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1 **Low-frequency signals produced by Northeast Atlantic killer whales**

2 *(Orcinus orca)*

3

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22 **Abstract**

23 Killer whale acoustic behavior has been extensively investigated, however most studies  
24 have focused on pulsed calls and whistles. This study reports the production of low-  
25 frequency signals by killer whales at frequencies below 300 Hz. Recordings were made  
26 in Iceland and Norway when killer whales were observed feeding on herring, and no  
27 other marine mammal species were nearby. Low-frequency sounds were identified in  
28 Iceland and ranged in duration between 0.14 and 2.77 seconds and in frequency between  
29 50 and 270 Hz, well below the previously reported lower limit for killer whale tonal  
30 sounds of 500 Hz. Low-frequency sounds appeared to be produced close in time to tail  
31 slaps, which are indicative of feeding attempts, suggesting that these sounds may be  
32 related to a feeding context. However, their precise function is unknown and they could  
33 be the by-product of a non-vocal behavior, rather than a vocal signal deliberately  
34 produced by the whales. Although killer whales in Norway exhibit similar feeding  
35 behavior, this sound has not been detected in recordings from Norway to date. This study  
36 suggests that, like other delphinids, killer whales produce low-frequency sounds but  
37 further studies will be required to understand whether similar sounds exist in other killer  
38 whale populations.

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## 44 I. INTRODUCTION

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

54 The sound frequency of tonal signals appears to be negatively correlated to body size  
55 in cetaceans, with the larger baleen whales producing lower frequency signals than  
56 odontocetes (Ding *et al.*, 1995; Matthews *et al.*, 1999; Podos *et al.*, 2002). Once  
57 phylogeny is taken into account, this relationship only holds for minimum frequency, but  
58 not for maximum frequency (May-Collado *et al.*, 2007). However, low frequency (<1500  
59 Hz) tonal sounds have also been described for some delphinids. For example, bottlenose  
60 dolphins (*Tursiops truncatus*) produce low frequency narrow-band sounds (Schultz *et al.*,  
61 1995; Simard *et al.*, 2011; Gridley *et al.*, 2015), ‘gulps’ (dos Santos *et al.*, 1995) and  
62 ‘moans’ (van der Woude, 2009), as well as low-frequency pulsed calls, the ‘bray calls’  
63 (dos Santos *et al.*, 1995; Janik, 2000). Other low-frequency narrow-band sounds include  
64 Risso’s (*Grampus griseus*) and Pacific humpback dolphin (*Sousa chinensis*) ‘grunts’  
65 (Corkeron and Van Parijs, 2001; Van Parijs and Corkeron, 2001) and Atlantic spotted  
66 (*Stenella frontalis*) and bottlenose dolphin ‘barks’ (Herzing, 1996). Contextual

67 production suggests these sounds are generally associated with socializing (e.g. Simard *et*  
68 *al.*, 2011), and feeding behaviors (Janik, 2000; Gridley *et al.*, 2015). The minimum  
69 frequency of delphinid low-frequency sounds can be as low as 39 Hz and well within the  
70 frequency range of baleen whale ‘moans’ and ‘tonal calls’ (van der Woude, 2009).

71 Killer whale (*Orcinus orca*) tonal signals are also referred to as ‘whistles’ and  
72 although few quantitative descriptions have been conducted, whistle frequency  
73 characteristics appear to vary between populations or ecotypes. For example, while  
74 resident and transient killer whales in the North Pacific appear to produce whistles in the  
75 audible range (<20 kHz; Thomsen *et al.*, 2001; Riesch and Deecke, 2011), others in the  
76 North Pacific, North Atlantic and Antarctic also produce whistles in the ultrasonic range  
77 (>20 kHz; Samarra *et al.*, 2010; Simonis *et al.*, 2012; Filatova *et al.*, 2012; Trickey *et al.*,  
78 2014). Ultrasonic whistles of killer whales in Iceland and Norway appear to have higher  
79 fundamental frequency, shorter duration and more variable time-frequency contours than  
80 those of whales in the Pacific Ocean (Samarra *et al.*, 2015). Quantitative descriptions of  
81 the whistles produced by Northeast Pacific resident and transient killer whales show that  
82 duration ranges between 0.06 and 18.3 s, and the fundamental frequency ranges from 2.4  
83 to 16.7 kHz (Thomsen *et al.*, 2001; Riesch and Deecke, 2011), although minimum  
84 frequency can be as low as 1.5 kHz (Ford, 1989). In the Northwest Atlantic tonal signals  
85 with minimum frequency of 0.5 kHz were reported (Steiner *et al.*, 1979). Whistles are  
86 mostly produced during socializing or high-arousal contexts (Ford, 1989; Thomsen *et al.*,  
87 2002) and some have stereotyped frequency contours that are often produced in complex  
88 sequences (Riesch *et al.*, 2006, 2008).

89           Although the vocal behavior of killer whales has been extensively studied in several  
90 locations, most studies have focused on pulsed calls, the most common vocalization  
91 produced (e.g., Moore *et al.*, 1988; Ford, 1989; Strager, 1995; Filatova *et al.*, 2007).  
92 Killer whale social groups produce unique and stable repertoires of stereotyped pulsed  
93 calls that are used in different behavioral contexts (Ford 1989, 1991). In Iceland and  
94 Norway killer whale call production increases significantly during feeding (Simon *et al.*,  
95 2007). Both populations are thought to feed primarily on Atlantic herring (*Clupea*  
96 *harengus*; Sigurjónsson *et al.*, 1988; Similä *et al.*, 1996), using coordinated group feeding  
97 where whales encircle herring schools and use underwater tail slaps to debilitate their  
98 prey before feeding (Similä and Ugarte, 1993; Simon *et al.*, 2007; Samarra and Miller,  
99 2015). Underwater tail slaps produce a characteristic broadband multipulsed sound  
100 (Simon *et al.*, 2005) that can be used as an acoustic cue of a feeding attempt (Samarra and  
101 Miller, 2015). Pulsed calls produced during feeding are thought to be used for group  
102 coordination (Similä and Ugarte 1993; Shapiro 2008; Samarra and Miller 2015) and  
103 because herring respond to killer whale sounds (Doksæter *et al.*, 2009; Sivle *et al.*, 2012),  
104 these acoustic stimuli may serve to help modify the herrings' behavior (Similä and Ugarte  
105 1993).

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

112 Quantitative descriptions of calls produced by killer whales in Norway report frequencies  
113 between 0.04 and 4.8 kHz and durations ranging between 0.11-2.2 s (Strager, 1993,  
114 1995), while in Iceland mean frequencies varied between 0.16 and 3.28 kHz and mean  
115 duration between 0.355 and 2.142 s (Moore *et al.*, 1988;). In Iceland, a distinctive long,  
116 low frequency call is produced exclusively during feeding just before an underwater tail  
117 slap, termed ‘herding call’ (Simon *et al.* 2006). This call was recently also recorded in  
118 Shetland (UK) also in association with feeding upon herring (Deecke *et al.*, 2011). The  
119 herding call has a relatively flat time-frequency contour and peak fundamental  
120 frequencies may vary between 406 and 1414 Hz while duration ranges from 0.83 to 8.5 s  
121 (Samarra, 2015). Due to its low frequency, presumably unsuitable for intra-specific  
122 communication, but within the frequency range that herring is sensitive to, the herding  
123 call is thought to function in prey manipulation (Simon *et al.*, 2006). It is thought that  
124 herding call production leads to an anti-predator response of the herring, which schools  
125 tighter. By helping compact the herring school prior to an underwater tail slap this call  
126 likely increases feeding efficiency (Simon *et al.*, 2006).

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

133

## 134 **II. METHODS**

135 **A. Data collection**

136 Acoustic recordings were made in Iceland and Norway in multiple years and multiple  
137 locations (Table I, Figure 1). All recordings were collected in fjords or open water  
138 locations where killer whales were observed feeding on herring. We used a variety of  
139 recording systems, including a 16-element towed hydrophone array recording onto an  
140 Alesis© ADAT-HD24 XR (frequency response 0.022-44 kHz,  $\pm 0.5$  dB; Miller and  
141 Tyack, 1998; Alesis, Cumberland, RI); a 2 element towed array with Benthos© AQ-4  
142 (Teledyne Benthos, Falmouth, MA) and Magrec© HP-02 pre-amplifiers (Magrec Ltd.,  
143 Lifton, UK; frequency response 0.1-40 kHz,  $\pm 3$  dB) towed array recording onto a  
144 Marantz© PMD671 (frequency response 0.02-44 kHz,  $\pm 0.5$  dB; Marantz America LLC,  
145 Mahwah, NJ) or a Sound Devices© 702 (frequency response 0.001-40 kHz,  $\pm 0.5$  dB;  
146 Sound Devices LLC, Reedsburg, WI); a 4-element vertical array (High Tech Inc© 94-  
147 SSQ with pre-amplifiers; frequency response 0.002-30 kHz; High Tech Instruments,  
148 Long Beach, MS) connected to an Edirol© FA-101 soundcard (frequency response 0.02-  
149 40 kHz,  $\pm 0/-2$  dB; Roland Corporation US, Los Angeles, CA) and recording onto a  
150 laptop using PAMGUARD (Gillespie *et al.*, 2008) or connected to a Roland© R-44  
151 (frequency response 0.02-40 kHz,  $\pm 0/-3$  dB; Roland Corporation US, Los Angeles, CA);  
152 a single hydrophone (High Tech Inc© 94-SSQ with pre-amplifiers; flat frequency  
153 response 0.002–30 kHz) recording onto a laptop using Adobe Audition 2.0©, or  
154 recording onto a M-Audio Microtrack II (M-Audio, Cumberland, RI); and movement and  
155 sound recording tags attached to killer whales using suction cups ('Dtags'; flat frequency  
156 response 0.6-45 kHz; Johnson and Tyack, 2003). With the exception of Dtags, all  
157 recording systems had a lower frequency response varying between 0.002-0.1 kHz.



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

176

## 177 **B. Acoustic analysis**

178 All recordings were inspected using Adobe Audition 2.0 (Adobe Systems Inc., San  
179 Jose CA) using the following FFT settings: Blackmann-Harris window; FFT=8192 or  
180 16384, for 64 or 96 kHz and 192 kHz sampling rates, respectively; 100% window width;

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

195 To compare how these sounds differed from other killer whale low frequency sounds  
196 previously described in the literature we compared these measurements to measurements  
197 taken from herding calls (the same sample as in Samarra, 2015). We first compared the  
198 parameter distributions using Mann-Whitney U-tests, to account for the non-normality of  
199 most parameter distributions (Shapiro-Wilk normality tests:  $P < 0.0001$ , except for LFS  
200 end frequency with  $P=0.006$  and LFS maximum frequency with  $P=0.25$ ). We used a  
201 Bonferroni correction to adjust the significance level to account for multiple comparisons  
202 ( $0.05/5 = 0.01$ ). We further input these measurements into a multivariate discriminant  
203 function analysis where sound type (herding call or LFS) was used as the grouping

204 variable and we used a jackknife cross-validation technique implemented in the *lda*  
205 function of package MASS version 7.3-16 (Venables and Ripley, 2002) in R 3.2.2 for  
206 Mac OS X (R Core Team, 2015). The overall proportion of correct classifications and the  
207 proportion of correct classifications by location were calculated and compared to the  
208 proportion of by-chance accuracy, which was assumed to be equal (50%) for both sound  
209 types.

210

### 211 **C. Behavioral context**

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

226 times to generate a probability distribution of mean expected intervals to nearest tail slap  
227 and compared it to the observed values.

228

### 229 **III. RESULTS**

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

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

243 In general, LFSs showed little frequency modulation and were characterized by an  
244 inverted ‘u’ increase in frequency followed by a decrease (Figure 1). In most cases (90%)  
245 analyzed LFSs had one or more harmonics at least partially visible (Figure 1). The  
246 sinusoidal waveform suggests that these are tonal signals (Figure 1). Figure 2 shows the  
247 distributions of all LFS parameters measured. LFS duration ranged between 0.14 and  
248 2.77 s with a mean  $\pm$  standard deviation of  $0.67 \pm 0.31$  s. All sounds analyzed were

249 produced exclusively below 300 Hz (Figure 2). LFS had a mean  $\pm$  standard deviation  
250 (minimum-maximum) start frequency of  $136 \pm 27$  Hz (67-219), end frequency of  $131 \pm$   
251  $29$  Hz (67-233), minimum frequency of  $113 \pm 22$  Hz (50-216) and maximum frequency  
252 of  $189 \pm 26$  Hz (113-270).

253 Comparisons between the time and frequency parameters of LFSs and herding calls  
254 revealed significant differences in all parameters measured, including start frequency  
255 (mean  $\pm$  standard deviation of  $136 \pm 27$  Hz for LFS vs.  $860 \pm 284$  Hz for herding calls;  
256 Mann-Whitney U-test:  $W=79001$ ;  $P<0.0001$ ), end frequency ( $131 \pm 29$  Hz for LFS vs.  
257  $1050 \pm 286$  Hz for herding calls; Mann-Whitney U-test:  $W=79002$ ;  $P<0.0001$ ), minimum  
258 frequency ( $113 \pm 22$  Hz for LFS vs.  $823 \pm 267$  Hz for herding calls; Mann-Whitney U-  
259 test:  $W=79000$ ;  $P<0.0001$ ), maximum frequency ( $189 \pm 26$  Hz for LFS vs.  $1070 \pm 285$  Hz  
260 for herding calls; Mann-Whitney U-test:  $W=79002$ ;  $P<0.0001$ ) and duration ( $0.67 \pm 0.31$   
261 s for LFS vs.  $2.9 \pm 1.0$  s for herding calls; Mann-Whitney U-test:  $W=78466$ ;  $P<0.0001$ ).  
262 The discriminant function analysis also showed good discrimination between the two  
263 signal types with an overall correct classification rate of 99%, with 100% of LFS and  
264 99% of herding calls being correctly assigned to type. Only 4 of 418 herding calls were  
265 incorrectly assigned to the LFS category.

266 Figure 3 displays the dive profile and concurrent sound production of a Dtag  
267 deployed on a killer whale off the Vestmannaeyjar archipelago in Iceland in the summer  
268 of 2009 (deployment oo09\_201a). This deployment appears to have captured some non-  
269 feeding behavior, including silent periods which likely represent travelling, as well as a  
270 feeding event initiated near the end of the deployment, characterized by deep diving,  
271 increased clicking and calling, and production of tail slaps (detailed view in Figure 3 top).

272 The majority of LFS are recorded during the bottom of these feeding dives, just prior to a  
273 tail slap, suggesting contextual production of LFS during feeding. The mean interval to  
274 nearest tail slap throughout this record was 83 s, which was significantly lower than  
275 chance (mean interval of randomizations = 32 minutes;  $P < 0.005$ ). However, a different  
276 Dtag deployment (oo09\_200a) in the same location in Iceland, which also included  
277 feeding behavior did not contain LFS, suggesting that if specific to a feeding context,  
278 LFS production is not ubiquitous during all feeding events.

279

#### 280 **IV. DISCUSSION**

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

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

316 concurrently with killer whale sounds, strongly points to killer whales to be the species  
317 that produced these sounds.

318 Unlike other delphinids that appear to produce low-frequency sounds mostly during  
319 socializing contexts (Schultz *et al.*, 1995; Simard *et al.*, 2011; Gridley *et al.*, 2015), the  
320 signals reported here appear linked to feeding by killer whales, which is a social,  
321 coordinated behavior. However, these sounds were not reported in all feeding events thus  
322 further data is necessary to confirm the contextual production of LFSs. Bottlenose  
323 dolphins also produce low-frequency sounds during feeding, the ‘bray calls’ (Janik,  
324 2000). However, studies of the function of LFS will be necessary before comparisons can  
325 be drawn between the use of low-frequency sounds across different species.

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

335 It is possible that LFSs may be a non-vocal by-product of another behavior. For  
336 example, bottlenose dolphin ‘moans’ appear to be produced concurrently with  
337 bubblestream and it is unclear if the sounds are produced in association with the  
338 bubblestream or as a result of it (van der Woude, 2009). LFSs show similarities in



339 frequency content to these signals, thus could similarly be associated with bubble  
340 production in killer whales. Similä and Ugarte (1993) report bubble production by  
341 Norwegian killer whales feeding on herring that is thought to help herd the herring  
342 further and our own field observations suggest this also occurs in Iceland. However, the  
343 fact that LFS were not recorded in all feeding events and were not recorded in Norway,  
344 where killer whales are known to produce bubbles when feeding (Similä and Ugarte,  
345 1993), suggests that these sounds may not be a by-product of bubble production by killer  
346 whales, although a larger sample size may be necessary to rule this out. However, LFSs  
347 could still be the by-product of movement or other type of unknown behavior. LFSs were  
348 not recorded frequently suggesting that if these sounds are produced as the by-product of  
349 a behavior or movement, this behavior only happens rarely. Alternatively, LFSs may be a  
350 vocal signal deliberately produced by killer whales for communication or to manipulate  
351 prey behavior.

352       Based on the known hearing sensitivity of killer whales a communicative function is  
353 perhaps unlikely. The frequency range of LFSs is considerably below the best hearing  
354 sensitivity of killer whales (18-42 kHz; Szymanski *et al.*, 1999). Measurements of killer  
355 whale hearing sensitivity at the frequency of the signals reported here have not been  
356 conducted, however hearing sensitivity is considerably decreased at 1kHz (Hall and  
357 Johnson, 1972; Szymanski *et al.*, 1999). Estimates of LFS source level and killer whale  
358 hearing sensitivity at frequencies below 1 kHz would be required to test whether killer  
359 whales can perceive these sounds, even if only at close range, as has been demonstrated  
360 for the low-frequency sounds produced by other delphinids (Simard *et al.*, 2011). On the  
361 other hand, herring is most sensitive at frequencies between 100-1200 Hz (Enger, 1967)

362 thus LFS could be directed at prey. Since Icelandic killer whales are known to produce  
363 feeding-specific calls of low frequency that are thought to function in prey manipulation  
364 (Simon *et al.*, 2006), LFSs could be an additional signal serving a similar function.  
365 However, our analysis shows that LFSs are significantly different from herding calls and  
366 in comparison to herding calls, LFSs appear to have lower amplitude thus might not be  
367 effective signals for prey manipulation. In addition, it is unclear why the whales would  
368 require two different sound types with a redundant functionality. Further data will be  
369 required to address these questions, particularly using animal-attached tags that could  
370 provide high-resolution data on the behavioral context and help identify contextual  
371 variations that could help explain the function of LFS and the factors driving its  
372 production in some contexts.

373       Intra-specific variability in acoustic signals produced during feeding may represent  
374 individual variation or an adaptation to prey-targeted or environmental characteristics.  
375 For example, humpback whales (*Megaptera novaeangliae*) in Alaska produce feeding  
376 calls that have not been recorded from feeding humpbacks elsewhere (Jurasz and Jurasz,  
377 1979; D'Vincent *et al.*, 1985; Cerchio and Dahlheim, 2001), while in the Northwest  
378 Atlantic feeding humpbacks produce short pulses of broadband sound termed  
379 'megapclicks' (Stimpert *et al.*, 2007) and paired pulses (Parks *et al.*, 2014) that also  
380 appear to be exclusive to this location. Similarly only killer whales in Iceland and  
381 Shetland have been recorded producing herding calls when feeding on herring (Simon *et*  
382 *al.*, 2006; Deecke *et al.*, 2011; Samarra, 2015). Despite feeding on the same prey, feeding  
383 strategies adopted by killer whales in Iceland and Norway differ (Samarra and Miller,  
384 2015). It is possible that, like herding calls (Simon *et al.*, 2006), LFSs are produced as

385 part of a feeding behavior that is exhibited by killer whales in Iceland, but not in Norway.  
386 Nevertheless, we cannot rule out the possibility that the absence of these sounds in our  
387 Norwegian sample is simply due to sampling limitations or differences in some of the  
388 recordings methods (Table I).

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

404 This study contributes to our knowledge of the acoustic repertoire of killer whales,  
405 however, additional data will be required to understand the production mechanism,  
406 function, and behavioral context of LFS and whether they are exclusively produced by  
407 only a few populations. Although our findings suggest that some Northeast Atlantic killer

408 whales can produce sounds across a wide range of fundamental frequencies (50 Hz to 75  
409 kHz, Samarra *et al.*, 2010), there are clear distinctions between these signals, which likely  
410 serve different functions. Our study shows that, like other delphinids, killer whales also  
411 produce low-frequency sounds, suggesting these are common among delphinids. The  
412 inclusion of such sounds in future evolutionary studies of cetacean tonal signal frequency  
413 may be worthwhile.

414

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428

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- 1 **Table I.** Summary of recordings analyzed. Recordings were made using towed (TA) or vertical hydrophone arrays (VA), a single  
 2 hydrophone (SH), an Ecological Acoustic Recorder (EAR, Lammers et al. 2008) or Dtags (Johnson and Tyack, 2003). Recordings  
 3 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)
	Breiðafjörður	“	“	“	SH	96	4	05:36	117 (32)
		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)

1 **Figure Legends**

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

6  
7 **Figure 2.** Distribution of frequency parameters (start, end, minimum and maximum  
8 frequency) and duration extracted from analyzed LFS. For each box the central line gives  
9 the median and the edges represent the 25<sup>th</sup> and 75<sup>th</sup> percentiles. Whiskers extend to the  
10 most extreme values and outliers are plotted as single points. Duration is plotted  
11 separately due to its different y-axis scale.

12  
13 **Figure 3.** Dive profile of tag oo09\_201a attached to a large juvenile killer whale in  
14 Vestmanaeyjar (SW Iceland) in July 2009, in which seven high quality LFS were  
15 recorded: A) example spectrogram of one of the LFSs detected during the first deep dive  
16 of the deployment; B) detailed dive profile of a section of the deployment when a feeding  
17 event begins, with increased clicking, calling and production of underwater tail slaps that  
18 are preceded by LFS in three deep dives; C) dive profile of the entire deployment  
19 highlighting periods of tail slap, call, click train and LFS production.

20







