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SHORT NOTE

Humpback whale songs during winter in subarctic waters

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Abstract The songs of the male humpback whales (*Megaptera novaeangliae*) have traditionally been associated with mating at tropical and subtropical mating grounds during winter. However, songs also occur out of mating season, both on feeding grounds in spring, late summer and fall. This study provides the first report of humpback whale singing behaviour in the subarctic waters of Northeast Iceland (Skjálfandi Bay) using long-term bottom-moored acoustic recorders during September 2008–February 2009 and from April to September 2009. Singing started in late November and peaked in February, within the breeding season. No songs were detected from spring to fall, despite visual detections of humpback whales. Non-song sound signals from humpback whales were detected during all recording months. Songs were partly composed of fundamental units common with other known mating grounds, and partly of song units likely unique to the study area. The variety of song unit types in the songs increased at the end of the winter recordings, indicating a gradual change in the songs throughout the winter season; as has been shown on traditional mating grounds. The relative proportion of songs compared with non-song signals was higher during dark hours than daylight hours. The short light periods of the winter, and where food is available, likely influence the daily occurrence of humpback whales' songs in the subarctic.

Keywords Humpback whale · *Megaptera novaeangliae* · Songs · Non-songs · Subarctic waters

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Introduction

North Atlantic humpback whales (*Megaptera novaeangliae*) forage in various temperate to Arctic coastal waters from spring to fall (Stevick et al. 2003). Many undertake seasonal migrations where the winters are spent in the less productive tropical breeding grounds of the West Indies (Martin et al. 1984; Katona and Beard 1990; Stevick et al. 1998), or of the northwest coast of Africa (Charif et al. 2001). However, humpback whales and other migrating baleen whale species do sometimes stay until winter, or even overwinter, in the polar regions (Thiele et al. 2004; Moore et al. 2006; Stafford et al. 2007; Simon et al. 2010; Acevedo et al. 2011). It is not known if portions of these populations have always overwintered on high-latitude feeding grounds. Nonetheless, humpback whales are regularly seen on Icelandic feeding grounds during winter following the capelin (*Mallotus villosus*) migration (Víkingsson 2004; Magnúsdóttir 2007), and they have been sighted during winter on northern feeding grounds for decades (Ingebrigtsen 1929; Christensen et al. 1992). At present, limited information exists about the abundance, behaviour and movement of humpback whales wintering in a subarctic region.

On lower latitude breeding grounds, wintering male humpback whales produce long and complex songs, comprising ascending hierarchical series of units, phrases and themes (Payne and McVay 1971; Mattila et al. 1987; Cerchio et al. 2001; Mercado et al. 2003). Within each breeding ground, all males sing the same or very similar songs at any given time (Winn and Winn 1978) but songs tend to change gradually throughout the mating season (Payne et al. 1983; Payne and Guinee 1983; Payne and Payne 1985; Cerchio et al. 2001); only male humpback whales have to date been detected singing (Smith et al. 2008; Herman et al. 2013).

Humpback whale songs have been detected at higher latitudes, outside of the breeding grounds and reproductive periods, both on migratory routes during early and late autumn (Clapham and Mattila 1990; Norris et al. 1999; Charif et al. 2001), and in spring and mid-winter on the southernmost feeding grounds of the North Atlantic (Clark and Clapham 2004; Vu et al. 2012). The function of songs outside of traditional breeding areas is not well understood, but they may serve as an opportunistic mating strategy or intra-sexual display (Clark and Clapham 2004; Smith et al. 2008; Wright and Walsh 2010).

Male singing is believed to have a role in reproduction (Tyack 1981; Mobley et al. 1988; Smith et al. 2008) and has so far only been associated with mating strategies (Darling and Bérubé 2001; Darling and Sousa-Lima 2005). Ovarian and testis data obtained from humpback whales caught on breeding grounds in the Northern Hemisphere (Ryukuan waters) showed that females ovulated and testis weight in mature males increased from January to April (Nishiwaki 1959, 1960, 1962). Thus, singing for mating purposes could also be expected by overwintering mature whales in the Arctic region.

This study describes an effort to investigate singing occurrence in the subarctic on a year-round basis. The aim was to evaluate the structure and development of the songs, changes in the incidences and properties of the song components as the mating period progressed (as has been shown on traditional mating grounds), if songs in the subarctic could also have a reproductive purpose, and if the extreme light conditions of the subarctic could affect the singing behaviour.

Materials and methods

Two bottom-moored microprocessor-based autonomous ecological acoustic recorders (EARs; Lammers et al. 2008) were deployed in Skjálfandi Bay from September 2008 to February 2009 and from April 2009 to September 2009. Skjálfandi Bay is located on the northeast coast of Iceland (at 66°07′N, 17°32′W) (Fig. 1). During the winter darkness

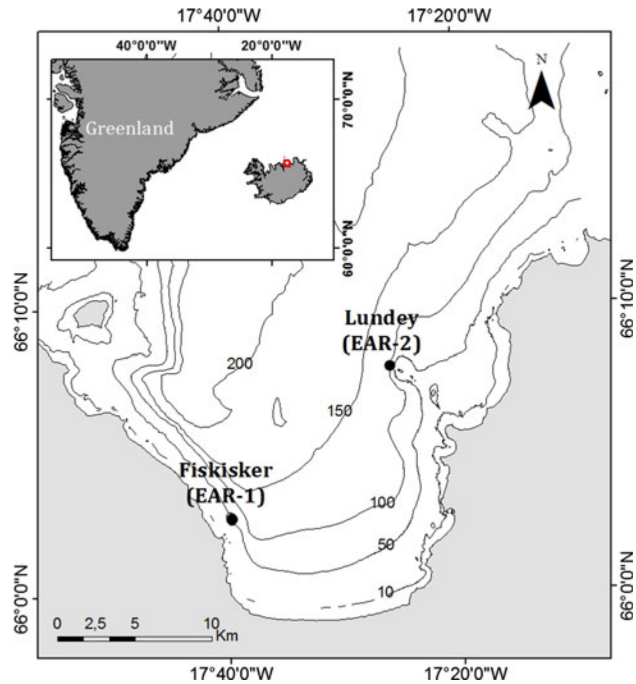

Fig. 1 The study area in Skjálfandi bay, NE Iceland. The *two black circles* represent the location of each EAR recording unit. Depth contours are in metres. *Source* (1) Hydrographic Department of the Icelandic Coast Guard, 2012, (2) National Land Survey of Iceland, 2012 and (3) Esri, DeLorme Publishing Company, Inc. The map was created using ArcGIS® software (version 10.1) by Esri

prevails (average ~3 h of daylight) and the water temperature is near freezing (~+2 °C) in contrast to the summer months where the days are long (average ~18 h of daylight) and the water temperature rises up to ~+8 °C (Jónsson 2004). EAR-1 "Lundey" was placed on an outcrop at about depths of 65 m named Lundey (66°08′N, 17°26′W), and EAR-2 "Fiskisker" was placed approximately 12.5 km away on a slope named Fiskisker (66°03′N, 17°40′W) at about 62 m depth. EAR-1 "Lundey" was retrieved on 28 February 2009, and EAR-2 "Fiskisker" was retrieved on 23 March 2009. Both EARs were redeployed to their same exact locations on 3 April 2009 and retrieved on 9 September 2009.

The EARs were programmed to record for 1 min every 15 min at a sampling rate of 64 kHz to collect a broad range of sounds from as many cetacean species as possible, over a long period, approximately 5 months per deployment. The detection range of the EARs for humpback whale signals below 1 kHz, based on the minimum (171 dB) and maximum (189 dB) source levels, are 12 and 28 km, respectively, assuming spherical spreading.

Acoustic data were analysed using the software packages Ishmael 2.0 (Mellinger 2002; Mellinger et al. 2011) and Osprey (Mellinger 2000). A frequency contour algorithm was employed to detect tonal signals ranging in frequency from 100 to 1,000 Hz (FFT 0.2048 s., 75 %

overlap, Hamming). To reduce the background noise in the recordings, one second of spectrogram equalization was applied (Mellinger 2002; Mellinger et al. 2011). Each detected signal was inspected visually and aurally to verify detections.

The humpback whale signals evaluated in this study were categorized as: (1) song units and (2) non-song signals. Song units were defined as signals found in rhythmic context (i.e. phrases). Non-song signals were defined as randomly occurring signals with no rhythmic context and not considered a part of a song (Dunlop et al. 2008). Due to the nature of the data sampling scheme (i.e. 1-min sound files recorded every 15 min), it was not always possible to obtain whole phrases and never whole themes. Therefore, the focus was placed on describing these smaller units. For each sound, the start and end times, the high and low frequencies and the frequency change were measured. Types were categorized visually by their shape and frequency range, and aurally. The units were named alphabetically as they occurred during inspection. Only sound files with clear signals where frequency parameters could be easily measured were used for measuring the frequency and duration of song units. These sound files were all obtained from Lundey (EAR-1) during 13 December 2008–12 February 2009. That period was divided into 12 5-day sub-periods to search for evidence of changes in song structure and song variability as the mating season progressed. The R-based *pastecs* package (version 1.3-11) was used to obtain descriptive statistics for the occurrence of units per sub-period. The number of sound files from each EAR containing song units was counted for and a paired *t* test was used to look for statistical differences in the number of detected sound files on each EAR.

All detections of humpback whale song units and non-song units, from both recording periods, were used to examine the effect of light conditions on the occurrence and combinations of song and non-song units. The null hypothesis was that the levels of calling are the same for all light regimes and that the relative proportions of song detections were independent of non-song detections during different light regimes. Three light regimes, light, dusk and dark hours, were defined by the altitude of the sun as described in Stafford et al. (2005). The timing of each light regime was determined by measurements of the United States Naval Observatory Astronomical Applications Department website (http://aa.usno.navy.mil) for the location 66°07′N, 17°32′W for each hour of data analysed. Since there was a substantial variance in the number of detected humpback whale signals between days, the mean number of sound signals each day was subtracted from the number of sound signals per hour for each day (Hjellvik et al. 2001; Stafford et al. 2005).

Diel trends in acoustic detections were analysed using Cochrane–Orcutt autocorrelation in the R-based *orcutt* package (version 1.1). The difference in the adjusted average number of calls per light period was tested using a one-way ANOVA and Tukey's HSD (honestly significant difference) test. Finally, Fishers exact test was used to investigate the relative proportions of song detections and non-song detections during different light regimes.

Results

Occurrence of songs and non-songs

The EAR-1 "Lundey" recorded for 162 days, and the EAR-2 "Fiskisker" recorded for 146 days during the winter (first deployment). The first humpback whale song units were detected at Lundey in September 2008, and at Fiskisker in December 2008; "Fiskisker" stopped recording earlier than expected. A total of 1,129, 1-min sound files containing humpback whale signals were detected during the winter (first deployment) of which 86 % included components of a song, and 14 % included non-song sounds. During the summer (second deployment), both EARs recorded for 165 days, resulting with just 79, 1-min sound files containing humpback whale signals, of which none were songs or traces of song units. Humpback whales were, however, visually observed in the area from June to September 2009 (pers. obs. by E.E. Magnúsdóttir, unpublished data).

The first occurrence of measureable song units was during mid-December 2008; the number of different song

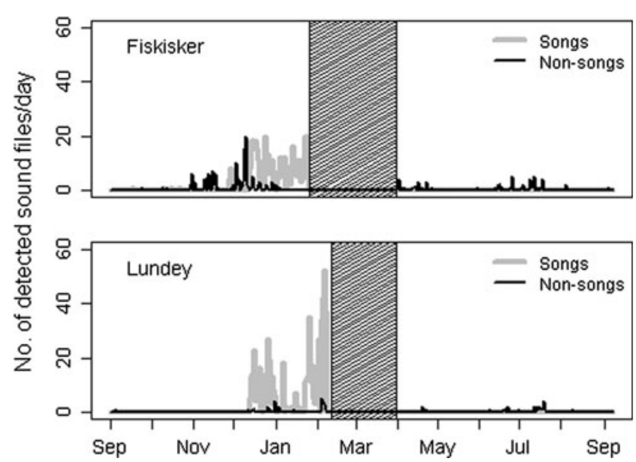

Fig. 2 Number of sound files per day containing humpback whale song units (*grey*) and non-song signals (*black*) from both locations during the two deployments, i.e. fall 2008 through spring 2009 and spring through fall 2009. The *shaded column* represents periods of no recording

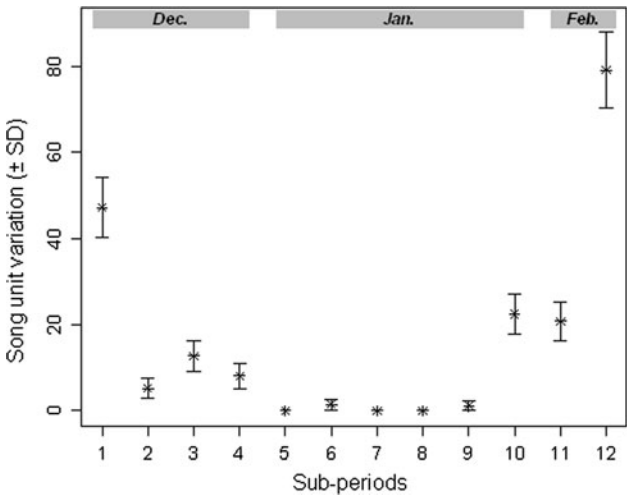

Fig. 3 Song unit variation within each of the 12 5-day sub-periods, during 13 December 2008–12 February 2009

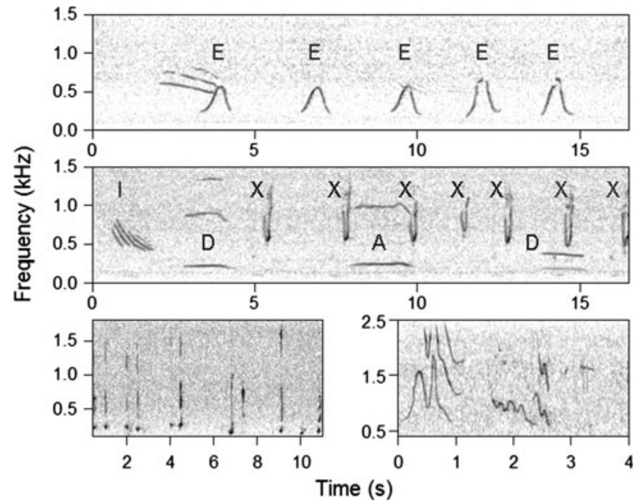

Fig. 4 Examples of some of the most commonly detected song units (*A*, *D*, *E* and *I*) embedded in phrases and song units from the end of the winter period (*X*). The *first two spectrograms* include song phrases, whereas the *two bottom spectrograms* display two recordings of different non-song signals, i.e. short up calls (*left*) and high-pitched screams (*right*). The top spectrogram includes a version of the I unit which is not produced by the same individual as of the *E* units. The second spectrogram includes one whole phrase (*I-X-X-X-X-X-X*) produced by one individual and a part of another phrase (*D-A-D*) produced by another individual

units produced varied throughout the singing period. The occurrence of humpback whale song units increased extensively in mid-December, and the greatest number of detections occurred in February despite only 12 days of recording that month (Fig. 2). Detections of non-song sounds started in September at both locations, whereas the number of detections increased considerably between November and December at Fiskisker and decreased again as the occurrence of songs increased. There was no significant difference in the number of song file detections per day between the two recording locations ($t = 1.08$, $df = 371$, $P = 0.28$). However, the detections of non-song sounds per day were significantly higher at Fiskisker ($t = 3.83$, $df = 371$, $P < 0.001$). The largest variety in song unit production, in terms of the number of occurrences per unit type, was observed during the last sub-period, (6–12 February), and the lowest during the mid-season corresponding to less song detection during those sub-periods (Fig. 3).

Song components

A total of 550 song units were measured, of which 23 different song units were identified (see Online Resource 1). The average duration of a single humpback whale song unit was 0.96 s (SE = ±0.02), average low frequency was 281.09 Hz (SE = ±4.48), average high frequency was 527.97 Hz (SE = ±8.47) and average frequency range was 246.9 Hz (SE = ±7.54). A special type of unit with down-swept harmonics not found in the literature was categorized as song unit I (Fig. 4). This unusual type of unit was almost exclusively observed in a pattern with other known song units and accordingly recognized as a humpback whale song unit.

The most commonly detected song unit was C followed by E, I, D and A (Fig. 4; see Online Resource 1) which all were detected throughout the entire period of singing activity. Unit C had the highest mean number of occurrences per sub-period. Other song units mostly occurred during specific sub-periods and peaked either during early or late winter (see Online Resource 2).

Diel trends in song and non-song signals

The detections of humpback whale songs and non-song signals showed no diel trends throughout the winter (Cochrane–Orcutt autocorrelation test: *songs*: $F_{3,1628} = 0.25$, $P = 0.86$; *non-songs*: $F_{2,1077} = 0.27$, $P = 0.77$). Additionally, there was no significant difference in the levels of song (ANOVA: $F_{2,1629} = 0.33$, $P = 0.72$) and non-song (ANOVA: $F_{2,1077} = 0.66$, $P = 0.52$) detections between the light regimes during the winter. However, compared with the detection of non-song signals, the relative proportion of songs was significantly higher during dark hours than daylight hours (Fishers exact test: $P = 0.02$, OR = 1.65), but was the same during dark and dusk hours (Fishers exact test: $P = 1$, OR = 0.98) and not considered significantly different between dusk and daylight hours (Fishers exact test: $P = 0.06$, OR = 1.68). In comparison, diel patterns were observed for non-song sounds during the summer (Cochrane–Orcutt autocorrelation test: $F_{1,1054} = 4.62$, $P = 0.004$) and a statistically significant difference in the mean level of detections between dark and light hours (TukeyHSD: $P = 0.002$) and dark and dusk hours (TukeyHSD: $P = 0.035$) but not between light and dusk hours (TukeyHSD: $P = 0.49$).

Discussion

This study investigated the occurrence of songs in subarctic waters on a year-round basis, whether there are evidences of changes in the song structure based on changes in song unit types as the winter progresses, and whether the limited daylight conditions of the subarctic winter could affect the occurrence of singing as has been shown for other baleen whale species. While it was not possible to address the structure of whole songs for comparison to those of humpback whales in other regions, due to the nature of the data sampling (1-min sound files recorded every 15 min), analysis of the occurrence and variability of different song units and changes in unit types produced per time during the mating season showed variability of phrases in song and that properties of song in this region change throughout the season. This study shows that humpback whales sing in subarctic waters during winter and that the types of song units used within an area can be useful for comparison to other feeding and breeding grounds.

While non-song signals were found in the same recordings as song units, this was not used as criterion for non-song signal classification and behaviours associated with the non-song signals were not analysed in this study. Non-song signals can be used by humpback whales for various purposes and be related to various group combinations, both during social interaction and feeding (Dunlop et al. 2008). Specific study on non-song sounds in Skjálfandi bay is being conducted that will investigate such behavioural correlates more thoroughly.

The songs found in this study were fundamentally characterized by five regularly occurring song units (A, C, D, E, and I), and the other units were added more sporadically to the songs. The occurrence of different song units changed gradually throughout the season. Of the 23 measured song units, only six were concentrated to the end of the period, indicating gradual changes in song construction throughout the winter as has been seen in other breeding areas (Payne et al. 1983; Payne and Guinee 1983; Payne and Payne 1985; Cerchio et al. 2001). Also, the variety of units in the songs increased at the end of the season suggesting greater effort in inter- or intra-sexual display when reaching the peak of the reproductive season, despite geographical location.

At least three of the fundamental song units (A, D and E) could be matched with song units described in the West Indies (Mattila et al. 1987) and on a western North Atlantic feeding ground (Clark and Clapham 2004). We are not aware of any other published studies that contain more extensive song descriptions for humpback whales in the North Atlantic for further comparison.

The song unit "I" differed from other reported stereotypical humpback whale song units. The structure of units can vary between areas, since they can change differently within each mating ground due to cultural innovation (Cerchio et al. 2001). It seems that a part of the units recorded in Skjálfandi Bay belongs to fundamental song components shared by other remote areas while a part of the song units could be special for this subarctic region.

The timing of increased singing activity in Iceland corresponds to the timing of songs for other distant breeding populations, such as in Hawaii (Herman et al. 1980; Au et al. 2000), but in contrast with studies from northern feeding grounds which have shown high singing activity before and after the peak mating season (Clark and Clapham 2004; Vu et al. 2012). Likely causes for these singing events are individuals that prolong their feeding season into the mating season or do not migrate at all. It has been shown that mature humpback whales often appear later on feeding (Gregr et al. 2000) and breeding grounds and also leave their breeding grounds later (Nishiwaki 1959, 1960, 1962). Therefore, mature males may start singing while still on their feeding grounds to gain access to more females. Humpback whale females, which commonly have two year reproductive cycle (Chittleborough 1958; Glockner-Ferrari and Ferrari 1984; Baker et al. 1987; Steiger and Calambokidis 2000), sometimes overwinter at high latitudes (Brown et al. 1995; Craig and Herman 1997; Smith et al. 1999). It could be a trade-off strategy for both sexes to overwinter in the subarctic or migrate late and attempt at mating while still having access to an abundance of food. Similar evidence has been found for fin whales (*Balaenoptera physalus*) during winter in the Davis Strait (Simon et al. 2010).

Studies from tropical mating grounds have shown diel variation in singing intensity (Au et al. 2000) and the observed behaviour of male humpback whales (Helweg and Herman 1994). However, this study showed no obvious diel trends in acoustic activity during the winter in relation to light conditions, only for non-song sounds during the summer. On the other hand, the results suggest that humpback whales spend a higher proportion of their time on singing during dark hours than during the few daylight hours of the winter. Fin whales detected in the Arctic during winter usually sing intensively during the dark period of the day while they are assumed to use the short daylight for feeding (Simon et al. 2010). The short light periods, and where food is available, likely influence the daily occurrence of humpback whales' songs in the subarctic.

Further studies are required with longer recording sessions to capture larger proportion of the songs in this area. Additionally, more intense visual observations along with skin sample or biopsy collection would be needed for a better understanding of the humpback whales sex ratio and behaviour during the winter in this part of the world.

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