

Samarra, Filipa I.P., Deecke, Volker B. and Miller, Patrick J.O. (2016) Low-frequency signals produced by Northeast Atlantic killer whales (*Orcinus orca*). *Journal of the Acoustical Society of America*, 139 (3). pp. 1149-1157.

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

2 *(Orcinus orca)*

3

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17 Submission date: 29 January 2016

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19 Running title: Killer whale low frequency sounds

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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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42 **PACS numbers:** 43.80.Ka

43

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, ± 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, ± 3 dB) towed array recording onto a
144 Marantz© PMD671 (frequency response 0.02-44 kHz, ± 0.5 dB; Marantz America LLC,
145 Mahwah, NJ) or a Sound Devices© 702 (frequency response 0.001-40 kHz, ± 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 22nd February and the 31st 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 ± 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 ± 27 Hz (67-219), end frequency of $131 \pm$
251 29 Hz (67-233), minimum frequency of 113 ± 22 Hz (50-216) and maximum frequency
252 of 189 ± 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 ± 27 Hz for LFS vs. 860 ± 284 Hz for herding calls;
256 Mann-Whitney U-test: $W=79001$; $P<0.0001$), end frequency (131 ± 29 Hz for LFS vs.
257 1050 ± 286 Hz for herding calls; Mann-Whitney U-test: $W=79002$; $P<0.0001$), minimum
258 frequency (113 ± 22 Hz for LFS vs. 823 ± 267 Hz for herding calls; Mann-Whitney U-
259 test: $W=79000$; $P<0.0001$), maximum frequency (189 ± 26 Hz for LFS vs. 1070 ± 285 Hz
260 for herding calls; Mann-Whitney U-test: $W=79002$; $P<0.0001$) and duration (0.67 ± 0.31
261 s for LFS vs. 2.9 ± 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

415 **Acknowledgments**

416 We sincerely thank everyone involved in the various field seasons, Dr. Marc
417 Lammers for providing the EAR for acoustic recordings in 2014 and Dr. Olga Filatova
418 and Ivan Fedutin for coordinating the collection of the EAR data. The field efforts of
419 2008-9 were conducted as part of the 3S collaborative research program. We would also
420 like to thank D. Risch for helpful discussions. Funding was provided by the BBC Natural
421 History Unit, Fundação para a Ciência e a Tecnologia (Grant Number
422 SFRH/BD/30303/2006), the Icelandic Research Fund (i. Rannsóknasjóður) through a
423 START Postdoctoral Fellowship (Grant Number 120248042), the National Geographic
424 Global Exploration Fund (Grant Number GEFNE65-12), the Office of Naval Research
425 (Grant Number N00014-08-10984) and Russell Trust Award from the University of St
426 Andrews. All field research was carried out in compliance with local regulations. We
427 thank two anonymous reviewers for very helpful comments.

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	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 25th and 75th 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





