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

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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 s 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. © *2016 Acoustical Society of America.*

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## 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),

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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 and 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 and 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) narrowband 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, Fig. 1, Mm. 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

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 | – |
| | Vestfjord | 2006 | Winter | TA; Dtag | 96 | 5 | 12:46 | – |
| | off Andenes | 2007 | Winter | TA | 96 | 5 | 13:39 | – |
| | Vestfjord | 2008 | Spring | TA | 96 | 1 | 04:37 | – |
| | Vestfjord | 2008 | Spring | Dtag | 192 | 1 | 15:43 | – |
| | off Vesterålen | 2009 | Spring | Dtag | 192 | 1 | 11:52 | – |
| | off Vesterålen | 2009 | Spring | Dtag | 96 | 1 | 13:21 | – |
| Iceland | Vestmannaeyjar | 2008 | Summer | VA | 96 | 7 | 16:07 | 73 (9) |
| | Vestmannaeyjar | 2009 | Summer | Dtag | 192 | 3 | 12:17 | 5 (2) |
| | Vestmannaeyjar | 2009 | Summer | Dtag | 96 | 1 | 04:12 | 8 (7) |
| | Vestmannaeyjar | 2009 | Summer | VA | 192 | 12 | 30:39 | 111 (7) |
| | Vestmannaeyjar | 2010 | Summer | SH | 48 | 3 | 02:10 | 57 (19) |
| | Vestmannaeyjar | 2010 | Summer | SH | 96 | 1 | 00:20 | 6 (2) |
| | Vestmannaeyjar | 2010 | Summer | TA | 96 | 4 | 06:54 | 91 (20) |
| | Vestmannaeyjar | 2013 | Summer | VA | 96 | 4 | 02:06 | 25 |
| | Vestmannaeyjar | 2014 | Summer | TA | 48 | 4 | 06:12 | 51 (11) |
| | Vestmannaeyjar | 2014 | Summer | TA | 192 | 6 | 12:00 | 103 (27) |
| | Vestmannaeyjar | 2014 | Summer | SH | 96 | 4 | 05:36 | 117 (32) |
| | Breiðafjörður | 2013 | Winter | VA | 96 | 14 | 10:36 | 50 (7) |
| | Breiðafjörður | 2013 | Winter | SH | 96 | 15 | 01:24 | 68 (19) |
| | Breiðafjörður | 2013 | Winter | Dtag | 240 | 3 | 04:48 | 4 |
| | Breiðafjörður | 2014 | Winter | SH | 96 | 7 | 03:00 | 1 (1) |
| | Breiðafjörður | 2014 | Winter | VA | 96 | 5 | 02:54 | 5 (3) |
| | Breiðafjörður | 2014 | Winter | EAR | 64 | 38 | 432:06 | 77 (23) |

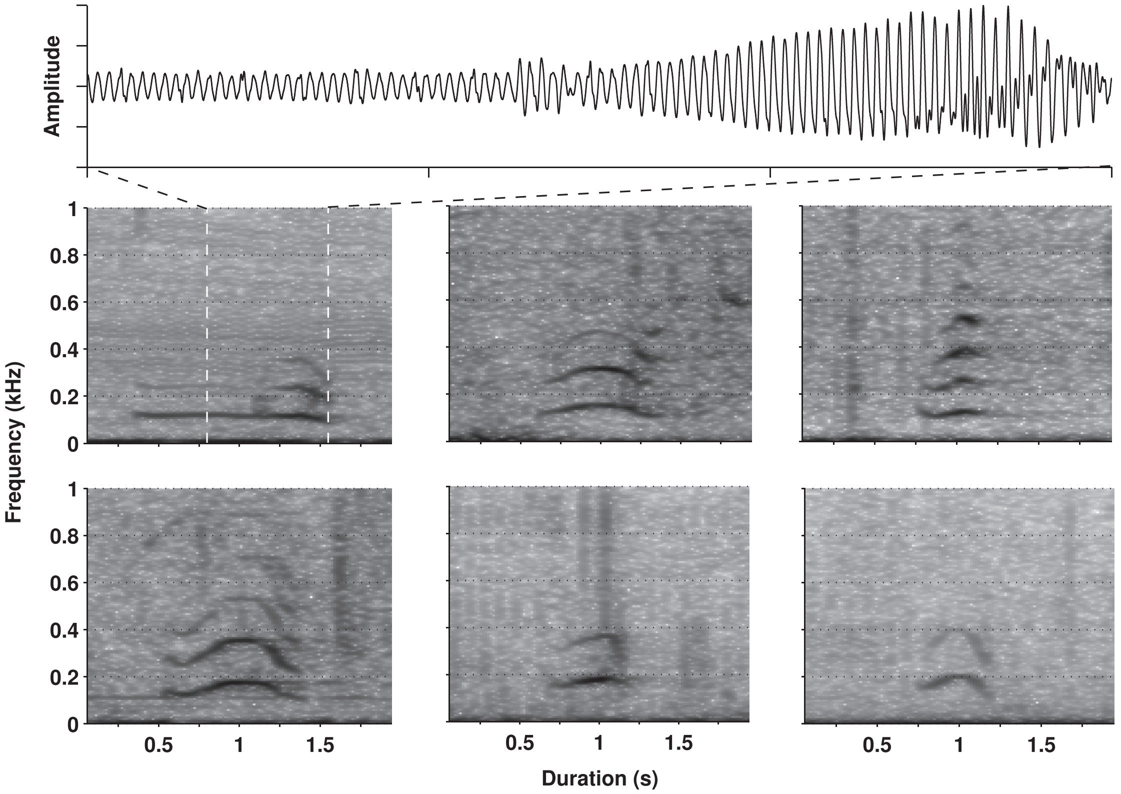

FIG. 1. Example spectrograms of low frequency sounds produced by killer whales in Iceland (see Mm. 1) with the waveform of one example shown at the top. Spectrogram parameters: FFT size: 256; overlap: 87.5%; window function: Hann; frequency resolution: 7.8 Hz; time resolution: 16 ms.

recording systems had a lower frequency response varying between 0.002 and 0.1 kHz.

Mm. 1. Audio example of a low-frequency sound produced by feeding killer whales. This sound corresponds to the spectrogram presented in Fig. 1, top left panel. This is a file of type "wav" (64.1 KB).

In 2014, an Ecological Acoustic Recorder (EAR, Lammers *et al.*, 2008) was deployed at a depth of ~30 m in inner Kolgrafafjörður, Iceland (Fig. 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 22 February and 31 March 2014, recording for 5 min every 10 min 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 LFS 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 16 384, for 64 or 96 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 16 384, for 64 or 96 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, low-pass 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 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 h of recordings from Iceland and 100.4 h of recordings from Norway (Table I). The difference in total recording time between Iceland and Norway is mainly due to the 432 h 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 LFS in Iceland but no similar sounds in Norway (Table I). A total of 189 LFS 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 LFS were only recorded concurrently with other killer whale vocalizations.

In general, LFS showed little frequency modulation and were characterized by an inverted "u" increase in frequency followed by a decrease (Fig. 1). In most cases (90%), analyzed LFS had one or more harmonics at least partially visible (Fig. 1). The sinusoidal waveform suggests that these are tonal signals (Fig. 1). Figure 2 shows the distributions of all LFS parameters measured. Low-frequency sound 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 (Fig. 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 LFS 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: $W = 79\,001$; $P < 0.0001$), end frequency (131 ± 29 Hz for LFS vs 1050 ± 286 Hz for herding calls; Mann-Whitney *U*-test: $W = 79\,002$; $P < 0.0001$), minimum frequency (113 ± 22 Hz for LFS vs 823 ± 267 Hz for herding calls; Mann-Whitney *U*-test: $W = 79\,000$; $P < 0.0001$), maximum frequency (189 ± 26 Hz for LFS vs 1070 ± 285 Hz for herding calls; Mann-Whitney *U*-test: $W = 79\,002$; $P < 0.0001$), and duration (0.67 ± 0.31 s for LFS vs 2.9 ± 1.0 s for herding calls; Mann-Whitney *U*-test: $W = 78\,466$; $P < 0.0001$). 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 low-frequency sound category.

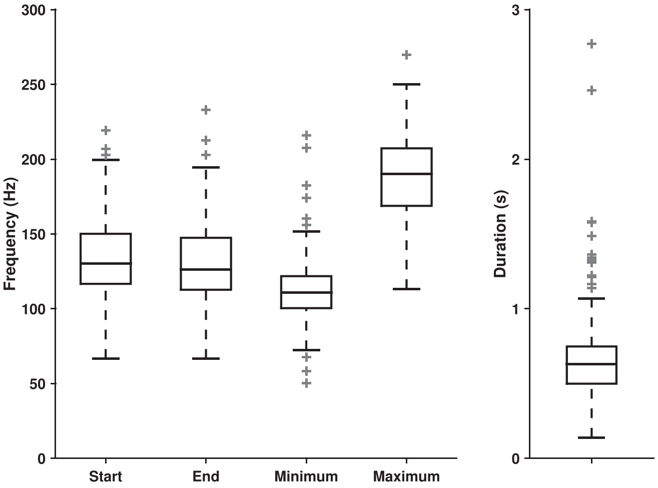

FIG. 2. Distribution of frequency parameters (start, end, minimum and maximum frequency) and duration extracted from analyzed LFS. For each box, the central line gives the median and the edges represent the 25th and 75th percentiles. Whiskers extend to the most extreme values and outliers are plotted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

Figure 3 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 that 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 Fig. 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 min; $P < 0.005$). 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, low-

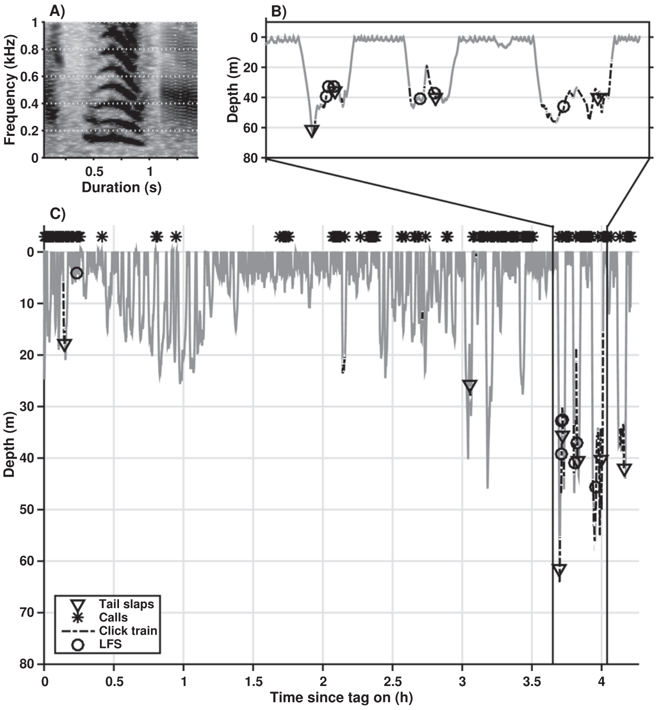

FIG. 3. Dive profile of tag oo09_201a attached to a large juvenile killer whale in Vestmannaeyjar (SW Iceland) in July 2009, in which seven high quality LFS were recorded: (A) example spectrogram of one of the LFS detected during the first deep dive of the deployment; (B) detailed dive profile of a section 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 low-frequency sound production.

frequency sound 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 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; this 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 LFS 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, LFS 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 (Fig. 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 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 (Fig. 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 are necessary to confirm the contextual production of LFS. 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 signals 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 LFS had little frequency modulation (Fig. 1). However, LFS were considerably longer than bottlenose dolphin low-frequency narrow-band sounds (mean of 0.05 s; 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 and 250 Hz. Based on these characteristics, this signal may have various putative functions.

It is possible that LFS 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). LFS show similarities in frequency content to these signals and 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, LFS could still be the by-product of movement or other type of unknown behavior. LFS 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, LFS 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 LFS 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 1 kHz (Hall and Johnson, 1972; Szymanski *et al.*, 1999). Estimates of low-frequency sound 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 LFS produced by other delphinids

(Simard *et al.*, 2011). On the other hand, herring is most sensitive at frequencies between 100 and 1200 Hz (Enger, 1967) thus LFS could be directed at prey. Because 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), LFS could be an additional signal serving a similar function. However, our analysis shows that LFS are significantly different from herding calls, and in comparison to herding calls, LFS appear to have lower amplitude and 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 low-frequency sounds 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), LFS 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 (Deecke, 2015). 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 LFS 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 LFS, suggesting these are common among delphinids. The inclusion of such sounds in future evolutionary studies of cetacean tonal signal frequency may be worthwhile.

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