ONE 8:e76507

Simon M, Stafford KM, Beedholm K, Lee CM, Madsen PT (2010) Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging. J Acoust Soc Am 128:3200–3210

Širović A, Hildebrand JA, Wiggins SM, McDonald MA, Moore SE, Thiele D (2004) Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. Deep Sea Res II 51:2327–2344

Širović A, Hildebrand JA, Wiggins SM, Thiele D (2009) Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. Mar Mamm Sci 25:125–136

Stafford KM (2019) Increasing detections of killer whales (*Orcinus orca*), in the Pacific Arctic. Mar Mamm Sci 35:696–706

Stafford KM, Nieukirk SL, Fox CG (2001) Geographic and seasonal variation of blue whale calls in the North Pacific. J Cetacean Res Manag 3:65–76

Stafford KM, Mellinger DK, Moore SE, Fox CG (2007) Seasonal variability and detection range modeling of baleen whale calls in the Gulf of Alaska, 1999–2002. J Acoust Soc Am 122:3378–3390

Stafford KM, Moore SE, Stabeno PJ, Holliday DV, Napp JM, Mellinger DK (2010) Biophysical ocean observation in the southeastern Bering Sea. Geophys Res Lett 37:L02606

Stafford KM, Moore SE, Berchok CL, Wiig Ø and others (2012) Spitsbergen's endangered bowhead whales sing through the polar night. Endang Species Res 18:95–103

Stafford KM, Castellote M, Guerra M, Berchok CL (2018) Seasonal acoustic environments of beluga and bowhead whale core-use regions in the Pacific Arctic. Deep Sea Res II 152:108–120

Storrie L, Lydersen C, Andersen M, Wynn RB, Kovacs KM (2018) Determining the species assemblage and habitat use of cetaceans in the Svalbard Archipelago, based on observations from 2002 to 2014. Polar Res 37:1463065

Thomisch K, Boebel O, Clark CW, Hagen W, Spiesecke S, Zitterbart DP, Van Opzeeland I (2016) Spatio-temporal patterns in acoustic presence and distribution of Antarctic blue whales *Balaenoptera musculus intermedia* in the Weddell Sea. Endang Species Res 30:239–253

Tweedie MCK (1984) An index which distinguishes between some important exponential families. In: Ghosh JK, Roy J (eds) Statistics: applications and new directions. Proc Indian Statistical Institute Golden Jubilee International Conference, Calcutta, 27 Sep–1 Oct 1982. Indian Statistical Institute, Calcutta, p 579–604

Vacquié-Garcia J, Lydersen C, Marques TA, Aars J and others (2017) Late summer distribution and abundance of ice-associated whales in the Norwegian High Arctic. Endang Species Res 32:59–70

Vihtakari M, Welcker J, Moe B, Chastel O and others (2018) Black-legged kittiwakes as messengers of Atlantification in the Arctic. Sci Rep 8:1178

Vikingsson GA, Pike DG, Valdimarsson H, Schleimer A and others (2015) Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? Front Ecol Evol 181:36–46

Watkins WA, Tyack P, Moore KE, Bird JE (1987) The 20-Hz signals of finback whales (*Balaenoptera physalus*). J Acoust Soc Am 82:1901–1912

Watkins WA, Daher MA, Reppucci GM, Greorge JE, Martin DL, DiMarzio NA, Gannon DP (2000) Seasonality and distribution of whale calls in the North Pacific. Oceanography (Wash DC) 13:62–67

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J R Stat Soc 73:3–36

Wood SN (2021) Package "mgcv": Mixed GAM computation vehicle with automatic smoothness estimation. https://cran.r-project.org/web/packages/mgcv/mgcv.pdf (accessed on 9 April 2021)

Wood SN, Pya N, Säfken B (2016) Smoothing parameter and model selection for general smooth models. J Am Stat Assoc 111:1548–1563

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