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BRIEF RESEARCH REPORT
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Humpback Whale (*Megaptera novaeangliae*) Song on a Subarctic Feeding Ground

*Saskia C. Martin[1,2], Ana S. Aniceto[3], Heidi Ahonen[4], Geir Pedersen[5] and Ulf Lindstrøm[2,6]**

[1] Department of Biology, Lund University, Lund, Sweden, [2] Department of Arctic and Marine Biology, Arctic University of Norway, Tromsø, Norway, [3] Faculty of Biosciences, Fisheries and Economics, Arctic University of Norway, Tromsø, Norway, [4] Norwegian Polar Institute, Tromsø, Norway, [5] Department of Marine Ecosystem Acoustics, Institute of Marine Research, Bergen, Norway, [6] Department of Marine Mammals, Institute of Marine Research, Tromsø, Norway

Male humpback whales (*Megaptera novaeangliae*) are known to produce long complex sequences of structured vocalizations called song. Singing behavior has traditionally been associated with low latitude breeding grounds but is increasingly reported outside these areas. This study provides the first report of humpback whale songs in the subarctic waters of Northern Norway using a long-term bottom-moored hydrophone. Data processed included the months January–June 2018 and December 2018–January 2019. Out of 189 days with recordings, humpback whale singing was heard on 79 days. Singing was first detected beginning of January 2018 with a peak in February and was heard until mid-April. No singing activity was found during the summer months and was heard again in December 2018, continuing over January 2019. A total of 131 song sessions, including 35 full sessions, were identified throughout the study period. The longest and shortest complete sessions lasted 815 and 13 min, respectively. The results confirm that singing can be heard over several months in winter and spring on a high latitude feeding ground. This provides additional evidence to the growing literature that singing is not an explicit behavior confined to low latitude breeding grounds. The peak of song occurrence in February appears to coincide with the reproductive cycle of humpback whales. Finally, this study indicates that song occurrence on a subarctic feeding ground likely aids the cultural transmission for the North Atlantic humpback whale population.

Keywords: passive acoustics, song occurrence, cetacean, Mysticeti, North Atlantic, Norway

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***Correspondence:**
Ulf Lindstrøm
ulf.lindstroem@hi.no

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INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are a highly migratory species, undertaking extensive annual migrations between high latitude summer feeding grounds in subpolar waters and low latitude winter breeding grounds in tropical waters (Dawbin, 1966). In the Eastern North Atlantic, the feeding grounds encompass subarctic waters of Iceland, Jan Mayen, Greenland, and Northern Norway to the Barents Sea (Stevick et al., 2006). Using sighting and catch data, humpback whales have been documented in Icelandic waters from May to September, peaking in June-July (Sigurjónsson and Víkingsson, 1997). Further north, in the Barents Sea, they have been observed

during the summer months with a peak abundance in September and along the Norwegian coast mainly between October and February (with a peak in January) (Ramm, 2020). Humpbacks have been reported to generally arrive on their breeding grounds in the West Indies and Cape Verde between February and April (Stevick et al., 2003, 2016). However, some studies proposed that not all humpbacks migrate annually but overwinter on feeding grounds (Van Opzeeland et al., 2013; Magnúsdóttir et al., 2015), thus, migratory behavior appears to vary by individuals (Magnúsdóttir and Lim, 2019).

Humpback whales frequently display long series of structured sound sequences known as song. To date, singing has only been observed for males and is strongly linked to breeding behavior (Payne and McVay, 1971; Cerchio et al., 2001; Cholewiak, 2008). The song of humpbacks is highly stereotypical and arranged in a nested hierarchy; the shortest, most basic element is called a "unit" which combine and form a string of individual sounds termed "phrase." Phrases, usually 2–20 units long, are then repeated in succession to form a "theme." A "song" is defined as the combination of distinct themes joined in a predictable sequence, which are then repeated multiple times in a "song session," lasting up to several hours (Payne and McVay, 1971; Cholewiak et al., 2013).

Singing has traditionally been associated with breeding in low latitude areas, however, growing evidence reports humpback whale song at higher latitudes, outside of breeding grounds, during feeding and migration (Gabriele and Frankel, 2002; Clark and Clapham, 2004; Vu et al., 2012; Garland et al., 2013; Magnúsdóttir et al., 2014; Gridley et al., 2018). The peak of song occurrence on breeding grounds around February–March (Au et al., 2000) appears to be in line with reproduction-specific traits such as the female ovulation period and increased testis weight in male humpback whales (Nishiwaki, 1959, 1960). This suggests that singing plays a role in reproduction (Tyack, 1981; Mobley et al., 1988; Smith et al., 2008). In the northern hemisphere, singing has been detected on feeding grounds on multiple occasions across ocean basins (Baker et al., 1985; Mattila et al., 1987; McSweeney et al., 1989; Clark and Clapham, 2004; Vu et al., 2012; Magnúsdóttir et al., 2014). Magnúsdóttir et al. (2015) reported regular singing activity during three consecutive winters on a subarctic feeding ground in Iceland. Icelandic waters have also been identified as a feeding ground and occasional passage route for Norwegian humpback whales, most likely aiding cultural transmission of songs within the North Atlantic (Magnúsdóttir and Lim, 2019). Recent data collection in Northern Norway is showing extensive humpback whale vocal activity during the winter months, mainly consisting of song. The objective of this study was to identify and describe the occurrence of the humpback whale song in Norwegian waters during migration and/or feeding.

MATERIALS AND METHODS

Data Collection

Launched in 2013, the Lofoten-Vesterålen (LoVe) Ocean Observatory was deployed in a cold-water coral area about 20 km offshore from the coast of Vesterålen, Norway, above the arctic circle (>66°33' N) (**Figure 1**). A hydrophone (Ocean Sonics SB35 ETH, 10 Hz–64 kHz) continuously records biologically generated sounds and anthropogenic noise within the area (Godø et al., 2014). Passive acoustic data processed in this study included the months January–June 2018 and December 2018–January 2019 and audio files were downloaded using the LoVe Ocean archive (Equinor and IMR, 2020) and processed using a combination of automated and manual methods.

Song Detection

To identify the occurrence of humpback whale vocalization, a long-term spectral average (LTSA) was generated using PamGuard software (version 2.01.04 beta; Gillespie et al., 2009) for every month with available data (**Figure 2**). Simultaneously with the LTSA, PamGuard's Whistle and Moan detector (WMD) for automated detection of humpback whale vocalizations was applied with the following settings: frequencies of 120–15,000 Hz, 4096 FFT, 50% overlap, Hann Window, detection threshold 8dB, remaining parameters as default by PamGuard. Including a WMD ensured the manual evaluation of false positives and false negatives, while assessing the occurrence of whale vocalizations. Areas of high activity generated by the LTSA and the WMD (see **Supplementary Figure 1**) were then investigated in detail using spectrograms in Raven Pro (version 1.6; Center for Conservation Bioacoustics, 2019) to determine start and end time of vocal activity as well as vocal categories (song or non-song). A song was defined by units found in a rhythmic context like phrases and themes (**Figure 3**). Randomly occurring sounds with no rhythmic

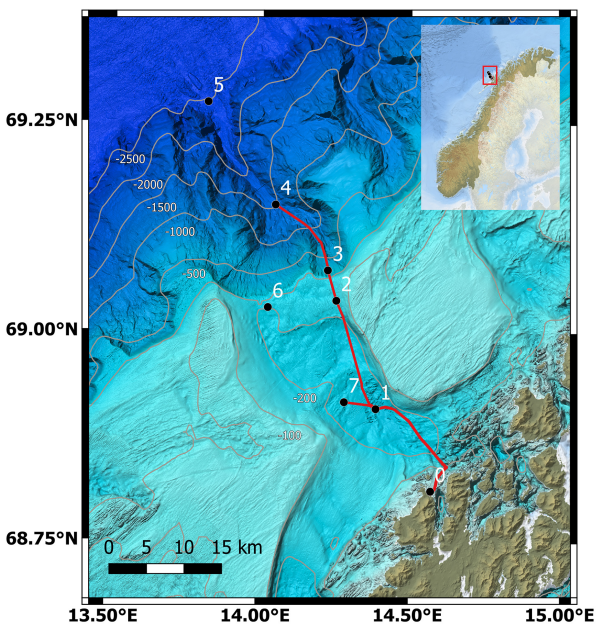

FIGURE 1 | Map of the sampling-nodes of the LoVe Ocean Observatory. Data used in this study were collected by node 1 (Equinor and IMR, 2020).

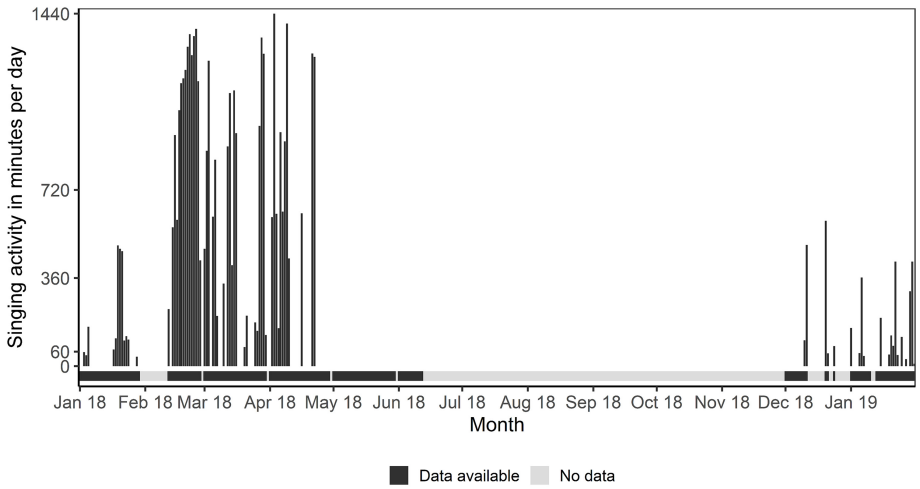

FIGURE 2 | Humpback whale song occurrence over the study period. The horizontal bottom bar indicates data availability.

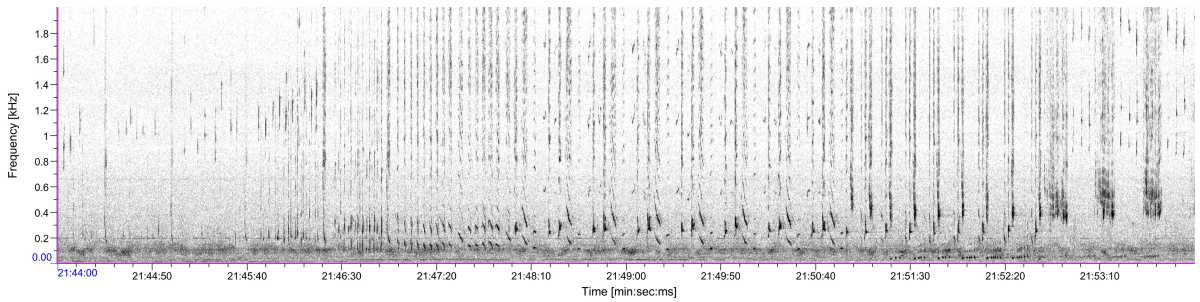

FIGURE 3 | Spectrographic view of an observed song cycle in January 2018; generated using Fast Fourier Transform (FFT) size 8092 Hann-window with a frequency resolution of 5.69 Hz and a 70% overlap. Audio is provided in **Supplementary Audio 2**.

pattern were considered non-song (Dunlop et al., 2008). Song sessions are usually sung in a continuous bout (Winn and Winn, 1978) and were delineated by a significant silent interval. Additionally, the number of chorusing singers was estimated using visual and auditory perceptual characteristics of overlapping units and phrases as applied by previous studies (Payne and Payne, 1985; Magnúsdóttir et al., 2015; Magnúsdóttir and Lim, 2019).

RESULTS

Song Occurrence

A total of 189 days of recordings were included in the analysis to investigate the presence of humpback whale song off the coast of Northern Norway. Humpback singing activity was detected on 42% of all recording days, occurring in six out of the eight months, with song detected in winter and spring between December and April (**Figure 2**).

The first occurrence of measurable song (units, phrases, themes, **Figure 3**) in the data available was on the 3rd of January 2018. In this month, a mean of 78 (± 147) minutes of singing activity per recording day was heard, the lowest activity throughout the study period (**Table 1**). This was followed by the peak month February, where song was detected on 15 out of 16 days, with a mean of 949 (± 440) min and the highest minimum of 233 min per recording day. March and April were also months of relatively high activity with singing detected for a mean of 448 (± 480) and 357 (± 504) minutes per recording day, respectively. On some occasions, singing was heard for more than 22 h within one day and in April, singing by multiple whales lasted one full recording day (1,440 min) and even beyond. No instances of singing were detected in May or June followed by a lack of data availability from July up to and including November. The next singing activity was detected on the 10th of December 2018 and continued until the end of January 2019 with no more data added to the analysis.

Song Sessions

Throughout the study period, a total of 131 song sessions were identified, with February and March having the highest numbers of more than 30 sessions (**Table 1**). With continuous data recordings available, it was possible to detect full song sessions (including start and end time) on multiple occasions. In total, 35 complete sessions were detected, with the highest amount

TABLE 1 | Summary of humpback whale song occurrence per recording day and song sessions.

Year Month	No. days recorded		Singing activity per recording day (min.)			No. song sessions*	No. full song sessions	Average song session length (min.)**			Max. no. singers in chorus***
	Total	w/song	Min	Max	Mean ± SD			Min	Max	Mean ± SD	
2018											
January	29	12	39	494	78 ± 147	15	1	112	112	–	2
February	16	15	233	1378	949 ± 440	33	2	14	52	33 ± 27	> 4
March	30	20	78	1343	448 ± 480	35	12	31	789	245 ± 234	3
April	29	12	155	1440	357 ± 504	17	7	17	815	200 ± 277	> 4
May	30	0	–	–	–	–	–	–			–
June	12	0	–	–	–	–	–	–			–
//											
December	14	5	53	594	95 ± 195	10	3	40	90	65 ± 25	2
2019											
January	29	15	10	427	84 ± 133	21	10	13	362	84 ± 105	2
Total	189	79	568	5676	238 ± 414	131	35	227	2220	159 ± 201	–

*No data indicated by hyphen (–). *No. song sessions, all sessions included, also when fading in/out, with too many singers chorusing then considered as one session; **Average song session length of full sessions, only sessions that included start and end time; ***Max. no. singers in chorus, singing at same time.*

of ten and twelve sessions in January 2019 and March 2018, respectively. For other months, such as January, February, and December 2018, only a small number of full song sessions were detected ($\leq$3). This was most likely a result of poor-quality recordings and/or too few data to determine the start and end time of a session in a meaningful measure. The lengths of full song sessions varied between several minutes and more than 12 h. The longest complete sessions occurred in March and April 2018 with more than 13 h and the shortest of only 13 min in January 2019.

Throughout 79 days of measured singing activity, multiple whales were found contemporaneously singing at a given time, with peaks of more than four singers in asynchronous chorus in February and April 2018. Although single singers were generally predominant throughout the study period (65%), multiple singers were detected for 35% of all detected song sessions (n = 131). Complete sessions (n = 35) resulted in similar ratios, with 63% sung by single whales and 37% by multiple animals.

DISCUSSION

This study provides the first account of humpback whale songs in the subarctic waters of Northern Norway. The results show that humpbacks can be heard singing over several months on a high latitude feeding ground, providing additional evidence to the growing literature that singing is not an explicit behavior confined to breeding grounds (e.g., Vu et al., 2012; Magnúsdóttir et al., 2014). The re-occurrence of singing activity over adjacent years demonstrates that this is most likely not an unusual but rather persistent event within this area. Whales were acoustically detected in coastal areas of Northern Norway in the period of December to April, with peak singing in February. This is in line with previous studies within the North-East Atlantic, with highest singing activity heard in February (Magnúsdóttir et al., 2014; Magnúsdóttir and Lim, 2019).

March and April were also months of relatively high song occurrence with the longest complete song sessions recorded. The observed variability in singing behavior might be driven by the abundance of whales in the area, specifically males which are the only ones that have been observed to engage in this vocal display (Winn and Winn, 1978; Baker and Herman, 1984; Darling and Bérubé, 2001; Darling et al., 2006; Herman et al., 2013). Recent studies showed that Norwegian fjords represent an important stopover in the southbound migration for humpback whales (Kettemer et al., 2019; Ramm, 2020). Peak sighting rates by Ramm (2020) using photo identification were generally highest in January with low to no observations in February and onwards. While visual studies report no humpback whale sightings in Norwegian waters after February (Broms et al., 2015; Ryan et al., 2015; Ramm, 2020), acoustic detections by Aniceto et al. (2020) and the present study reveal longer stays throughout spring. Although recordings in February only covered 57% of all days within this month, singing activity would still be highest if the missing 12 days were set as "song absent" (resulting in 542 min/recording day).

The increase of song occurrence in February is most likely correlated with the reproduction cycle as already suggested by Magnúsdóttir and Lim (2019). Peaks in singing overlap the ovulation periods of females (Nishiwaki, 1959) and might be driven by elevated testosterone levels in males (Clark and Clapham, 2004). However, other studies on North Atlantic feeding grounds provided opposing results with no song present in February and peaks in November (Vu et al., 2012). Furthermore, the increase in humpback whale song occurrence in February could identify the time period when most males arrive at Norwegian feeding grounds. Magnúsdóttir et al. (2014) reported visual observations of humpbacks without any song detected from spring to autumn. However, further abundance

investigations including sex ratios in February and beyond are necessary to confirm this hypothesis.

Humpback whales from the North-East Atlantic have been documented to generally arrive at the breeding sites in the West Indies and Cape Verde sometime between February and May (Stevick et al., 2003, 2016; Kettemer et al., 2019). The occurrence of song from December throughout April within the study area demonstrates that humpbacks start singing well before they have reached their breeding grounds. This might indicate that males start to migrate with a delay as proposed by Vu et al. (2012). However, Stevick et al. (2003) demonstrated evidence for sex segregation in migration with males arriving earlier at breeding areas than females. Additionally, pregnant female humpbacks have been documented to depart last from feeding grounds and arrive latest at breeding areas (Dawbin, 1966). As Ramm (2020) put forward, this suggests a dominance by females in the later winter-feeding seasons in Norway. Based on a sex ratio highly skewed toward male humpback whales in breeding areas, it has been proposed that females most likely remain in feeding areas to improve their body condition (Brown et al., 1995; Craig and Herman, 1997). A delayed departure or even remaining whales in the area could explain the lasting singing behavior by male humpbacks until April, suggesting a trade-off strategy for both sexes as indicated by Magnúsdóttir et al. (2014). Song session duration on breeding grounds has shown to be linked to the hormonal cycle in humpbacks. Tyack (1981) reported an increase in song bouts length as a result of decreasing female reproductive activity. This could account for the increased duration of full song sessions observed in March and April off Norway's coast. However, given the small number of identified complete song sessions in other months such as February, this result must be interpreted with caution.

The majority of singers detected at a given time within the area were single whales, much in contrast to the chorusing singers on low-latitude breeding grounds. This pre-dominance of solo singers is consistent with other studies of high latitude feeding grounds (Gabriele and Frankel, 2002; Vu et al., 2012), however, these findings are not in line with the high number of simultaneous singers in Icelandic waters (Magnúsdóttir and Lim, 2019). Following the trend of singing activity per day per month, it can be inferred that the number of males present within the study area seems to be the driver of this variation in song occurrence. Humpback whale songs are gradually and continuously evolving within any given population from year to year, but all males conform to the same version of song within the same area (Payne et al., 1983; Payne and Payne, 1985). This change of themes, phrases and even units over time is termed "song evolution" (Payne et al., 1983) and "song revolution" is characterized by the complete replacement of an existing song by a novel song (Noad et al., 2000). Another ongoing study of the same dataset (unpublished) indicates temporal variation in song structure in Northern Norway. As already proposed by Magnúsdóttir and Lim (2019), song exchange in high latitude feeding areas might be a key driving force behind cultural transmission for North Atlantic humpback whale populations. Detailed analyses of humpback song patterns over multiple years and comparisons of song types between feeding and breeding grounds as well as along migration routes may contribute to our understanding of singing behavior in subarctic waters. It would furthermore help to elucidate the importance of feeding grounds for song exchange at high latitude feeding grounds of the North Atlantic.

The results presented here are largely in line with previous findings of humpback whale song production in the North Atlantic. However, they also provoke further investigations in relation to feeding and breeding behavior and how humpback vocalizations might relate to environmental conditions in Norwegian waters.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

AA conceived the original idea. SM and AA designed the study. SM processed the data, performed the analysis, and took the lead in writing the manuscript. AA and UL supervised the project. AA, HA, GP, and UL provided critical feedback and helped shape the research, analysis and manuscript. All authors have read and approved this submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.669748/full#supplementary-material

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

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