

Singing behavior of fin whales in the Davis Strait with implications for mating, migration and foraging

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Most baleen whales undertake migrations between low-latitude breeding grounds and high-latitude feeding grounds. Though little is known about the timing of their migration from the Arctic, fin whales are assumed to undertake a similar migratory pattern. To address questions about habitat use and migrations, the acoustic activity of fin whales in Davis Strait, between Greenland and Canada, was monitored continuously for two years using three bottom-moored acoustic recorders. The acoustic power in the fin whale call frequencies peaked in November–December, showing that fin whales are present in Davis Strait much later in the year than previously expected. The closely timed peaks in song activity and conception time imply that not all fin whales migrate south to mate, but rather start mating at high latitudes rather than or before migrating. Singing activity was strongly linked to daylight hours, suggesting that fin whales might feed during the few daylight hours of the late fall and early Arctic winter. A negative correlation between the advancing sea ice front and power in fin whale frequencies indicates that future changes in sea ice conditions from global warming might change the distribution and migratory patterns of fin whales near the poles.

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I. INTRODUCTION

Long-range migratory behavior is found in a number of animal species including fish (Jakobsson and Østvedt, 1999), insects (Urquhart and Urquhart, 1977), mammals (Strelkov, 1969) and birds (Salomonsen, 1967). Though many ecological factors influence migratory behavior, seasonal variation in resources is often a major driving force for long distance migrations (Alerstam *et al.*, 2003). That is also believed to be the case for most baleen whale species who undertake long migrations between high latitude, productive feeding grounds during summer and warmer oligotrophic mating/ breeding grounds in the tropics during winter (Kellogg, 1929; Norris, 1967).

Long migratory routes have been mapped for humpback (*Megaptera novaeangliae*), right (*Eubalaena australis* and *E. glacialis*) and gray whales (*Eschrichtius robustus*) with identified high-latitude feeding and low-latitude breeding

grounds (e.g., Bannister *et al.*, 1999; Clapham, 1996; Kraus *et al.*, 1986; Pike, 1962). Discovery tag returns from commercial whaling suggest that blue whales (*Balaenoptera musculus*) and fin whales (*B. physalus*) may undertake similar migrations: feeding at high latitudes during summer and moving to lower latitudes for mating during winter (Kellogg, 1929; Norris, 1967; Mizroch *et al.*, 2009). That notion is supported by acoustic data for fin whales from the Pacific (Stafford *et al.*, 1999), and likely also Antarctica, showing a negative correlation between calling rate and increasing sea ice concentration (Širović *et al.*, 2004, 2009). Although no clear fin whale migratory routes have been identified, a number of studies suggest that most populations migrate between high and low latitudes while a few populations seemingly reside in the same area year-round (Lockyer, 1984; Mizroch *et al.*, 2009).

Fin whales are one of the most abundant cetaceans in the Davis Strait off Western Greenland, where they likely play an important role in an ecosystem that experiences large temporal and spatial fluctuations in primary and secondary production over the year (Laidre *et al.*, 2010). Though the Davis Strait is a fin whale summer feeding ground, little is known about how long and with what purposes other than feeding fin whales use the Davis Strait over the year. This lack of data on fin whales partly stems from difficulties in studying them over sufficiently large temporal and spatial scales. For high latitude populations in particular, harsh weather conditions make it challenging to study habitat use during the autumn and winter, as traditional sighting surveys are not feasible due to low light conditions, sea ice and heavy seas, underlining the need for other experimental methods.

Passive acoustic monitoring (PAM) is increasingly used as a tool to study the presence, relative abundance, migratory movements and behavior of large baleen whales (e.g., Moore *et al.*, 2006; Mellinger *et al.*, 2007). Singing fin whales lend themselves to PAM by producing repetitive, powerful low frequency (LF) 20-Hz pulses. The dominating LF part of the song consists of stereotyped ~ 1 s long down-sweeps centered at 20 Hz (Watkins *et al.*, 1987) that appear in bouts of either single calls or call doublets, repeated for up to many hours at a time with a regular inter-pulse-interval that varies among fin whale stocks (Thompson *et al.*, 1992; Watkins *et al.*, 1987; Clark *et al.*, 2002; Delarue *et al.*, 2009). Other than the LF pulse, the call often also contains a simultaneous high frequency (HF) component. The HF component may vary between populations of fin whales; Eastern Antarctic fin whales have a center frequency of 99 Hz while those near the Western Antarctic Peninsula and the Scotia Sea have a center frequency of 89 Hz (Širović *et al.*, 2004, 2009).

With an estimated source level of 170–190 dB re 1 μ Pa and call production in all the world's ocean basins, the song is believed to serve in long range acoustic communication (Payne and Webb, 1971; Charif *et al.*, 2002; Širović *et al.*, 2007; Thomson and Richardson, 1995). The occurrence of a peak in fin whale song just before the estimated peak conception time (Lockyer, 1984) and the identification of males as singers (Croll *et al.*, 2002), have led to the hypothesis that the song is part of a male mating display (Watkins *et al.*, 1987; Croll *et al.*, 2002).

Diel variation in baleen whale calling rates has been reported from several species and a correlation between feeding, sunlight and calling activity has been proposed (Stafford *et al.*, 2005; Baumgartner and Fratantoni, 2008) although such evidence for fin whales is relatively weak (Watkins *et al.*, 1984, 1987). Blue whales seem to have a clear diel variation in their acoustic activity by producing most B-calls during night and dusk, when prey may be less available to them and using D-calls during day time foraging (Stafford *et al.*, 2005; Wiggins *et al.*, 2005; Oleson *et al.*, 2007). Fin whale calls from Bermuda showed only slight, inconsistent differences in calling rates between day and night (Watkins *et al.*, 1987). However, radio tracking observations suggested that their behavioral states changed between these two light regimes (Watkins *et al.*, 1984).

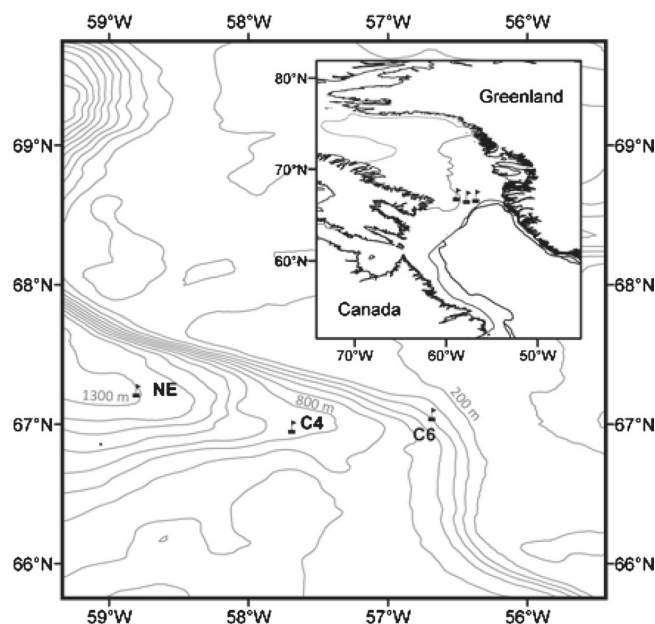


FIG. 1. Locations of the three instruments deployed at 300 m depth in the Davis Strait. The monthly extension of the sea ice edge from November 2006 to March 2007 is shown as lines in the inset map.

Very little is known about how fin whales use Arctic high latitude habitats from October to May and specifically if and why they migrate south. Using continuous passive acoustic monitoring in the Davis Strait from October 2006 to September 2008 we set out to investigate the temporal and spatial patterns of fin whale singing and address implications for fin whale migration, feeding and mating behavior. Here we use patterns in the power of fin whale frequency bands to address questions about how fin whale presence may be influenced by sea ice conditions, and we present the first measurements of fin whale song from the Davis Strait and estimate the difference in the active space of HF and the LF song components. The analysis of long term recordings in a very hostile environment show that singing fin whales are present in the Davis Strait in large numbers until the end of December demonstrating that at least part of the population does not move south in the early fall as expected. Rather they stay in the Davis Strait to use this Arctic habitat as a feeding and/or mating ground even when the dark winter has arrived, and they do not seem to start migrating before the sea ice forms from the north.

II. METHODS

Continuous acoustic recordings were made in the Davis Strait with three autonomous recording devices (HARU-Phone III) from 23 October 2006 to 5 October 2007 (Fig. 1). One of them (C6) was redeployed until 4 September 2008. There was a distance of 45–85 km between the instrument moorings. Each recorder consists of a 16 bit analog to digital converter stored in a 6.5 in. pressure housing (Fox *et al.*, 2001). They were all deployed at 300 m depth as part of a moored oceanographic array in areas with seafloor depths of 400 m (C6), 870 m (C4) and 1300 m (NE) (Fig. 1). All three instruments had a recording sensitivity of -160 dB re 1 V/ μ Pa. They sampled continuously at 2000 Hz with band

pass filtering between 0.1 and 970 Hz. The recordings were saved in 6-h *.dat files and time-marked with an internal clock. Files were converted from the stored big-endian 16 bit binary data to standard *.wav files in Matlab 7.5 (*Math-Works*) for further analysis.

A. Calibration

On-mooring RAFOS sound sources (40 s 5 Hz up-sweep between 777.5 Hz and 782.5 Hz) produced on and received by the NE and C4 moorings were used for calibration. The mean relative received level of sync pulses from mooring NE and recorded on instrument C4 was -52.8 dB re clipping (rms) ($sd=2.5$) and the mean received level of sweeps played by mooring C4 and recorded by instrument NE was -56.4 dB re clipping (rms) ($sd=2.3$).

B. Acoustic analysis of individual calls

Fin whale song in the Davis Strait consists of two elements. A frequency down-sweep centered around 20 Hz (LF) and a higher frequency pulse centered near 130 Hz (HF) [Fig. 2(A)]. From recordings on instrument C6, we selected calls with a signal to noise ratio of >10 dB, and clear HF and LF pulses for further analysis. We measured the inter-pulse-interval (IPI), peak frequency (fp), -10 dB bandwidth (-10 BW) and frequency centroid (fc, defined as the frequency dividing the spectra in two halves of equal energy) of the two call components. The recordings were down sampled with a factor 5 and the analysis was done with bin widths of 0.8 Hz for the HF component (FFT=512) and bin width 0.4 Hz for the LF component (FFT=1024). To estimate the difference in detection range between the HF and LF pulse, the energy flux density levels were computed for both pulses within the same call after band pass filtering (LF: 15–35 Hz and HF: 110–160 Hz with a 2-pole Butterworth filter) in Matlab.

C. Fin whale call detection

The fin whale “20-Hz” call is a commonly recorded animal sound in the North Atlantic (Clark, 1995) and during some months of the year it is so abundant that the calls form a continuous band around 20 Hz in spectrogram displays [Fig. 2(B)], rendering automatic kernel detections futile. Following Širović *et al.* (2004, 2009), we therefore quantified fin whale calls as the power in the frequency band around the fin whale calls relative to surrounding noise bands. Širović *et al.* (2009) made a power analysis on the HF pulse components in the fin whale calls. The LF down-sweep has a fairly constant frequency signature across different geographical areas but the frequency of the HF element clearly varies (Širović *et al.*, 2009). Also, the HF component was often not detectable in our recordings. We therefore opted for a power analysis on the primary pulse, using a frequency band that covered the LF pulse (F_{fin} , 19–28 Hz). To ensure that the power contribution of fin whale calls was measured and not background noise in the F_{fin} frequency band, the summed powers in surrounding frequency bands of 13–17 Hz and 33–37 Hz were also computed, assuming white noise characteristics of the ambient noise from 13 to 37 kHz. The fin

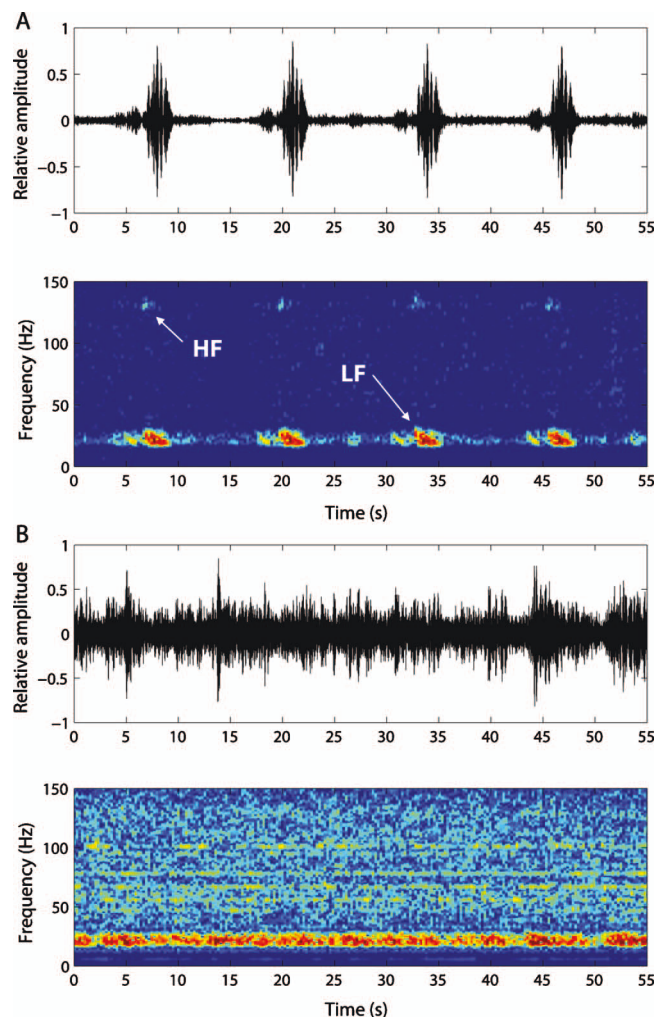


FIG. 2. (A) Time series and spectrogram of fin whale song with clearly separated calls consisting of high frequency (HF) and low frequency (LF) components. The pulses are recorded on top of a band of fin whale songs in the background. (B) Example of a band of LF fin whale signals too closely spaced in time to identify single pulses. FFT size: 2048, 50% overlap, window: 512.

whale call power was subsequently computed as the power level of the fin whale frequency band in 1 s blocks with a 50% overlap (Hann window). The noise power and fin whale signal power was referenced to the grand average of the noise frequency band power (F_{noise}). We chose not to reference the instantaneous F_{fin} to the instantaneous F_{noise} , because it would then not have been possible to discern for instance if an increase in the F_{fin} power relative to F_{noise} power ratio was caused by a decrease in the F_{noise} power or an increase in F_{fin} power. To aid interpretation the power in both the F_{fin} and the F_{noise} frequency bands are displayed in the figures.

D. Sea ice

The daily minimum distance from the mooring position to the sea ice edge was obtained from the National Ice Center, NOAA (<http://www.natice.noaa.gov>). In order to compare the ice data to the calling activity of the fin whales, we first averaged the acoustic power data to a per-day level and then determined the centralized rms-bandwidth of this reduced data set. The critical sampling period, which is the

reciprocal of twice the bandwidth of the time series, was determined to be 5 days. Sea ice data F_{fin} power and F_{noise} power were all averaged into 5 day bins. Using this information, binary data sets were then generated of “fin whales present” and “sea ice present” time bins. A “fin whale present” period was defined as one where F_{fin} power exceeded F_{noise} power in the same time bin. The “sea ice present” data was set to one when the sea ice edge was south of the mooring. When the sea ice edge was north of the mooring position, the sea ice data was set to zero. We then tested the probability of observing the counted number (or less) of coincidences between sea ice and fin whale bins, using a binominal distribution. Also a Pearson’s coefficient of correlation was calculated between distance to the sea ice edge and power in the fin whale frequency band and noise frequency band, respectively (all data sampled in bins of 5 days). As it might well have been the same whale recorded on several recorders we only tested the recording made on mooring C6 where we had data for both 2006 and 2007.

E. Diel variation

To visualize the daily pattern in fin whale calls, the summed power for both frequency bands, F_{fin} and F_{noise} , within 30-min time bins were arranged into a matrix, so that each column represented a single day and each row the individual half hours of the day. The matrices were then displayed as an image with signal power color-coded for comparison with the data for sunrise and sunset for the period in question. The time of sunrise and sunset at the mooring positions were obtained from the U.S. Naval Observatory (<http://aa.usno.navy.mil/index.php>).

The bandwidth of the F_{fin} power data averaged into half-hour bins was determined, and the critical period was in this case determined to be 6 h. However, to have a bin centered on noon, an odd number is called for, and we therefore used three 8-h bins instead. The average F_{fin} power per hour bin was calculated for the peak calling period, 12 November–22 December. A Jarque-Bera two-sided goodness-of-fit test was used to test the hypothesis that the data were not normally distributed, and in one case H_0 was accepted ($P < 0.05$) for the F_{noise} band, therefore a nonparametric analysis of medians was adopted for all data sets. A two-tailed Mann-Whitney U-test on the power data (expressed in dB) was used to test the null-hypothesis that the intensity of the F_{fin} frequency band was the same during the light (bin 2) and dark periods (bin 1 combined with bin 3) of the day. For each station, two control data sets were also created for a similar period delayed by 80 days. These control data sets were treated the same way as the sets recorded during the peak period of intense singing. As the same whale calls might have been recorded on several recorders we only tested the recording made on mooring C6, which had the most powerful F_{fin} signal.

III. RESULTS

A. Fin whale call parameters

Frequency characteristics were measured on a total of 539 fin whale calls recorded in the Davis Strait in ten differ-

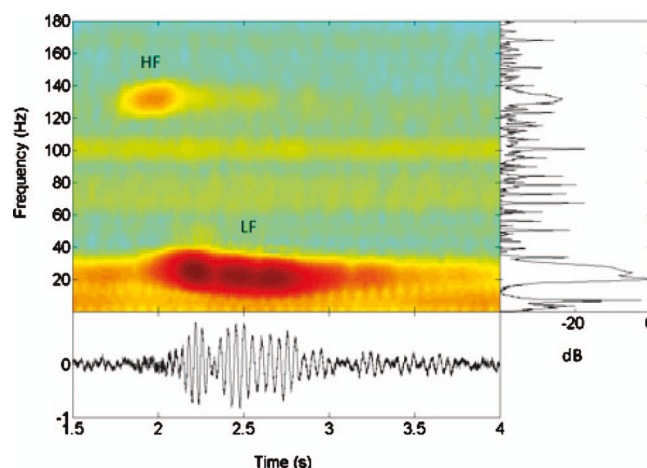


FIG. 3. Spectrogram, waveform and power spectrum of the time aligned average of 50 typical fin whale calls, showing the low frequency down-sweep (LF) and the secondary, lower amplitude high frequency pulse (HF). FFT size: 1024, 94% overlap, Hann window.

ent days between 23 October and 17 November 2006. The LF pulse of the calls (Fig. 3) consists of a 1 s long down-sweep, with a frequency centroid of 22.1 ± 0.63 Hz (mean $\pm$ std), peak frequency of 21.6 ± 1.38 Hz and a -10 dB bandwidth of 6.5 ± 1.28 Hz. The HF component (Fig. 3) consists of a ca. 0.3 s pulse with a frequency centroid of 131.9 ± 1.15 Hz, peak frequency of 132.2 ± 1.38 Hz and a -10 dB bandwidth of 14.8 ± 13.70 Hz. The mean interpulse interval (IPI) was 13.5 ± 2.44 s. There was a large (24.5 ± 2.60 dB) difference in the received energy flux density level between the HF and LF pulses within the same call, with the LF pulse having some 280 times more energy on average.

B. Call detections in Davis Strait

Fin whale calls were detected from June to January, but there was a clear seasonal peak in the frequency band of fin whale calls from November to the end of December [Figs. 4(A)–4(D)]. The F_{fin} peak was especially strong at instrument C6 [Fig. 4(A)], where it formed a peak rising more than 15 dB above the average ambient noise level (F_{noise}) during both years of monitoring. The seasonal peak was also clear at C4, though 5 dB lower than C6 [Fig. 4(B)]. Instruments C4 and C6 were deployed at similar latitudes, but C4 was 45 km further west in water that was 869 m deep (v. 390 m for C6). The seasonal peak in the power of the fin whale song frequency band was present, but weak on instrument NE [Fig. 4(C)]. Instrument NE was deployed about 85 km further north (water depth 1267 m) than C6 and C4 (Fig. 1).

C. Sea ice

The fin whale power peaks in November–December followed by an abrupt decline in December just as the sea ice edge cover the mooring site in both years of the deployment [Fig. 5(A)]. The distance to sea ice edge and the occurrence of fin whale song had a 0.002% probability of not depending on one another (binominal distribution $P = 0.00002$). There

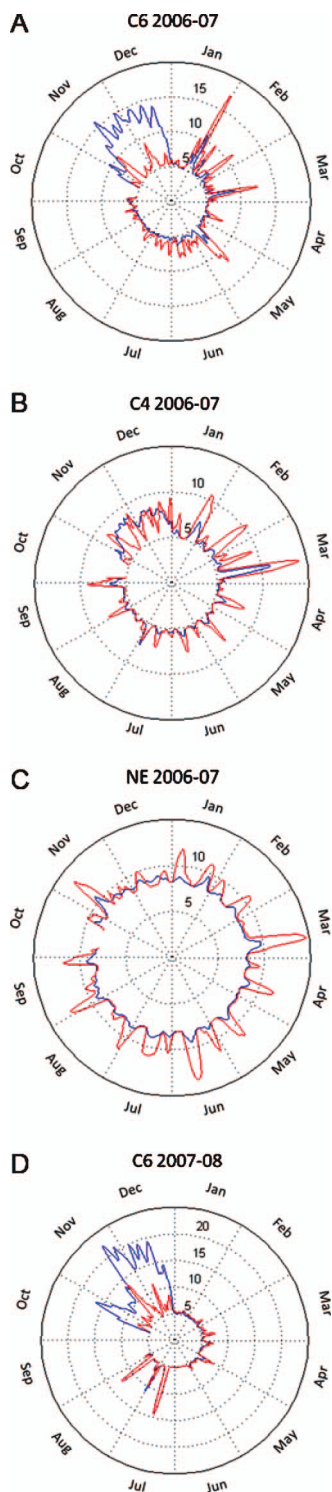


FIG. 4. Power analysis showing the seasonal output of the power in the fin whale frequency band, F_{fin} (blue) and the surrounding noise bands, F_{noise} (red). The power in both are bands expressed relative the yearly grand average of the background noise power.

was no significant correlation between the power in the noise frequency band and the distance to ice edge (Pearson's coefficient of correlation, $N=124$, $P>0.4$) indicating that the correlation between sea ice and fin whale song is not an artifact from noise correlating with formation or advance of sea ice [Figs. 5(A) and 5(B)].

D. Diel variation

During the peak singing period from November to December, all instruments showed a diel pattern in the F_{fin} power [Figs. 6(A)–6(D), upper panel]. At the onset of the song period (early November) the whales started singing at about 1400 (all times in local time calculated at the position of each recorder). They continued singing all night and stopped at about 0700 (Fig. 6). A similar pattern was observed throughout the peak singing period, with singing starting progressively earlier and ending later. By the end of the singing period, the singing started at about 1200 and stopped at about 0800.

The diel pattern to the fin whale singing activity in the period 12 November–22 December on mooring C6 in 2006 was significant (Mann-Whitney U-test, $P<1e-9$). The same was true for C6 in 2007 (Mann-Whitney U-test, $P<0.001$) and for mooring C4 (Mann-Whitney U-test, $P<0.0001$), but not for NE (Mann-Whitney U-test, $P>0.3$) where the F_{fin} signal was by far the weakest (Figs. 5 and 6). However, the diel pattern was still visually discernible in the recordings of NE [Fig. 6(C)]. In no cases did we see a lower F_{noise} acoustic power in bin 2 (noon) compared with bin 1 and bin 3 combined. The reduced F_{fin} energy during the hours surrounding noon, is not a pause, but merely a reduction in calling activity: the difference in median is only around 3 dB when it is most pronounced in location C6 in 2006.

The power of the F_{noise} did not show a similar diel pattern, confirming that the diel pattern observed in F_{fin} was not an artifact from ambient noise fluctuations [Figs. 6(A)–6(D), lower panels]. The oblique high-intensity lines seen in all these plots are most likely due to broadband low frequency strumming noise from tidal movements around the moorings [Figs. 6(A)–6(D), low panels].

IV. DISCUSSION

A. Spectral signatures of fin whale calls in the Davis Strait

We recorded very large numbers of LF pulses in the Davis Strait with spectral properties similar to those described from other areas (Thomson and Richardson, 1995; Širović *et al.*, 2004). The HF component of fin whales in the Davis Strait had a much higher frequency (131 Hz) compared to those reported from Antarctica (89 and 99 Hz). It is unknown if the production and pitch of the HF component in fin whale song are under control of the singing animal or if they are an anatomically induced by-product from making the 20 Hz pulse. Larger animals generally produce sound at lower frequencies compared to smaller animals (Fletcher, 2004). However, the mean size difference of ~ 2 m (some 10%) between southern and northern hemisphere fin whales (Brodie, 1975) is unlikely to generate the more than 30% increase in frequency observed in the Davis Strait fin whales. Rather, the difference in frequency of the HF pulse supports the notion put forward by Širović *et al.* (2009), that different populations of fin whales have different HF song components. If so, the center frequency of the secondary peak might be an acoustic indicator of fin whale population structures, and possibly serve a communicative function along

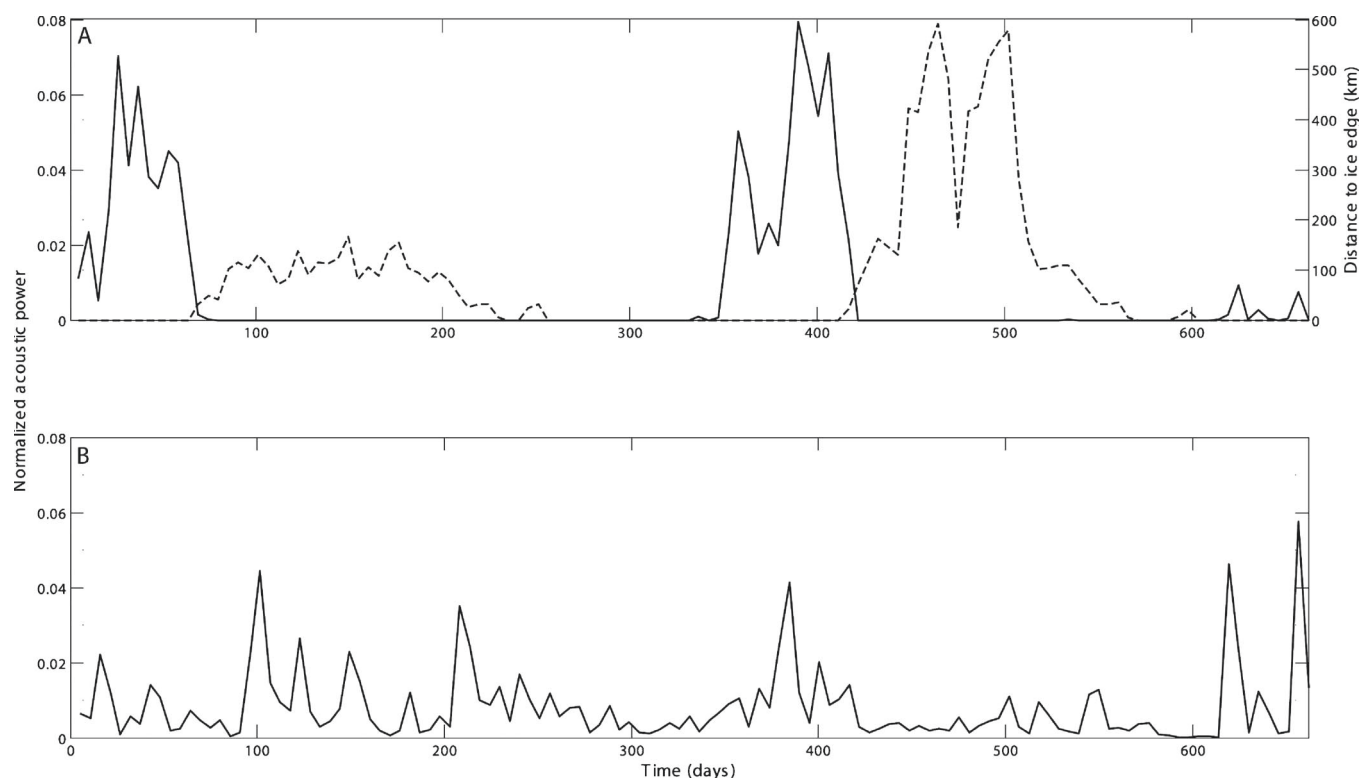


FIG. 5. Dynamics of normalized power in the fin whale (upper panel) and noise (lower panel) frequency bands and the distance to the ice edge (upper panel, broken lines) when the sea ice edge has covered the mooring. The distance was set to zero when the sea ice edge was north of the mooring. All data was computed as the mean of 5 days.

with the primary LF component at 20 Hz. For the same reason, it is not optimal to rely solely on detecting this HF pulse when analyzing data for occurrence of fin whales because of the high risk of missing calls with a changing frequency in the secondary peak on a spatial scale. This concern is accentuated by the fact that we did not always detect the HF component in our recordings, increasing the risk of missing detections.

This raises the question of why the high frequency pulse is not always detected along with the primary pulse at 20 Hz? First, it may simply be that the HF component can be turned on and off by the singing animals. However, if it indeed is a fixed part of the singing, it may relate to differences in source properties and propagation of the two pulses. Given the 6 times shorter wavelength, it may be envisioned that the HF pulse is more directional and thus only recorded when the whale is pointing in the direction of the recorders. Still with a wavelength (11 m) about half the size of the whale that produces it, the signal directionality is expected to be low for the HF component, and with whales in random orientation with respect to the recorders there should at least be a weak spectral band during the months with high peak fin whale detection. Given this, the explanation for the sometimes missing HF component is likely to be explained by differences in the active space of the two song elements; the energy flux density of the HF pulse was about 25 dB lower than the LF pulse within the same call.

Taking the difference in ambient noise at 20 Hz and 130 Hz (Wenz, 1962) into account the noise level is 17 dB higher around the LF pulse (20 Hz) compared to the HF pulse (130

Hz). Assuming spherical spreading, the LF pulse can therefore be detected minimum 3 times further compared to the HF pulse, resulting in a noise limited monitoring area ~ 9 times smaller, when using only the HF pulse for detection, compared to the LF pulse. We did not take the differences in frequency dependent absorption into account in these estimates, as it is negligible at these low frequencies. If it had been included it would in any case make the detection range of the HF pulse relatively lower (Urlick, 1983).

The differential active spaces mean that the song consists of two elements providing different cues when listening for conspecifics. A fin whale closely surrounded by singing individuals will be challenged in extracting directional cues from the LF pulse. That implies that this call component may be used for long-range communication, as suggested by Payne and Webb (1971). The larger active space of the LF pulse will let other whales detect one or more singing males at long ranges depending on ambient noise levels and propagation conditions. When whales close in on the singers, they will start detecting the HF pulses that via a shorter wavelength may be better for telling the direction to individuals, while possibly gaining information on the population identity from the pitch of the HF component.

The interpulse-interval (IPI) distributions of fin whale pulses differ between fin whale stocks and may as such serve as an alternative identification cue for fin whales (Delarue *et al.*, 2009). However, there seems to be a large disadvantage in using a temporal cue for transmitting information in a species often singing in large aggregations, such as the fin whale. As soon as more than a single animal is singing it will

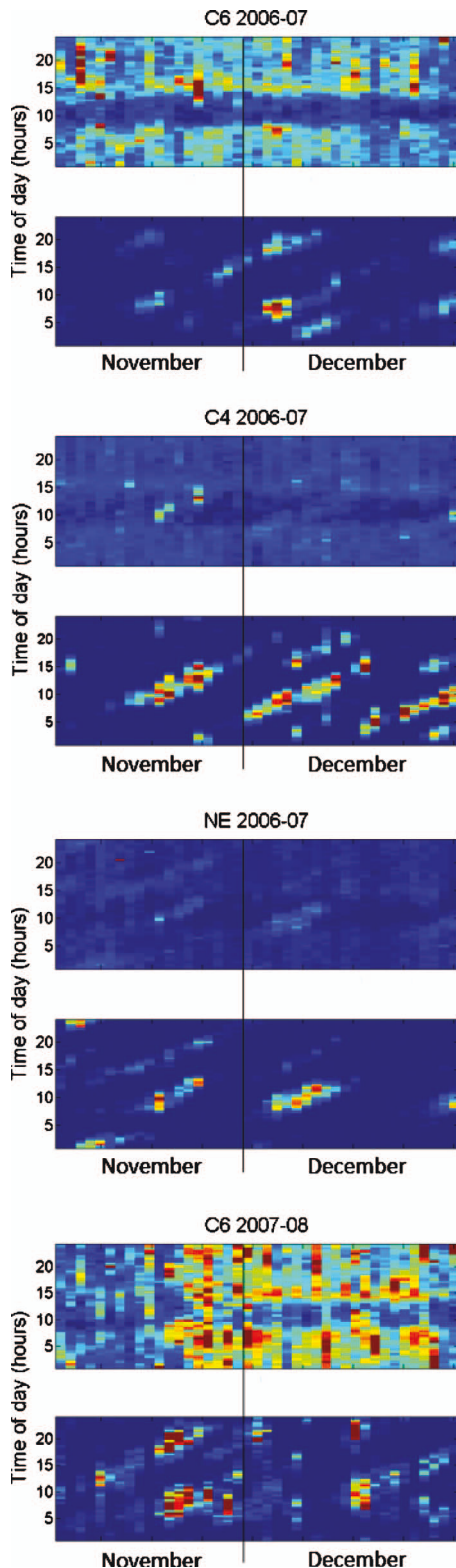


FIG. 6. Diel variation in the power of the F_{fin} (upper panel) and F_{noise} frequency band (lower panel). The x-axis shows the days from 12 November to 22 December. The y-axis shows the time of the day in hours. The image displays show the relative intensity in the frequency bands with increasing intensities illustrated by blue to red color scale. There is a clear diel pattern with the whales singing most of the day with a clear decrease in singing activity a few hours in the middle of the day.

be hard to extract the IPI information and in the peak singing season the IPI would be impossible to extract from the choir of singing whales [Fig. 2(B)]. If the peak singing is con-

nected to mating aggregations, a time where population identity should be important, it seems that the information on population identity in fin whales is better transmitted as a frequency cue perhaps in the form of the HF pulse of the song.

B. Detection ranges of fin whale calls

There were similar power levels of the F_{noise} signal on all three instruments but large differences in the received power levels of the F_{fin} relative to F_{noise} (Fig. 4). The northernmost deployed instrument, NE, had a very weak fin whale signature. Compared to instrument NE the signal was much stronger on instrument C4, and instrument C6 had the strongest signal with the same relative level in the second year of deployment [Figs. 4(A)–4(D)]. The back and forth calibration of the RAFOS signals confirmed that, assuming spherical spreading, the sensitivities of the recorders were similar ($< \pm 3$ dB). Therefore, the large differences in fin whale detections between recorders deployed only 85 km apart likely reflect that more whales were singing closer to the southeastern-most buoy (C6) south of the sea ice edge.

It is reasonable to assume that the detection of 20 Hz pulses both on our recorders and by fin whales are limited by background noise. Therefore the detection range of the recorders also provides a cue to how far fin whales might detect other fin whales. Payne and Webb (1971) estimated that if fin whale song suffered from spherical spreading and the ambient noise was moderate, fin whales should have a detection range of roughly 90 km. The maximum distance for using multiple path propagation of fin whale calls off the western Antarctic Peninsula was modeled to be 56 km while estimated detection ranges of fin whale calls in the Gulf of Alaska varied with ambient noise levels from 10 km–100 km (Širović *et al.*, 2007; Stafford *et al.*, 2007). Here we found that the summed power of fin whale calls was strong on the southeastern instrument (C6) but almost non-detectable on instrument NE, approximately 85 km away. So while the calling fin whales are not necessarily right next to the southernmost mooring (C6), the large drop in summed power in the fin whale call band show that the calling whales must have been much closer to that instrument than to the NE instrument and that their detection range in the physical environment of the Davis Strait in November–December was unlikely to extend much further than 85 km (the distance between the two recorders).

C. Implications for passive acoustic monitoring

The difference in detection range of the two call components is an important point to consider in the light of ambient noise profiles when choosing which part of the song to use for fin whale detections. Knowledge of the range over which a monitoring instrument can detect a sound in question, makes it easier to design a study in accordance with the research questions posed. For instance, if the detection range of fin whale LF calls is about 100 km, monitoring instruments deployed with less than 200 km distance, will result in areas with overlapping coverage from several instruments, potentially allowing for acoustic tracking and localization of

singing individuals. On the other hand if instruments are deployed with more than twice the distance of the detection range, areas will be left unmonitored. Under these conditions, however, it is then certain that animals recorded on one instrument are different individuals from those recorded at the same time on another instrument, leading to minimum estimates of the number of singing whales.

D. Seasonality in fin whale presence in the Davis Strait

It has been assumed that the majority of fin whales migrate south in the fall to warmer waters to mate and breed during winter (e.g., Norris, 1967; Heide-Jørgensen *et al.*, 2008). Sighting surveys and catch statistics have shown that fin whales are numerous in West Greenland from July to October (Heide-Jørgensen *et al.*, 2008; Simon *et al.*, 2007). Ten aerial cetacean surveys were conducted in the Davis Strait in March–April 1981–2008 (Heide-Jørgensen *et al.*, 1993; Koski and Davis, 1994; Heide-Jørgensen and Reeves, 1996; Heide-Jørgensen and Acquarone, 2002; Heide-Jørgensen *et al.*, 2007). None of these surveys had sightings of fin whales, making it unlikely that fin whales were present in the Davis Strait in March–April in the years of the surveys. However, the apparent seasonality inferred from catches and surveys is heavily biased by weather, daylight and sea ice conditions. There is a lack of information on the presence or absence of whales during winter. Except for a single satellite tracked fin whale, that stayed in West Greenland until 20 December, when the tag stopped transmitting (Heide-Jørgensen *et al.*, 2003), we have almost no information on fin whale presence in the Davis Strait from October to February. Here we used acoustics to document the presence of fin whales during these months. As in all PAM studies, a lack of acoustic detections does not necessarily mean that no whales are present, only that they are not singing. We recorded sporadic fin whale calls from June to October; few acoustic detections during a period when fin whales are known to be abundant from catch reports and visual surveys (e.g., Heide-Jørgensen *et al.*, 2008). On the other hand, we also detected a very strong peak in singing activity in November and December, when sighting effort is low or absent. The intense singing activity with overlapping continuous bands of fin whale calls is strong evidence that a large number of singing fin whales are present in the Davis Strait in November and December. This changes the view on fin whale seasonal migratory patterns by showing that at least part of the population does not migrate south in the fall, but rather stay at least until the end of December. This in turn raises the questions of 1) What are they doing until the early winter in the Davis Strait?, 2) When do the fin whales start migration and 3) Which factors drive them to migrate? As for the first question, there are two likely answers: feeding and mating. Here we use the call patterns to test for the hypotheses proposing fin whale feeding and mating in the Davis Strait from October to December.

E. Fin whales and sea ice

Širović *et al.* (2004) reported a negative correlation between the occurrence of fin whale calls and sea ice cover in

the Antarctic, implying that fin whales migrate when the sea ice forms. Our data corroborates this finding. Starting in November the sea ice expands in the Davis Strait from the northeast, and all three instruments were covered with sea ice from December 2006 to June 2007 (Fig. 1). The weak fin whale signal on instrument NE compared to instrument C6 (Fig. 4) suggests that the singing whales were closer to instrument C6, south of the sea ice edge during the peak singing period, indicating that sea ice dictates the northern limit of the distribution of singing fin whales in the Davis Strait during winter. Second, we observed that the short period of intense singing activity ended abruptly by the end of December (Fig. 5). That, in combination with the differences in song power on the buoys described above, suggests that the advance of sea ice may possibly affect the fin whales in different ways: i. fin whales stay in the area, despite increasing sea ice cover, but discontinue singing when the sea ice forms. ii. The advancing sea ice triggers fin whales to end their singing and migrate south to lower latitudes or iii. The fin whales continue singing but move further south just ahead of the expanding sea ice. Scenarios i or ii would imply that a certain sea ice distribution threshold exists for fin whale singing and/or migration and that this threshold was reached in 2006 just as the sea ice covered mooring C6. Therefore, if such a threshold exists, we were fortunate enough to deploy the mooring just at the threshold latitude. This seems unlikely, and the third scenario whereby fin whales continue to sing, but move further south when the sea ice moves in from the north, seems to be the most parsimonious explanation. Thus, both Antarctic and Davis Strait fin whale calling activity is strongly negatively correlated with the expansion of sea ice (Širović *et al.*, 2009), suggesting that similar circumstances exist for singing fin whales near the two poles: sea ice limits their distribution toward higher latitudes and changing sea ice may therefore lead to changes in distribution of singing fin whales. Whether this is due to the physical presence of sea ice that impedes normal breathing and surface swimming or if it relates to secondary oceanographic effects on prey availability remains to be tested. Regardless, it seems that changes in sea ice cover related to climate changes are likely to affect fin whale distribution in Davis Strait during winter with the potential to cause overall changes in how these large predators exploit Arctic waters for mating, breeding and feeding in a warmer less icy future.

F. Mating in the cold?

Fin whale calls are usually recorded year round in different areas of the world's oceans, but with a clear seasonal peak in the singing activity, lasting for about four months (Thomson and Richardson, 1995; Stafford *et al.*, 2007; Watkins *et al.*, 1987; Thompson *et al.*, 1992; Moore *et al.*, 1998). The annual peak in fin whale singing coincides with the estimated conception time, suggesting that the song is part of a mating display, possibly to attract mates (Watkins *et al.*, 1987; Moore *et al.*, 1998; Croll *et al.*, 2002; Payne and Webb, 1971). This contention is supported by genetic evidence that all singing fin whales, that have been sexed, were

males (Croll *et al.*, 2002). The peak singing period in the Davis Strait in November and December is unusually short compared to fin whales recorded in other areas, including further south in the North Atlantic and Pacific (Watkins *et al.*, 1987; Stafford *et al.*, 2007). The peak conception time in the North Atlantic centers on January (Lockyer, 1984). From the contemporaneous occurrence of the intense fin whale singing and the conception time we infer that at least part of the population of the Davis Strait fin whales may likely mate while still at high latitudes. The bimodal pattern of feeding at high latitudes and breeding/mating at low latitudes is too simplistic to fully account for fin whale ecology and migration patterns.

G. Feeding and singing in the Arctic winter

Several studies have shown that baleen whales have diel variations in their song behavior, with blue and fin whales singing in the dark period of the day from dusk to dawn, suggesting a causal link between song activity and the absence of sunlight (Stafford *et al.*, 2005; Watkins *et al.*, 1987). Fin and blue whales are lunge feeders, ingesting large volumes of prey filled water (Croll *et al.*, 2001; Goldbogen *et al.*, 2006; Pivorunas, 1979). This feeding strategy is most efficient if the prey occur in dense aggregations (Croll and Tershy, 2002). Most baleen whale prey perform daily vertical migrations up and down the water column controlled by the light intensity, appearing in dense aggregations at depth during the day to reduce predation and dispersed in the water column during night when sunlight is gone. Stafford *et al.* (2005) suggested that the higher call rates in blue whales during night/dusk were associated with the vertical migration of the prey. The blue whales fed during day when krill densities were highest and then sang during night when krill were dispersed in the whole water column and perhaps not in great enough concentrations for cost-efficient feeding (Stafford *et al.*, 2005). Sei whales (*Balaenoptera borealis*) are, contrary to fin and blue whales, most vocally active during daytime (Baumgartner and Fratantoni, 2008). This difference among three large closely related rorquals has been explained by the differences in prey choice and feeding behavior. Where the lunge feeding fin and blue whales might benefit from feeding at depth during daylight, when krill swarms are concentrated at depth, sei whales were reported to skim feed on copepods near the surface at night (Baumgartner and Fratantoni, 2008). Despite these differences, the singing activity of all three rorquals seems linked to the light intensity (whether positively or negatively), through the light-induced vertical migration and dispersion of prey.

In the present study, there was a significant diel pattern in the fin whale song activity in November and December with fin whales singing continuously from early afternoon until early morning (Fig. 6). Diel variation in calling activities of rorquals has previously only been reported from temperate and tropical areas (Baumgartner and Fratantoni, 2008; Stafford *et al.*, 2005; Watkins *et al.*, 1987; Wiggins *et al.*, 2005). Here we show that even in the dark Arctic winter with minimal hours of daylight, the calling activity follows the dark period of the day. This provides strong circumstantial

evidence that the calling activity is light-induced either directly or through the migratory behavior of the prey.

The clear diel signature in the fin whale singing activity, however, does not directly justify the conclusion that there is a causal correlation between the prey migration and fin whale feeding behavior. A recent study showed that Arctic zooplankton continues the light-induced vertical migration through the polar night (Berge *et al.*, 2009). Fin whales prey on krill that follow the vertical migration of their planktonic prey (Sourisseau *et al.*, 2008). As the song activity follows the same pattern as the vertical migrations performed by fin whale prey it is conceivable that the reduction in fin whale singing during the daylight was due to whales feeding on dense prey patches at depth. If such a relationship exists, it would imply that fin whales that stay in the Arctic during early winter are feeding during the short daylight hours, which contrasts the paradigm that balaenopterids only feed during summer.

V. CONCLUSIONS

We have demonstrated that fin whales are acoustically active and hence present in the Davis Strait from June to December, much later in the year than previously thought. The contemporaneous peaks in song activity and estimated conception time suggest that not all fin whales migrate south to mate, but rather stay at high latitudes perhaps to exploit food niches that are not available at lower latitudes while mating. The latter notion is supported by the fact that the singing activity of fin whales in the Davis Strait is strongly linked to daylight hours, and could be controlled possibly by the vertical migratory behavior of their prey. This suggests that fin whales might feed during the few daylight hours of the late fall and early Arctic winter. The difference in magnitude of fin whale signal detections among the three recorders shows that the distribution of fin whales in the Davis Strait may in part be controlled by the advance of the sea ice edge during winter. Further, we observed a negative correlation between fin whale song and sea ice whereby the song stopped when the sea ice covered the mooring. Consequently, changing sea ice conditions may change the winter distribution of singing fin whales in the future and such changes may be monitored successfully by using PAM.

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