Low-frequency signals produced by Northeast Atlantic killer whales (*Orcinus orca*)

Filipa I. P. Samarra[1]
Marine Research Institute, Skulagata 4, PO Box 1390, 121 Reykjavík, Iceland
fipsamarra@gmail.com

Volker B. Deecke
Centre for Wildlife Conservation, University of Cumbria, Rydal Road, Ambleside, Cumbria, LA22 9BB, United Kingdom

Patrick J. O. Miller
Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews KY16 8LB, United Kingdom
pm29@st-andrews.ac.uk

Submission date: 29 January 2016

Running title: Killer whale low frequency sounds

[1] Author to whom correspondence should be addressed. Electronic mail: fipsamarra@gmail.com

Abstract

Killer whale acoustic behavior has been extensively investigated, however most studies have focused on pulsed calls and whistles. This study reports the production of low-frequency signals by killer whales at frequencies below 300 Hz. Recordings were made in Iceland and Norway when killer whales were observed feeding on herring, and no other marine mammal species were nearby. Low-frequency sounds were identified in Iceland and ranged in duration between 0.14 and 2.77 seconds and in frequency between 50 and 270 Hz, well below the previously reported lower limit for killer whale tonal sounds of 500 Hz. Low-frequency sounds appeared to be produced close in time to tail slaps, which are indicative of feeding attempts, suggesting that these sounds may be related to a feeding context. However, their precise function is unknown and they could be the by-product of a non-vocal behavior, rather than a vocal signal deliberately produced by the whales. Although killer whales in Norway exhibit similar feeding behavior, this sound has not been detected in recordings from Norway to date. This study suggests that, like other delphinids, killer whales produce low-frequency sounds but further studies will be required to understand whether similar sounds exist in other killer whale populations.

PACS numbers: 43.80.Ka

I. INTRODUCTION

Cetaceans produce a variety of acoustic signals, generally divided into clicks, pulsed calls, and tonal signals, for communication and echolocation (see Richardson *et al*., 1995 for a review). Tonal signals are usually sounds with a continuous sinusoidal waveform and narrow-band frequency, typically with harmonics. Different terminology is used to describe them depending on species group; in odontocetes tonal signals are generally referred to as 'whistles', although this terminology may not be appropriate due to these sounds being produced by tissue vibrations rather than by resonating air volumes (Madsen *et al*., 2012). In mysticetes, tonal signals are generally designated as 'moans' or 'tonal calls' (Richardson *et al*., 1995).

The sound frequency of tonal signals appears to be negatively correlated to body size in cetaceans, with the larger baleen whales producing lower frequency signals than odontocetes (Ding *et al*., 1995; Matthews *et al*., 1999; Podos *et al*., 2002). Once phylogeny is taken into account, this relationship only holds for minimum frequency, but not for maximum frequency (May-Collado *et al*., 2007). However, low frequency (<1500 Hz) tonal sounds have also been described for some delphinids. For example, bottlenose dolphins (*Tursiops truncatus*) produce low frequency narrow-band sounds (Schultz *et al*., 1995; Simard *et al*., 2011; Gridley *et al*., 2015), 'gulps' (dos Santos *et al*., 1995) and 'moans' (van der Woude, 2009), as well as low-frequency pulsed calls, the 'bray calls' (dos Santos *et al*., 1995; Janik, 2000). Other low-frequency narrow-band sounds include Risso's (*Grampus griseus*) and Pacific humpback dolphin (*Sousa chinensis*) 'grunts' (Corkeron and Van Parijs, 2001; Van Parijs and Corkeron, 2001) and Atlantic spotted (*Stenella frontalis*) and bottlenose dolphin 'barks' (Herzing, 1996). Contextual production suggests these sounds are generally associated with socializing (e.g. Simard *et al*., 2011), and feeding behaviors (Janik, 2000; Gridley *et al*., 2015). The minimum frequency of delphinid low-frequency sounds can be as low as 39 Hz and well within the frequency range of baleen whale ‘moans’ and ‘tonal calls’ (van der Woude, 2009).

Killer whale (*Orcinus orca*) tonal signals are also referred to as ‘whistles’ and although few quantitative descriptions have been conducted, whistle frequency characteristics appear to vary between populations or ecotypes. For example, while resident and transient killer whales in the North Pacific appear to produce whistles in the audible range (<20 kHz; Thomsen *et al*., 2001; Riesch and Deecke, 2011), others in the North Pacific, North Atlantic and Antarctic also produce whistles in the ultrasonic range (>20 kHz; Samarra *et al*., 2010; Simonis *et al*., 2012; Filatova *et al*., 2012; Trickey *et al*., 2014). Ultrasonic whistles of killer whales in Iceland and Norway appear to have higher fundamental frequency, shorter duration and more variable time-frequency contours than those of whales in the Pacific Ocean (Samarra *et al*., 2015). Quantitative descriptions of the whistles produced by Northeast Pacific resident and transient killer whales show that duration ranges between 0.06 and 18.3 s, and the fundamental frequency ranges from 2.4 to 16.7 kHz (Thomsen *et al*., 2001; Riesch and Deecke, 2011), although minimum frequency can be as low as 1.5 kHz (Ford, 1989). In the Northwest Atlantic tonal signals with minimum frequency of 0.5 kHz were reported (Steiner *et al*., 1979). Whistles are mostly produced during socializing or high-arousal contexts (Ford, 1989; Thomsen *et al*., 2002) and some have stereotyped frequency contours that are often produced in complex sequences (Riesch *et al*., 2006, 2008).

Although the vocal behavior of killer whales has been extensively studied in several locations, most studies have focused on pulsed calls, the most common vocalization produced (e.g., Moore *et al*., 1988; Ford, 1989; Strager, 1995; Filatova *et al*., 2007). Killer whale social groups produce unique and stable repertoires of stereotyped pulsed calls that are used in different behavioral contexts (Ford 1989, 1991). In Iceland and Norway killer whale call production increases significantly during feeding (Simon *et al*., 2007). Both populations are thought to feed primarily on Atlantic herring (*Clupea harengus*; Sigurjónsson *et al*., 1988; Similä *et al*., 1996), using coordinated group feeding where whales encircle herring schools and use underwater tail slaps to debilitate their prey before feeding (Similä and Ugarte, 1993; Simon *et al*., 2007; Samarra and Miller, 2015). Underwater tail slaps produce a characteristic broadband multipulsed sound (Simon *et al*., 2005) that can be used as an acoustic cue of a feeding attempt (Samarra and Miller, 2015). Pulsed calls produced during feeding are thought to be used for group coordination (Similä and Ugarte 1993; Shapiro 2008; Samarra and Miller 2015) and because herring respond to killer whale sounds (Doksæter *et al*., 2009; Sivle *et al*., 2012), these acoustic stimuli may serve to help modify the herrings' behavior (Similä and Ugarte 1993).

The low-frequency component of calls produced by Northeast Atlantic killer whales has slightly higher median frequency than calls of North Pacific resident whales and significantly higher than transient killer whales, with the majority of calls having a median frequency between 0.5-1 kHz (Filatova *et al*., 2015). Generally, killer whale pulsed calls have pulse repetition rates between 0.25 and 2 kHz, with most energy between 1 and 6 kHz, and durations from less than 50 ms to over 10 s (Ford, 1989).

Quantitative descriptions of calls produced by killer whales in Norway report frequencies between 0.04 and 4.8 kHz and durations ranging between 0.11-2.2 s (Strager, 1993, 1995), while in Iceland mean frequencies varied between 0.16 and 3.28 kHz and mean duration between 0.355 and 2.142 s (Moore *et al*., 1988;). In Iceland, a distinctive long, low frequency call is produced exclusively during feeding just before an underwater tail slap, termed 'herding call' (Simon et al. 2006). This call was recently also recorded in Shetland (UK) also in association with feeding upon herring (Deecke *et al*., 2011). The herding call has a relatively flat time-frequency contour and peak fundamental frequencies may vary between 406 and 1414 Hz while duration ranges from 0.83 to 8.5 s (Samarra, 2015). Due to its low frequency, presumably unsuitable for intra-specific communication, but within the frequency range that herring is sensitive to, the herding call is thought to function in prey manipulation (Simon *et al*., 2006). It is thought that herding call production leads to an anti-predator response of the herring, which schools tighter. By helping compact the herring school prior to an underwater tail slap this call likely increases feeding efficiency (Simon *et al*., 2006).

Although the characteristics of killer whale signals have been investigated in some locations, low-frequency sounds such as those produced by some other delphinids have, to our knowledge, not been previously reported for this species. Here we report distinctly low frequency (<300 Hz) narrow-band sounds produced by Northeast Atlantic killer whales, hereafter termed LFS. We analyze recordings of killer whales in Iceland and Norway to investigate the production of such sounds across different populations.

II. METHODS

A. Data collection

Acoustic recordings were made in Iceland and Norway in multiple years and multiple locations (Table I, Figure 1). All recordings were collected in fjords or open water locations where killer whales were observed feeding on herring. We used a variety of recording systems, including a 16-element towed hydrophone array recording onto an Alesis© ADAT-HD24 XR (frequency response 0.022-44 kHz, ±0.5 dB; Miller and Tyack, 1998; Alesis, Cumberland, RI); a 2 element towed array with Benthos© AQ-4 (Teledyne Benthos, Falmouth, MA) and Magrec© HP-02 pre-amplifiers (Magrec Ltd., Lifton, UK; frequency response 0.1-40 kHz, ±3 dB) towed array recording onto a Marantz© PMD671 (frequency response 0.02-44 kHz, ±0.5 dB; Marantz America LLC, Mahwah, NJ) or a Sound Devices© 702 (frequency response 0.001-40 kHz, ±0.5 dB; Sound Devices LLC, Reedsburg, WI); a 4-element vertical array (High Tech Inc© 94-SSQ with pre-amplifiers; frequency response 0.002-30 kHz; High Tech Instruments, Long Beach, MS) connected to an Edirol© FA-101 soundcard (frequency response 0.02-40 kHz, +0/-2 dB; Roland Corporation US, Los Angeles, CA) and recording onto a laptop using PAMGUARD (Gillespie *et al*., 2008) or connected to a Roland© R-44 (frequency response 0.02-40 kHz, +0/-3 dB; Roland Corporation US, Los Angeles, CA); a single hydrophone (High Tech Inc© 94-SSQ with pre-amplifiers; flat frequency response 0.002–30 kHz) recording onto a laptop using Adobe Audition 2.0©, or recording onto a M-Audio Microtrack II (M-Audio, Cumberland, RI); and movement and sound recording tags attached to killer whales using suction cups (‘Dtags’; flat frequency response 0.6-45 kHz; Johnson and Tyack, 2003). With the exception of Dtags, all recording systems had a lower frequency response varying between 0.002-0.1 kHz.

In 2014 an Ecological Acoustic Recorder (EAR, Lammers *et al*., 2008) was deployed at a depth of ~30 m in inner Kolgrafafjörður, Iceland (Figure 1). The inner part of the fjord was only accessible through a narrow and shallow man-made channel, with very strong currents, and was the location where large quantities of herring (*Clupea harengus*) were found in 2014. Killer whales were often observed passing through the narrow channel to feed on herring in the inner part of the fjord. The EAR was deployed between the 22nd February and the 31st March 2014, recording for 5 minutes every 10 minutes at a sampling rate of 64 kHz. No other marine mammals were observed (or acoustically detected) in the vicinity during acoustic recordings of killer whales in Iceland and Norway, except for the winter of 2014 when occasionally white-beaked dolphins (*Lagenorhynchus albirostris*) and pinnipeds were observed in the same area but never in close proximity to the killer whales. Visual observations were usually conducted from the observation boat during all acoustic recordings with the exception of EAR recordings, which continued in bad weather conditions or at night when the research vessel was absent. Thus, low frequency sounds detected in these conditions were assumed to be produced by killer whales if produced concurrently with other killer whale sounds. Nevertheless, no other sounds were clearly detected on the EAR recordings that would suggest the presence of other marine mammal species.

B. Acoustic analysis

All recordings were inspected using Adobe Audition 2.0 (Adobe Systems Inc., San Jose CA) using the following FFT settings: Blackmann-Harris window; FFT=8192 or 16384, for 64 or 96 kHz and 192 kHz sampling rates, respectively; 100% window width;

or Audacity 2.0.3 (Audacity Development Group, Pittsburgh, PA) using the settings: Hanning window; FFT=8192 or 16384, for 64 or 96 kHz and 192 kHz sampling rates, respectively; 100% window width). The beginning and end time of each LFS was marked. In general, LFS were easily distinguishable from other sounds, but if any ambiguous sounds were detected these were not marked or used for further analyses. Each detected LFS was then extracted from the main recording, lowpass filtered to avoid aliasing and the sampling frequency was converted to 2 kHz. Start, end, minimum and maximum frequency and duration were measured from each LFS with cursors directly from the spectrogram display created in MATLAB R2013a. The precision of these measurements was probably in the order of 50-100 ms, thus measurements from signals with duration of 100 ms or less should be interpreted with care. We only extracted parameters from LFS clearly visible in the spectrogram with signal to noise ratios >10 dB and not overlapped with noise (e.g., from movements of the hydrophone or loud flow noise).

To compare how these sounds differed from other killer whale low frequency sounds previously described in the literature we compared these measurements to measurements taken from herding calls (the same sample as in Samarra, 2015). We first compared the parameter distributions using Mann-Whitney U-tests, to account for the non-normality of most parameter distributions (Shapiro-Wilk normality tests: $P < 0.0001$, except for LFS end frequency with $P=0.006$ and LFS maximum frequency with $P=0.25$). We used a Bonferroni correction to adjust the significance level to account for multiple comparisons ($0.05/5 = 0.01$). We further input these measurements into a multivariate discriminant function analysis where sound type (herding call or LFS) was used as the grouping variable and we used a jackknife cross-validation technique implemented in the *lda* function of package MASS version 7.3-16 (Venables and Ripley, 2002) in R 3.2.2 for Mac OS X (R Core Team, 2015). The overall proportion of correct classifications and the proportion of correct classifications by location were calculated and compared to the proportion of by-chance accuracy, which was assumed to be equal (50%) for both sound types.

C. Behavioral context

To investigate whether LFS might be produced in a feeding context we analyzed a Dtag deployment containing different behavioral contexts, where several LFS were detected with sufficient quality for analysis. This Dtag was deployed on a large juvenile killer whale in Iceland in July 2009 and the whale was tracked from an observation boat throughout the deployment duration. Sounds used in the analysis were assumed to have been produced by the tagged whale or by whales in its immediate vicinity, at similar depth and engaged in the same behavior. We restricted our analysis to this sample as the majority of the other acoustic recordings where we detected high quality LFS were restricted to a feeding context. This preliminary analysis was conducted to study possible contextual production but results should be interpreted with care given these are based on one sample. We calculated the time interval between each LFS and the nearest tail slap (which can be used as an acoustic cue of a feeding attempt; Samarra and Miller 2015) and then randomized LFS timing by linking the start and end of the deployment and rotating the LFS production sequence a random amount of time. We repeated this step 100,000 times to generate a probability distribution of mean expected intervals to nearest tail slap and compared it to the observed values.

III. RESULTS

We collected 553.4 hours of recordings from Iceland and 100.4 hours of recordings from Norway (Table I). The difference in total recording time between Iceland and Norway is mainly due to the 432 hours of recordings collected with a stationary hydrophone in the winter season of 2014 in Iceland. The methodologies used in both locations differed somewhat; in Norway only towed arrays and Dtags were used while in Iceland vertical arrays, single hydrophones and a stationary hydrophone were also used (Table I).

We detected 852 LFSs sounds in Iceland but no similar sounds in Norway (Table I). A total of 189 LFSs were selected for parameter measurements, 50 from winter and 139 from summer. LFS were recorded in several years, different locations and always concurrently with other killer whale sounds. Recordings collected with a stationary hydrophone also included several hours of recordings with no killer whale sounds, but LFSs were only recorded concurrently with other killer whale vocalizations.

In general, LFSs showed little frequency modulation and were characterized by an inverted ‘u’ increase in frequency followed by a decrease (Figure 1). In most cases (90%) analyzed LFSs had one or more harmonics at least partially visible (Figure 1). The sinusoidal waveform suggests that these are tonal signals (Figure 1). Figure 2 shows the distributions of all LFS parameters measured. LFS duration ranged between 0.14 and 2.77 s with a mean ± standard deviation of 0.67 ± 0.31 s. All sounds analyzed were produced exclusively below 300 Hz (Figure 2). LFS had a mean ± standard deviation (minimum-maximum) start frequency of 136 ± 27 Hz (67-219), end frequency of 131 ± 29 Hz (67-233), minimum frequency of 113 ± 22 Hz (50-216) and maximum frequency of 189 ± 26 Hz (113-270).

Comparisons between the time and frequency parameters of LFSs and herding calls revealed significant differences in all parameters measured, including start frequency (mean ± standard deviation of 136 ± 27 Hz for LFS vs. 860 ± 284 Hz for herding calls; Mann-Whitney U-test: W=79001; P<0.0001), end frequency (131 ± 29 Hz for LFS vs. 1050 ± 286 Hz for herding calls; Mann-Whitney U-test: W=79002; P<0.0001), minimum frequency (113 ± 22 Hz for LFS vs. 823 ± 267 Hz for herding calls; Mann-Whitney U-test: W=79000; P<0.0001), maximum frequency (189 ± 26 Hz for LFS vs. 1070 ± 285 Hz for herding calls; Mann-Whitney U-test: W=79002; P<0.0001) and duration (0.67 ± 0.31 s for LFS vs. 2.9 ± 1.0 s for herding calls; Mann-Whitney U-test: W=78466; P<0.0001). The discriminant function analysis also showed good discrimination between the two signal types with an overall correct classification rate of 99%, with 100% of LFS and 99% of herding calls being correctly assigned to type. Only 4 of 418 herding calls were incorrectly assigned to the LFS category.

Figure 3 displays the dive profile and concurrent sound production of a Dtag deployed on a killer whale off the Vestmannaeyjar archipelago in Iceland in the summer of 2009 (deployment oo09_201a). This deployment appears to have captured some non-feeding behavior, including silent periods which likely represent travelling, as well as a feeding event initiated near the end of the deployment, characterized by deep diving, increased clicking and calling, and production of tail slaps (detailed view in Figure 3 top).

The majority of LFS are recorded during the bottom of these feeding dives, just prior to a tail slap, suggesting contextual production of LFS during feeding. The mean interval to nearest tail slap throughout this record was 83 s, which was significantly lower than chance (mean interval of randomizations = 32 minutes; $P<0.005$). However, a different Dtag deployment (oo09_200a) in the same location in Iceland, which also included feeding behavior did not contain LFS, suggesting that if specific to a feeding context, LFS production is not ubiquitous during all feeding events.

IV. DISCUSSION

Killer whales produce a variety of acoustic signals, but to date low-frequency signals as seen in other delphinids had not been reported. In this study we report a characteristic low-frequency sound (termed LFS) that was recorded in the presence of Icelandic killer whales. Although this population is known to produce low frequency calls, termed ‘herding’ calls (Simon *et al*., 2006) our comparisons showed that LFS are significantly different from herding calls. LFS are exclusively produced below 300 Hz, which is much lower than the typical herding call frequencies of approximately 700 Hz or above (Simon et al. 2006; Samarra, 2015). In addition, herding calls are generally long (~3 s), while low frequency sounds have an average duration of ~0.7 s. Finally, herding calls also appear to have different time-frequency contours, generally flat often ending with a slight upsweep, while LFS described here typically have an inverted ‘u’ shape. Thus, the sounds we describe here represent a novel sound type previously unreported for the Icelandic killer whale population.

When describing a novel sound type, particularly using recordings where the signaler cannot be identified with certainty, it is important to establish whether any other species could have produced the sounds. Herring are known to produce sounds when releasing air from the anal duct, however LFS are unlike those previously described sounds (Wahlberg and Westerberg, 2003; Wilson *et al*., 2004). In addition, LFSs were not detected in the EAR recordings in the absence of killer whales but when herring were presumably present in the area. To the best of our knowledge, sounds such as those described here have not been previously recorded from herring. It also seems unlikely that these sounds were produced by another species of cetacean or pinniped, as LFS were consistently recorded only in the presence of other killer whale sounds, and close in time with their feeding activity (Figure 3). No other marine mammals were ever seen feeding in close spatial proximity to feeding killer whales in any of our daytime recordings. In addition, one recording site was a small (approximately 5 km total length), shallow fjord, Kolgrafafjörður (maximum depth ~40 m), where the presence of any baleen whale within acoustic range would have been detected. During recordings collected with the autonomous recorder, which included day and night-time recordings as well as days with and without killer whales present, there were many hours of silence. LFS sounds were only detected concurrently with other killer whale sounds in these recordings. Finally, clear examples of the sound recorded on the Dtag attached to a killer whale provide further evidence that they were produced by the tagged individual or a nearby whale (Figure 3). The large acoustic recording sample we used, spanning several years, recording locations and methodologies, together with the consistent production of LFS concurrently with killer whale sounds, strongly points to killer whales to be the species that produced these sounds.

Unlike other delphinids that appear to produce low-frequency sounds mostly during socializing contexts (Schultz *et al*., 1995; Simard *et al*., 2011; Gridley *et al*., 2015), the signals reported here appear linked to feeding by killer whales, which is a social, coordinated behavior. However, these sounds were not reported in all feeding events thus further data is necessary to confirm the contextual production of LFSs. Bottlenose dolphins also produce low-frequency sounds during feeding, the 'bray calls' (Janik, 2000). However, studies of the function of LFS will be necessary before comparisons can be drawn between the use of low-frequency sounds across different species.

Like previously described low frequency sounds of other delphinids, such as the low frequency narrow-band sounds and moans of bottlenose dolphins (Schultz *et al*., 1995; van der Woude, 2009; Simard *et al*., 2011) killer whale LFSs sounds had little frequency modulation (Figure 1). However, LFSs were considerably longer than bottlenose dolphin low frequency narrow-band sounds (mean of 0.05 sec; Schultz *et al*., 1995), shorter than moans (mean of 2.08; van der Woude, 2009) but had a similar frequency range to that of bottlenose dolphin moans (150-240 Hz, van der Woude, 2009), with the fundamental frequency ranging between 100-250 Hz. Based on these characteristics, this signal may have various putative functions.

It is possible that LFSs may be a non-vocal by-product of another behavior. For example, bottlenose dolphin 'moans' appear to be produced concurrently with bubblestream and it is unclear if the sounds are produced in association with the bubblestream or as a result of it (van der Woude, 2009). LFSs show similarities in frequency content to these signals, thus could similarly be associated with bubble production in killer whales. Similä and Ugarte (1993) report bubble production by Norwegian killer whales feeding on herring that is thought to help herd the herring further and our own field observations suggest this also occurs in Iceland. However, the fact that LFS were not recorded in all feeding events and were not recorded in Norway, where killer whales are known to produce bubbles when feeding (Similä and Ugarte, 1993), suggests that these sounds may not be a by-product of bubble production by killer whales, although a larger sample size may be necessary to rule this out. However, LFSs could still be the by-product of movement or other type of unknown behavior. LFSs were not recorded frequently suggesting that if these sounds are produced as the by-product of a behavior or movement, this behavior only happens rarely. Alternatively, LFSs may be a vocal signal deliberately produced by killer whales for communication or to manipulate prey behavior.

Based on the known hearing sensitivity of killer whales a communicative function is perhaps unlikely. The frequency range of LFSs is considerably below the best hearing sensitivity of killer whales (18-42 kHz; Szymanski *et al*., 1999). Measurements of killer whale hearing sensitivity at the frequency of the signals reported here have not been conducted, however hearing sensitivity is considerably decreased at 1kHz (Hall and Johnson, 1972; Szymanski *et al*., 1999). Estimates of LFS source level and killer whale hearing sensitivity at frequencies below 1 kHz would be required to test whether killer whales can perceive these sounds, even if only at close range, as has been demonstrated for the low-frequency sounds produced by other delphinids (Simard *et al*., 2011). On the other hand, herring is most sensitive at frequencies between 100-1200 Hz (Enger, 1967) thus LFS could be directed at prey. Since Icelandic killer whales are known to produce feeding-specific calls of low frequency that are thought to function in prey manipulation (Simon *et al*., 2006), LFSs could be an additional signal serving a similar function. However, our analysis shows that LFSs are significantly different from herding calls and in comparison to herding calls, LFSs appear to have lower amplitude thus might not be effective signals for prey manipulation. In addition, it is unclear why the whales would require two different sound types with a redundant functionality. Further data will be required to address these questions, particularly using animal-attached tags that could provide high-resolution data on the behavioral context and help identify contextual variations that could help explain the function of LFS and the factors driving its production in some contexts.

Intra-specific variability in acoustic signals produced during feeding may represent individual variation or an adaptation to prey-targeted or environmental characteristics. For example, humpback whales (*Megaptera novaeangliae*) in Alaska produce feeding calls that have not been recorded from feeding humpbacks elsewhere (Jurasz and Jurasz, 1979; D'Vincent *et al*., 1985; Cerchio and Dahlheim, 2001), while in the Northwest Atlantic feeding humpbacks produce short pulses of broadband sound termed 'megapclicks' (Stimpert *et al*., 2007) and paired pulses (Parks *et al*., 2014) that also appear to be exclusive to this location. Similarly only killer whales in Iceland and Shetland have been recorded producing herding calls when feeding on herring (Simon *et al*., 2006; Deecke *et al*., 2011; Samarra, 2015). Despite feeding on the same prey, feeding strategies adopted by killer whales in Iceland and Norway differ (Samarra and Miller, 2015). It is possible that, like herding calls (Simon *et al*., 2006), LFSs are produced as part of a feeding behavior that is exhibited by killer whales in Iceland, but not in Norway. Nevertheless, we cannot rule out the possibility that the absence of these sounds in our Norwegian sample is simply due to sampling limitations or differences in some of the recordings methods (Table I).

The low-frequency characteristics of these sounds make them easily masked by low frequency noise sources (e.g. boat noise), thus LFS may go unnoticed. For example, the use of towed hydrophone arrays deployed from a moving vessel or Dtags with flow noise can influence the ability to detect these signals. Poor low-frequency response of recording systems or deliberate low-frequency cutoffs to reduce noise may further reduce the ability to detect these signals, which in addition to different research focuses (e.g., on pulsed calls or whistles) could explain the absence of these sounds from studies in other populations. It is likely that such low-frequency sounds exist in other populations but due to their infrequent production have not been previously described. For example, in Shetland a small sample of low-frequency sounds were detected (V. B. Deecke, unpublished data). Different terminology may also have been assigned to LFS-like sounds detected in other populations (e.g., ‘grunts’ or ‘moans’) but to the best of our knowledge quantitative descriptions to allow comparison have not been provided. Further investigation of acoustic recordings from other populations would be valuable to investigate if occurrence of low-frequency sounds is widespread.

This study contributes to our knowledge of the acoustic repertoire of killer whales, however, additional data will be required to understand the production mechanism, function, and behavioral context of LFS and whether they are exclusively produced by only a few populations. Although our findings suggest that some Northeast Atlantic killer whales can produce sounds across a wide range of fundamental frequencies (50 Hz to 75 kHz, Samarra *et al*., 2010), there are clear distinctions between these signals, which likely serve different functions. Our study shows that, like other delphinids, killer whales also produce low-frequency sounds, suggesting these are common among delphinids. The inclusion of such sounds in future evolutionary studies of cetacean tonal signal frequency may be worthwhile.

Acknowledgments

We sincerely thank everyone involved in the various field seasons, Dr. Marc Lammers for providing the EAR for acoustic recordings in 2014 and Dr. Olga Filatova and Ivan Fedutin for coordinating the collection of the EAR data. The field efforts of 2008-9 were conducted as part of the 3S collaborative research program. We would also like to thank D. Risch for helpful discussions. Funding was provided by the BBC Natural History Unit, Fundação para a Ciência e a Tecnologia (Grant Number SFRH/BD/30303/2006), the Icelandic Research Fund (i. Rannsóknasjóður) through a START Postdoctoral Fellowship (Grant Number 120248042), the National Geographic Global Exploration Fund (Grant Number GEFNE65-12), the Office of Naval Research (Grant Number N00014-08-10984) and Russell Trust Award from the University of St Andrews. All field research was carried out in compliance with local regulations. We thank two anonymous reviewers for very helpful comments.

References

Corkeron, P. J., and Van Parijs, S. M. (**2001**). "Vocalizations of eastern Australian Risso's dolphins, *Grampus griseus*," Can. J. Zool. **79**, 160-164.

Deecke, V. B., Nykänen, M., Foote, A. D., and Janik, V.M. (**2011**). "Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK". Aquat. Biol. **13**, 79–88.

Ding, W., Würsig, B., and Evans, W. (**1995**). "Comparisons of whistles among seven odontocete species," in: *Sensory Systems of Aquatic Mammals*, edited by R. A. Kastelein, J. A. Thomas and P. E. Nachtigall (De Spil Publishers, Woerden, The Netherlands), pp. 299-323.

Doksæter, L., Godø, O. R., Handegard, N. O., Kvadsheim, P. H., Lam, F. P. A., Donovan, C., and Miller, P. J. O. (**2009**). "Behavioral responses of herring (*Clupea harengus*) to 1–2 and 6–7 kHz sonar signals and killer whale feeding sounds," J. Acoust. Soc. Am. **125**, 554–564.

dos Santos, M. E., Ferreira, A. J., and Harzen, S. (**1995**). "Rhythmic sound sequences emitted by aroused bottlenose dolphins in the Sado Estuary, Portugal," in *Sensory Systems of Aquatic Mammals*, edited by R. A. Kastelein, J. A. Thomas and P. E. Nachtigall (De Spil, Woerden, The Netherlands), pp. 325–334.

Enger, P.S. (**1967**). "Hearing in herring," Comp. Biochem. Physiol. **22**, 527-538.

Filatova, O. A., Fedutin, I. D., Burdin, A. M., and Hoyt, E. (**2007**). "The structure of the discrete call repertoire of killer whales *Orcinus orca* from southeast Kamchatka," Bioacoustics **16**, 261-280.

Filatova, O. A., Ford, J. K. B., Matkin, C. O., Barrett-Lennard, L. G., Burdin, A. M., and Hoyt, E. (**2012**). "Ultrasonic whistles of killer whales (*Orcinus orca*) recorded in the North Pacific (L)," J. Acoust. Soc. Am. **132**, 3618-3621.

Filatova, O. A., Miller, P. J. O., Yurk, H., Samarra, F. I. P., Hoyt, E., Ford, J. K. B., Matkin, C. O., and Barrett-Lennard, L. G. (**2015**). "Killer whale call frequency is similar across the oceans, but varies across sympatric ecotypes," J. Acoust. Soc. Am. **138**, 251-257.

Ford, J. K. B. (**1989**). "Acoustic behavior of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia," Can. J. Zool. **67**, 727-745.

Ford, J. K. B. (**1991**). "Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia," Can. J. Zool. **69**, 1454–1483.

Gillespie, D., Gordon, J., McHugh, R., McLaren, D., Mellinger, D., Redmond, P., Thode, A., Trinder, P., and Deng, X.Y. (**2008**). "PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans," Proc. Inst. Acoust. **30**, Pt 5, 54-62.

Gridley, T., Nastasi, A., Kriesell, H. J., and Elwen, S. H. (**2015**). "The acoustic repertoire of wild common bottlenose dolphins (*Tursiops truncatus*) in Walvis Bay, Namibia," Bioacoustics **24**, 153-174.

Hall, J. D., and Johnson, C. S. (**1972**). "Auditory thresholds of a killer whale *Orcinus orca* Linnaeus," J. Acoust. Soc. Am. **51**, 515-517.

Herzing, D. L. (**1996**). "Vocalizations and associated underwater behavior of free-ranging Atlantic spotted dolphins, *Stenella frontalis* and bottlenose dolphins, *Tursiops truncatus*," Aquat. Mamm. **22**, 61-79.

Janik, V. J. (**2000**). “Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*),” Proc. Roy. Soc. **267**, 923-927.

Johnson, M. P., and Tyack, P. L. (**2003**). “A digital acoustic recording tag for measuring the response of wild marine mammals to sound,” IEEE J. Ocean. Eng. **28**, 3-12.

Lammers, M.O., Brainard, R.E., Au, W.L., Mooney, T.A., and Wong, K.B. (**2008**). “An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other marine habitats,” J. Acoust. Soc. Am. **123**, 1720-1728.

Madsen, P. T., Jensen, F. H., Carder, D., and Ridgway, S. (**2012**). “Dolphin whistles: a functional misnomer revealed by heliox breathing,” Biol. Lett. **8**, 211-213.

May-Collado, L. J., Agnarsson, I., and Wartzok, D. (**2007**). Reexamining the relationship between body size and tonal signals frequency in whales: a comparative approach using a novel phylogeny. Mar. Mamm. Sci. **23**, 524-552.

Matthews, J. N., Rendell, L. E., Gordon, J. C. D., and Macdonald, D. W. (**1999**). “A review of frequency and time parameters of cetacean tonal calls,” Bioacoustics **10**, 47-71.

Miller, P. J., and Tyack P. L. (**1998**). “A small towed beamforming array to identify vocalizing resident killer whales (*Orcinus orca*) concurrent with focal behavioural observations,” Deep-Sea Res. II **45**, 1389-1405.

Moore, S. E., Francine, J. K., Bowles, A. E., and Ford, J. K. B. (**1988**). “Analysis of calls of killer whales, *Orcinus orca*, from Iceland and Norway,” Rit Fisk. **11**, 225-250.

Podos, J., da Silva, V. M. F., and Rossi-Santos, M. R. (**2002**). "Vocalizations of Amazon river dolphins, *Inia geoffrensis*: insights into the evolutionary origins of delphinid whistles," Ethol. **108**, 601-612.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Richardson, W. J., Greene, C. R. J., Malme, C. I., and Thomson, D. H. (**1995**) "Marine mammals and noise," Academic Press, New York, NY, pp. 159–189.

Riesch, R. and Deecke, V. B. (**2011**). "Whistle communication in mammal-eating killer whales (*Orcinus orca*): further evidence for acoustic divergence between ecotypes," Behav. Ecol. Sociobiol. **65**, 1377-1387.

Riesch, R., Ford, J. K. B., and Thomsen, F. (2006). "Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia," Anim. Behav. **71**, 79–91.

Riesch, R., Ford, J. K. B., and Thomsen, F. (**2008**). "Whistle sequences in wild killer whales (*Orcinus orca*)," J. Acoust. Soc. Am. **124**, 1822–1829.

Samarra, F. I. P. (**2015**). "Variations in killer whale food-associated calls produced during different prey behavioural contexts," Behav. Proc. **116**, 33-42.

Samarra, F. I. P., Deecke, V. B., Vinding, K., Rasmussen, M. H., Swift, R. J., and Miller P. J. O. (**2010**). "Killer whales (*Orcinus orca*) produce ultrasonic whistles," J. Acoust. Soc. Am. **128**, EL205-EL210.

Samarra, F. I. P., and Miller, P. J. O. (2015) "Prey-induced behavioural plasticity of herring-eating killer whales," Mar. Biol. **162**, 809-821.

Samarra, F. I. P., Simonis, A. E., Deecke, V. B., and Miller, P. J. O. (**2015**). “Geographic variation in the time-frequency characteristics of high-frequency whistles produced by killer whales (*Orcinus orca*),” Mar. Mamm. Sci. **31**, 688-706.

Schultz, K. W., Cato D. H., Corkeron, P. J., and Bryden, M. M. (**1995**). “Low frequency narrow-band sounds produced by bottlenose dolphins,” Mar. Mamm. Sci. **11**, 50-509.

Shapiro, A. D. (**2008**). “Orchestration: the movement and vocal behavior of free-ranging Norwegian killer whales (*Orcinus orca*),” PhD thesis, Massachusetts Institute of Technology and Woods Hole Oceanographic Institution, USA.

Sigurjónsson, J., Lyrholm, T., Leatherwood, S., Jónsson, E., and Víkingsson, G. (**1988**). “Photoidentification of killer whales, *Orcinus orca*, off Iceland, 1981 through 1986,” Rit. Fisk. **11**, 99-114.

Simard, P., Lace, N., Gowans, S., Quintana-Rizzo, E., Kuczaj II, S. A., Wells, R. S., and Mann, D. A. (**2011**). “Low-frequency narrow-band calls in bottlenose dolphins (*Tursiops truncatus*): signal properties, function, and conservation implications,” J. Acoust. Soc. Am. **130**, 3068-3076.

Similä, T., and Ugarte, F. (**1993**). “Surface and underwater observations of cooperatively feeding killer whales in northern Norway,” Can. J. Zool. **71**, 1494-1499.

Similä, T., Holst, J. C., and Christensen, I. (**1996**) “Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring,” Can. J. Fish. Aq. Sci. **53**, 769-779.

Simon, M., Wahlberg, M., Ugarte, F., and Miller, L. A. (**2005**). "Acoustic characteristics of underwater tail slaps used by Norwegian and Icelandic killer whales (*Orcinus orca*) to debilitate herring (*Clupea harengus*)," J. Exp. Biol. **208**, 2459-2466.

Simon, M., Ugarte, F., Wahlberg, M., and Miller, L. (**2006**). "Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus,*" Bioacoust. **16**, 57-74.

Simon, M., McGregor, P.K., and Ugarte, F. (**2007**) "The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*)," Acta Ethologica **10**, 47–53.

Simonis, A. E., Baumann-Pickering, S., Oleson, E., Melcón, M. L., Gassmann, M., Wiggins, S. M., and Hildebrand, J. A. (**2012**). "High-frequency modulated signals of killer whales (*Orcinus orca*) in the North Pacific," J. Acoust. Soc. Am. **131**, EL295-EL301.

Sivle, L. D., Kvadsheim, P. H., Ainslie, M. A., Solow, A., Handegard, N. O., Nordlund, N., and Lam, F. P. A. (**2012**). "Impact of naval sonar signals on Atlantic herring (*Clupea harengus*) during summer feeding," ICES J. Mar. Sci. **69**, 1078–1085.

Steiner, W. W., Hain, J. H., Winn, H. E., and Perkins, P. J. (**1979**). "Vocalizations and feeding behavior of the killer whale (*Orcinus orca*)," J. Mammal. **60**, 823-827.

Strager, H. (**1993**). "Catalogue of underwater calls from killer whales (*Orcinus orca*) in northern Norway," M.Sc. thesis, University of Århus, Denmark.

Strager, H. (**1995**). "Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca*, Linnaeus, 1758, in the waters of northern Norway," Can. J. Zool. **73**, 1037-1047.

Szymanski, M. D., Bain, D. E., Kiehl, K., Pennington, S., Wong, S., and Henry, K. R. (**1999**). "Killer whale (*Orcinus orca*) hearing: auditory brainstem response and behavioral audiograms," J. Acoust. Soc. Am. **106**, 1134-1141.

Thomsen, F., Franck, D., and Ford, J. K. B. (**2001**). "Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia," J. Acoust. Soc. Am. **109**, 1240-1246.

Thomsen, F., Franck, D., and Ford, J. K. B. (**2002**). "On the communicative significance of whistles in wild killer whales (*Orcinus orca*)," Naturwissenschaften **89**, 404-407.

Trickey, J. S., Reyes, M. V. R., Baumann-Pickering, S., Melcón, M. L., Hildebrand, J. A., and Iñíguez, M. A. (**2014**). "Acoustic encounters of killer and beaked whales during the 2014 SORP cruise," IWC report SC/65b/SM12.

Van der Woude, S. E. (**2009**). "Bottlenose dolphins (*Tursiops truncatus*) moan as low in frequency as baleen whales," J. Acoust. Soc. Am. **126**, 1552-1562.

Van Parijs, S., and Corkeron, P. (**2001**). "Vocalizations and behaviour of Pacific humpback dolphins *Sousa chinensis*," Ethol. **107**, 701-716.

Venables, W. N., and Ripley, B. D. (**2002**). "Modern applied statistics with S", Fourth edition, Springer, New York, NY.

Wahlberg, M., and Westerberg, H. (**2003**). "Sounds produced by herring (*Clupea harengus*) bubble release," Aq. Liv. Res. **16**, 271-275.

Wilson, B., Batty, R. S., and Dill, L. M. (**2004**). "Pacific and Atlantic herring produce burst pulse sounds," Biol. Lett. **271**, S95–S97.

Table I. Summary of recordings analyzed. Recordings were made using towed (TA) or vertical hydrophone arrays (VA), a single hydrophone (SH), an Ecological Acoustic Recorder (EAR, Lammers et al. 2008) or Dtags (Johnson and Tyack, 2003). Recordings made during each day were used as a proxy for number of encounters.

Location	Region	Year	Season	Recording method	Sampling rate (kHz)	No. of encounters	Recording duration (hh:mm)	LFS recorded (analyzed)
Norway	Vestfjord	2005	Winter	TA; Dtag	96	13	28:26	-
	“	2006	“	TA; Dtag	96	5	12:46	-
		2007	“	TA	96	5	13:39	-
	Vestfjord	2008	Spring	TA	96	1	04:37	-
	“	“	“	Dtag	192	1	15:43	-
		2009	“	Dtag	192	1	11:52	-
		“	“	Dtag	96	1	13:21	-
Iceland	Vestmannaeyjar	2008	Summer	VA	96	7	16:07	73 (9)
	“	2009	“	Dtag	192	3	12:17	5 (2)
	“	“	“	Dtag	96	1	04:12	8 (7)
	“	“	“	VA	192	12	30:39	111 (7)
	“	2010	“	SH	48	3	02:10	57 (19)
	“	“	“	SH	96	1	00:20	6 (2)
	“	“	“	TA	96	4	06:54	91 (20)
	“	2013	“	VA	96	4	02:06	25
	“	2014	“	TA	48	4	06:12	51 (11)
	“	“	“	TA	192	6	12:00	103 (27)
	“	“	“	SH	96	4	05:36	117 (32)
	Breiðafjörður	2013	Winter	VA	96	14	10:36	50 (7)
	“	“	“	SH	96	15	01:24	68 (19)
	“	“	“	Dtag	240	3	04:48	4
	“	2014	“	SH	96	7	03:00	1 (1)
	“	“	“	VA	96	5	02:54	5 (3)

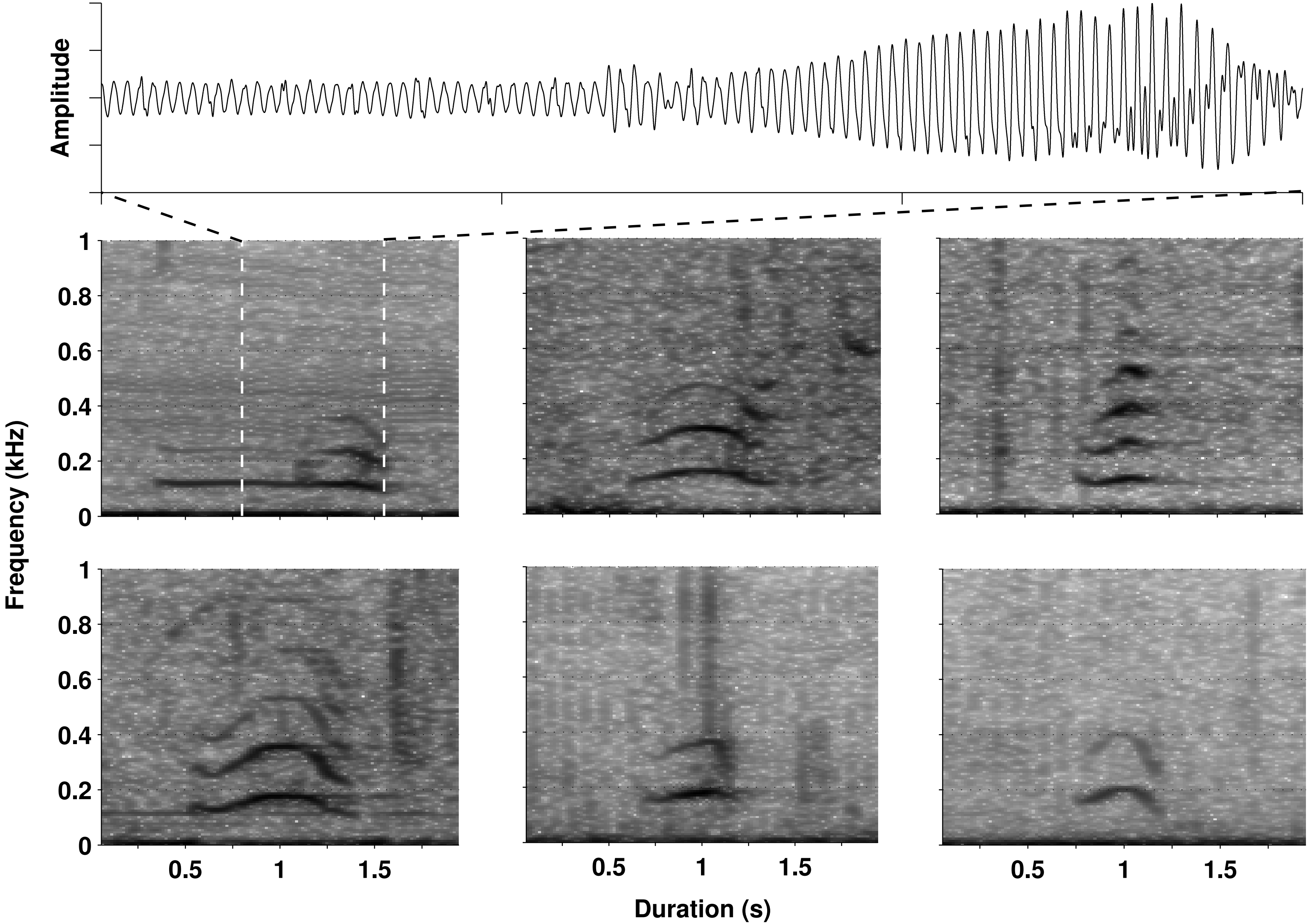
1	“	“	“	EAR	64	38	432:06	77 (23)

Figure Legends

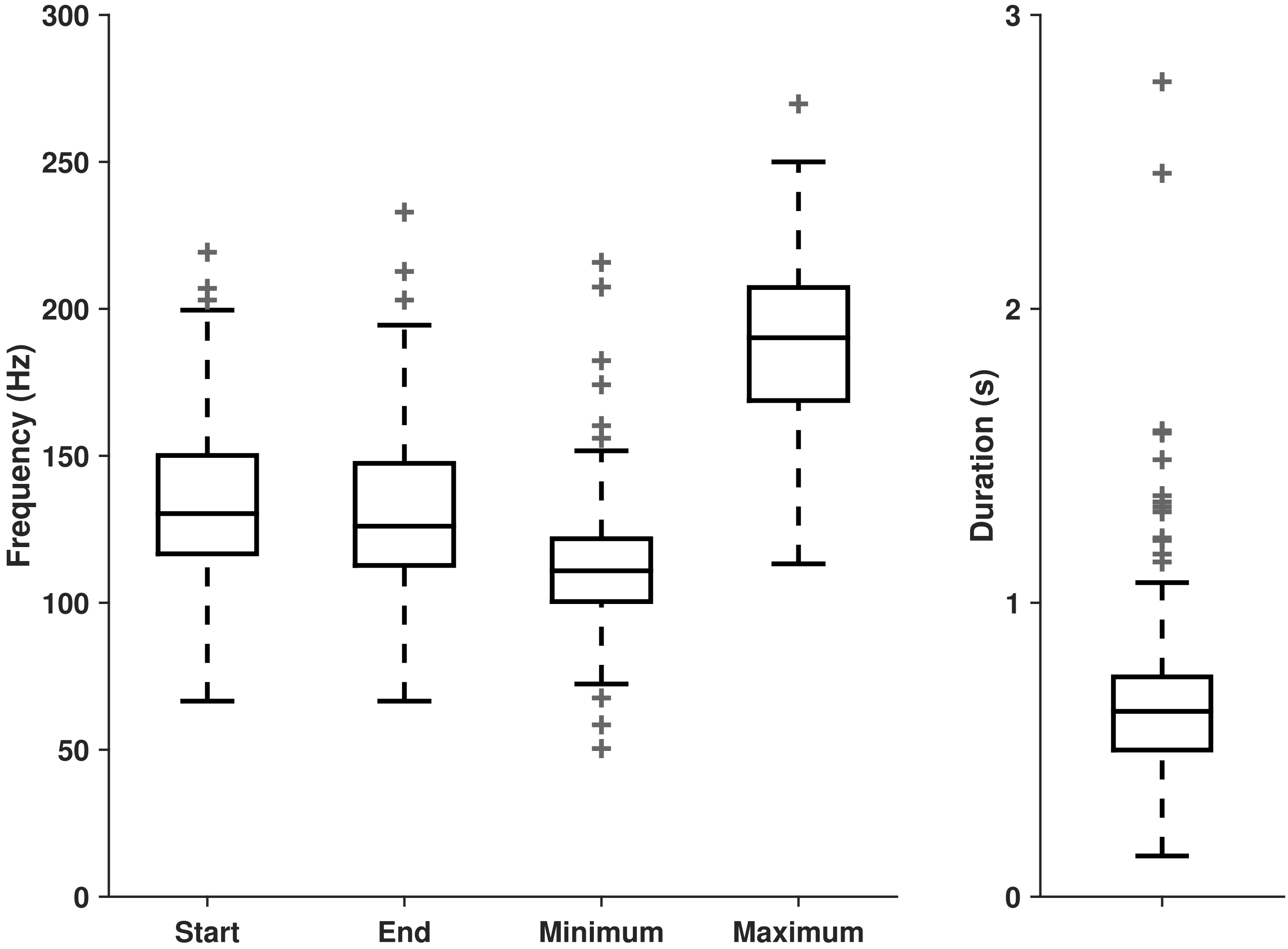
Figure 1. Example spectrograms of low frequency sounds produced by killer whales in Iceland (see Supplemental material), with the waveform of one example shown at the top. Spectrogram parameters: FFT size: 256; overlap: 87.5%; window function: Hann; frequency resolution: 7.8 Hz; time resolution: 16 ms.

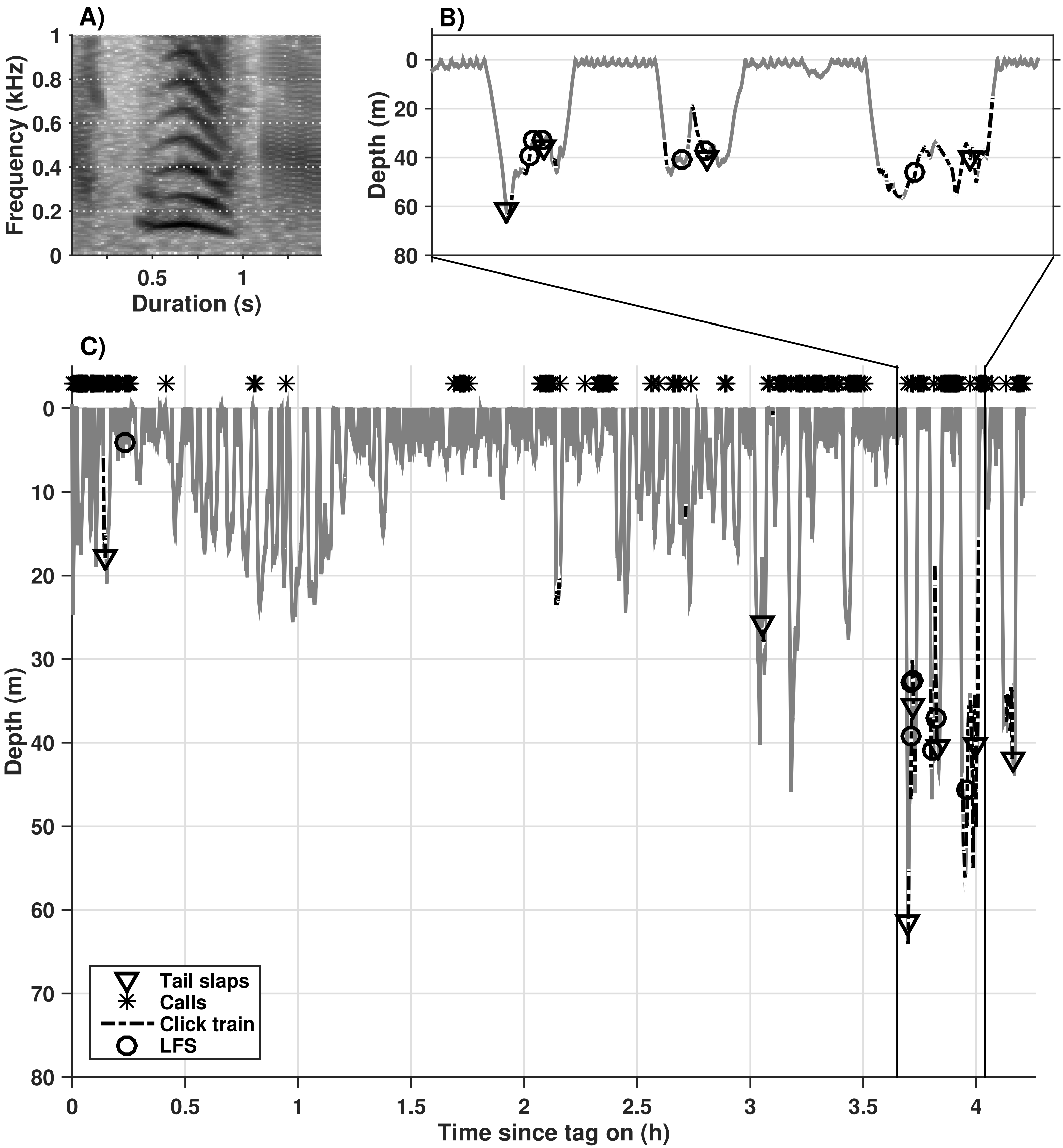
Figure 2. Distribution of frequency parameters (start, end, minimum and maximum frequency) and duration extracted from analyzed LFS. For each box the central line gives the median and the edges represent the 25^{th} and 75^{th} percentiles. Whiskers extend to the most extreme values and outliers are plotted as single points. Duration is plotted separately due to its different y-axis scale.

Figure 3. Dive profile of tag oo09_201a attached to a large juvenile killer whale in Vestmanaeyjar (SW Iceland) in July 2009, in which seven high quality LFS were recorded: A) example spectrogram of one of the LFSs detected during the first deep dive of the deployment; B) detailed dive profile of a section of the deployment when a feeding event begins, with increased clicking, calling and production of underwater tail slaps that are preceded by LFS in three deep dives; C) dive profile of the entire deployment highlighting periods of tail slap, call, click train and LFS production.



Amplitude
Frequency (kHz)
1
0.8
0.6
0.4
0.2
0
0.5
1
1.5
Duration (s)


Frequency (Hz)
300
250
200
150
100
50
0
Start
End
Minimum
Maximum
Duration (s)
3
2
1
0


A)
Frequency (kHz)
1
0.8
0.6
0.4
0.2
0
0.5
1
Duration (s)
B)
Depth (m)
0
20
40
60
80
C)
Depth (m)
0
10
20
30
40
50
60
70
80
0
0.5
1
1.5
2
2.5
3
3.5
4
Time since tag on (h)
Tail slaps
Calls
Click train
LFS