

1 **A comparison of Northeast Atlantic killer whale (*Orcinus orca*) stereotyped call**  
2 **repertoires**

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24 **Abstract**

25 Killer whale call repertoires can provide information on social connections among groups  
26 and populations. Killer whales in Iceland and Norway exhibit similar ecology and behavior,  
27 are genetically related, and are presumed to have been in contact before the collapse of the  
28 Atlanto-Scandian herring stock in the 1960s. However, photo-identification suggests no  
29 recent movements between Iceland and Norway but regular movement between Iceland and  
30 Shetland. Acoustic recordings collected between 2005–2016 in Iceland, Norway, and  
31 Shetland were used to undertake a comprehensive comparison of call repertoires of Northeast  
32 Atlantic killer whales. Measurements of time and frequency parameters of calls from Iceland  
33 ( $n = 4,037$ ) and Norway ( $n = 1,715$ ) largely overlapped in distribution, and a discriminant  
34 function analysis had low correct classification rate. No call type matches were confirmed  
35 between Iceland and Norway or Shetland and Norway. Three call types matched between  
36 Iceland and Shetland. Therefore, this study suggests overall similarities in time and frequency  
37 parameters but some divergence in call type repertoires. This argues against presumed past  
38 contact between Icelandic and Norwegian killer whales and suggests that they may not have  
39 been one completely mixed population.

40

41 **KEYWORDS**

42 acoustic behavior, geographic variation, killer whale, *Orcinus orca*, Northeast Atlantic,  
43 repertoire

## 44 1 INTRODUCTION

45

46 Geographic variation in acoustic signals occurs between spatially separated populations that  
47 do not mix, while dialects are usually defined as differences on a local scale, within  
48 populations or between neighboring populations that potentially mix (Au & Hastings, 2008;  
49 Nottebohm, 1969). Dialects mostly occur in species that are capable of vocal learning  
50 (Conner, 1982) and have been described in many species of birds (Baker & Cunningham,  
51 1985) but seem to be rare in mammals. The only cetaceans known to have dialects to date are  
52 sperm whales (*Physeter macrocephalus*; Weilgart & Whitehead, 1997), killer whales  
53 (*Orcinus orca*; Ford, 1991), and short-finned pilot whales (*Globicephala macrorhynchus*; van  
54 Cise, Mahaffy, Baird, Mooney & Barlow, 2018). Geographical variation, however, can be the  
55 result of genetic differentiation and is common in both birds and mammals (e.g., Krebs &  
56 Kroodsma, 1980; Mitani, Hunley, & Murdoch, 1999; Slobodchikoff, Ackers, & van Ert,  
57 1998).

58 Killer whale vocalizations are generally divided into three categories: echolocation  
59 clicks, whistles, and pulsed calls (Ford, 1989; Schevill & Watkins, 1966; Thomsen, Franck,  
60 & Ford, 2001). Pulsed calls (hereafter calls) are the most commonly produced sound and are  
61 composed of clicks emitted at high repetition rates (Ford, 1989). Calls that have a stereotyped  
62 time-frequency contour and can be assigned to distinct categories, are known as discrete calls  
63 (Ford, 1989). In some populations, group-specific call repertoires have been described that  
64 have been shown to be learned, rather than genetically encoded (Deecke, Ford, & Spong,  
65 2000; Foote et al., 2006; Ford, 1991). Differences in repertoires are thought to accumulate  
66 over time as groups split apart, leading to the formation of dialects (Ford, 1991; Miller &  
67 Bain, 2000). Calls provide a measure of maternal relatedness, with shared calls indicating a  
68 relationship between individuals and matrilineal groups (Deecke, Barrett-Lennard, Spong &

69 Ford, 2010; Ford, 1991; Yurk, Barret-Lennard, Ford, & Matkin, 2002). The main  
70 mechanisms of call divergence are thought to be learning errors, innovation, horizontal  
71 transmission, and cultural selection (Deecke et al., 2010; Filatova, Burdin, & Hoyt, 2010,  
72 2013; Filatova et al., 2012; Filatova & Miller, 2015; Ford, 1991; Yurk et al., 2002). In  
73 captivity, killer whales introduced to new social environments can modify their repertoire  
74 considerably within as few as three years (Crance, Bowles, & Garver, 2014) but rates of  
75 change in the wild appear much lower, with calls being relatively stable over decades (Foote  
76 & Nystuen, 2008; Ford, 1991).

77         In addition to differences in their acoustic repertoires, killer whale populations show  
78 dietary, behavioral, morphological, and genetic differentiation (e.g., Barrett-Lennard, Ford, &  
79 Heise, 1996; Ford et al., 1998; Morin et al. 2010; Pitman & Ensor, 2003). Dietary preferences  
80 are a key factor determining movements and connectivity between groups and populations  
81 (Ford et al., 1998; Pitman & Ensor, 2003). In the North Atlantic, killer whale occurrence  
82 around Iceland and Norway is associated with North Atlantic herring (*Clupea harengus*)  
83 movements (Foote et al., 2011) and previous studies suggest that killer whales there  
84 specialize on herring as their main prey (Sigurjónsson, Lyrholm, Leatherwood, Jónsson, &  
85 Víkingsson, 1988; Similä, Holst, & Christensen, 1996; Simon, McGregor, & Ugarte, 2007).  
86 They are morphologically similar, genetically closely related (Foote, Newton, Piertney,  
87 Willerslev, & Gilbert, 2009; Morin et al., 2010), and share similar feeding strategies  
88 (Samarra & Miller, 2015; Similä & Ugarte, 1993).

89         Before its collapse in the 1960s, the Atlanto-Scandian herring stock migrated between  
90 Iceland and Norway (Jakobsson & Østvedt, 1999). Killer whale catch locations from whalers  
91 indicate a strong association with herring occurrence, as well as a continuous distribution of  
92 killer whales between Iceland and Norway or migration between the two locations (Jonsgård  
93 & Lyshoel, 1970). The collapse of the Atlanto-Scandian herring stock led to a change in the

94 herring distribution and resulted in the herring retreating closer to the coastal areas of Iceland  
95 and Norway (Jakobsson & Stefánsson, 1999; Kvamme et al., 2003). Comparisons of  
96 identification photographs collected in Iceland and Norway since the 1980s found no matches  
97 of killer whales between Iceland and Norway, indicating that little or no movement occurs  
98 between the populations (Foote, Similä, Víkingsson, & Stevick, 2010; Sigurjónsson et al.,  
99 1988). However, little dedicated photo-identification effort was invested in Iceland, hindering  
100 a full analysis of movements between the two regions. On the other hand, a small number of  
101 killer whales has been shown to undertake seasonal movements between Iceland and  
102 Shetland (Foote et al., 2010; Samarra & Foote, 2015), indicating that the movement patterns  
103 of Icelandic killer whales are not limited to Icelandic coastal waters. Updated comparisons of  
104 photo-identification catalogs from different regions of the North Atlantic have not been  
105 conducted yet, hindering our understanding of the connectivity of different killer whale  
106 populations in this ocean basin.

107         The acoustic behavior of Icelandic and Norwegian killer whales is very similar: both  
108 have high rates of echolocation and calling during feeding but are mostly silent when  
109 travelling (Samarra & Miller, 2015; Simon et al., 2007). Similarly, herring-eating killer  
110 whales in Shetland are highly vocal during feeding but whales in the same areas predated on  
111 seals are relatively quiet during hunting (Deecke et al., 2011). High frequency whistles have  
112 been recorded in Iceland, Norway, and Shetland (Samarra et al., 2010). The repertoires and  
113 time-frequency parameters of these whistles are similar between Iceland and Norway but  
114 different from those of the North Pacific (Samarra, Deecke, Simonis, & Miller, 2015). On the  
115 other hand, low frequency signals (<300 Hz) have been reported from killer whales in Iceland  
116 and Shetland but have not been found in recordings from Norway (Samarra, Deecke, &  
117 Miller, 2016). Similarly, the ‘herding call’, Icelandic call type I36, seems to play a  
118 particularly important role in the feeding strategy of Icelandic killer whales and has also been

119 recorded in Shetland (call type NASH08), but not in Norway (Deecke et al., 2011; Samarra,  
120 2015; Simon, Ugarte, Wahlberg, & Miller, 2006).

121 Call repertoires have not been studied in detail in the Northeast Atlantic. In Shetland,  
122 there are no shared call types between killer whales preying on seals and those feeding on  
123 herring (Deecke et al., 2011). Norwegian killer whales are presumed to live in stable  
124 matrilineal groups (Bisther & Vongraven, 1995) and were found to have group-specific call  
125 repertoires, similar to those of the North Pacific resident populations (Strager, 1995). Group-  
126 specific call repertoires have been suggested for Icelandic killer whales in an earlier study but  
127 results were considered preliminary due to the small sample size of recordings used (Moore,  
128 Francine, Bowles, & Ford, 1988). Recent studies show that Icelandic killer whales live in a  
129 fluid, multilevel society showing fission-fusion dynamics (Tavares, Samarra, & Miller,  
130 2017). Due to this dynamic social structure, it is often difficult to obtain recordings from  
131 isolated groups, hence to date we have little knowledge whether Icelandic killer whales  
132 exhibit group-specific repertoires.

133 Comparisons of the call repertoire of Northeast Atlantic killer whales have been  
134 attempted to various degrees. An earlier study comparing a small set of recordings from  
135 Iceland and Norway suggested that the two populations have calls of similar frequency but  
136 distinct repertoires with no shared call types (Moore et al., 1988). Using a larger sample size  
137 from Norway, Strager (1995) matched two call types from Norway to call types reported by  
138 Moore et al. (1988) from Iceland, but also found one match from Norway to the Canadian  
139 resident population and one to Alaska. Both call types matched to Iceland were only recorded  
140 from one Norwegian pod, which is the most socially isolated of the pods described (Strager,  
141 1995). However, small sample sizes, particularly for Iceland, have precluded a more  
142 thorough comparison of the repertoire of these populations. Data collection for both studies  
143 occurred between 1983 and 1992 and Icelandic data had only been collected in the east of

144 Iceland during two consecutive winters. More recently, Shamir et al. (2014) investigated the  
145 performance of an automated image comparison method to classify calls recorded from killer  
146 whales in Iceland and Norway and found that the algorithm automatically separated the calls  
147 between the two locations without prior information on their origin. Danishevskaya et al.  
148 (2020) investigated whether independent observers could correctly detect differences in  
149 repertoires of killer whale populations from different ecotypes, different oceans, and from  
150 different subpopulations of the same population. While both North Pacific resident killer  
151 whales and North Atlantic killer whales were easily distinguished from North Pacific  
152 transient killer whales, Icelandic and Norwegian call repertoires were difficult to distinguish  
153 from North Pacific resident type killer whales. Finally, Deecke et al. (2011) compared calls  
154 recorded in Shetland to calls recorded in Iceland (Moore et al., 1988; Simon et al., 2006) and  
155 found two call type matches, suggesting some shared call repertoire between these locations.

156         While these earlier studies have attempted to some degree to compare the call  
157 repertoires of killer whales in Iceland, Norway, and Shetland, an updated, comprehensive  
158 analysis using large sample sizes collected over several years and locations has not yet been  
159 conducted. The fact that past and present connectivity between these locations has either been  
160 shown or implied from catch distributions, suggests that there is potential for call type  
161 sharing. Here we use killer whale calls recorded between 2008 and 2016 in Iceland, between  
162 2005 and 2009 in Norway and in 2008 and 2009 in Shetland to attempt a comprehensive  
163 comparison of the call repertoires of Northeast Atlantic killer whales. This study aims to  
164 compare acoustic repertoire sharing to current knowledge of movement connectivity between  
165 these locations to provide insights into population structure and social relationships among  
166 Northeast Atlantic killer whales.

167

## 168 2 METHODS

169

### 170 2.1 Data collection

171 Acoustic recordings were made at different locations in Iceland, Norway, and Shetland  
172 (Figure 1) between 2005 and 2016 (Table 1). In order to use as many recordings as possible,  
173 acoustic data collected in various projects with different research priorities and recording set-  
174 ups were included (Table 1). In Iceland, killer whales are regularly seen during summer in  
175 Vestmannaeyjar, a spawning ground of the Icelandic summer-spawning (ISS) herring, and  
176 during winter in Breiðafjörður, an overwintering ground of ISS herring. In both areas, killer  
177 whales are often seen in large aggregations of 50-100 whales. Therefore, it can be difficult to  
178 discern isolated groups and establish group affiliation and social networks (Beck, Kuningas,  
179 Esteban, & Foote, 2012; Sigurjónsson et al., 1988; Tavares et al., 2017). Generally,  
180 recordings were made when whales were feeding on herring, which is also the behavior when  
181 these whales are most vocal (Samarra & Miller, 2015; Simon et al., 2007). The targeted prey  
182 could not be identified in all cases, but feeding on marine mammals was not observed.

183 Identification photographs were collected during recordings in Iceland, except for recordings  
184 obtained from an Ecological Acoustic Recorder (EAR, Lammers, Brainard, Au, Mooney, &  
185 Wong, 2008), deployed in 2014 (22 February to 31 March) at ~30 m depth in Breiðafjörður.

186 In Norway, killer whales aggregated in fjords during the winter, where they were  
187 feeding on herring. While Norwegian killer whales are presumed to live in stable,  
188 moderately-sized matrilineal groups (Bisther & Vongraven, 1995), large aggregations were  
189 also frequently observed. The research focus in Norway was on individual tagged whales and  
190 their group. Photo-identification records of these focal groups were not always complete but  
191 group size was estimated and identification of pods was possible in most cases. During some  
192 Dtag deployments in Norway, animals were exposed to simulated sonar signals as part of a



193 controlled exposure experiment (Miller et al., 2011). Only data prior to the start of sound  
194 transmissions were used from those deployments.

195         Recordings in Shetland were undertaken around small groups of killer whales (1-15  
196 individuals) hunting seals and larger groups (20+ individuals) feeding on herring. The  
197 majority of individuals present were photographed and identified (Deecke et al., 2011).

198         In all locations the situation was dynamic, often with several groups of whales around  
199 and large aggregations of individuals. Thus, the number of individuals present are minimum  
200 estimates. For Iceland and Shetland, group size was determined from photo-identification  
201 records and for Norway, it was estimated in the field. It is possible that the acoustic  
202 recordings include vocalizations of additional whales in the area that were not part of focal  
203 groups. However, in all cases the data collection effort was focused on the group(s) closest to  
204 the hydrophone and it is unlikely that high quality calls that would be included in the analysis  
205 were recorded from farther groups.

206         In Iceland, other marine mammals were observed or acoustically detected on three  
207 occasions. In the winter of 2014, white-beaked dolphins (*Lagenorhynchus albirostris*), and  
208 pinnipeds were occasionally observed but never in close proximity to the killer whales. In  
209 2015 and 2016, long-finned pilot whales (*Globicephala melas*) were recorded visually and  
210 acoustically. Due to the familiarity gained with the Icelandic killer whale calls during  
211 analysis, pilot whale vocalizations were easily separated. Usually there was little or no  
212 overlap between vocalizations of killer and pilot whales; nevertheless, killer whale calls  
213 recorded during phases of pilot whale vocalization were not included in the analysis. In  
214 Norway and Shetland no other marine mammals were observed or acoustically detected,  
215 except for seals preyed upon by seal-hunting killer whales in Shetland.

216

## 217 2.2 Acoustic analysis

218 All recordings from Iceland were analyzed aurally and visually from spectrograms using  
219 Audacity 2.1.2 (Audacity Team) with a Hann window, FFT = 8,192 for 96, 192 and 240 kHz  
220 sampling rates and FFT = 4,096 for 48 and 64 kHz sampling rates. Recordings from Norway  
221 were analyzed using Adobe Audition 2.0 (Adobe Inc., San Jose, USA) using a Blackmann-  
222 Harris window, FFT = 2,048 or 4,096, for 96 and 192 kHz sampling rates, respectively. Calls  
223 were defined as burst-pulse sounds as opposed to whistles that are tonal sounds. Killer whale  
224 whistles are frequency-modulated sounds with or without harmonic overtones and typically  
225 have high frequency (average dominant frequency of 8.3 kHz) and long duration (Thomsen et  
226 al., 2001). Calls consist of rapidly repeated broadband pulses. Thus, they appear as  
227 continuous frequency-modulated contours in the spectrogram with a fundamental frequency  
228 and many harmonics (Wellard, Erbe, Fouda, & Blewitt, 2015). The large majority of calls  
229 from a number of different populations have lower frequency components below 4 kHz  
230 (Filatova et al., 2016). Nevertheless, calls and whistles may be considered two extremes on a  
231 continuum and killer whales are known to produce call types that resemble whistles  
232 (Filatova, Fedutin, Burdin, & Hoyt, 2007; Murray, Mercado, & Roitblat, 1998). The start and  
233 end of each call was marked, and each call was assigned a quality from 1 (poor) to 3 (high)  
234 based on signal-to-noise ratio, overlap with other sounds and clarity of the call. Only quality  
235 3 calls were used for further analysis. Recordings from Shetland were analyzed in a previous  
236 study that determined the call categories used here (Deecke et al., 2011).

237

## 238 2.3 Call classification and comparison

239 Calls from Iceland and Norway were classified based on visual and aural examination of  
240 spectrograms (Ford, 1987; Strager, 1995). The majority of killer whale calls are discrete.  
241 They have a distinctive structure, are repetitive and can be classified into call types and

242 subtypes (Ford, 1989). Aberrant calls are based on a discrete call type but are highly modified  
243 and variable calls cannot be arranged into clear categories (Ford, 1989). Features that appear  
244 readily discernible in spectrograms can usually be perceived acoustically (Wellard, Pitman,  
245 Durban & Erbe, 2020; Yurk et al. 2002; Sharpe, Castellote, Wade & Cornick, 2017).  
246 Classification was based on the shape of the call contour, the number of subunits (defined  
247 below), and to a lesser extent, call duration. Subtypes were assigned if a subunit was added or  
248 subtracted from a call, if a major change in a subunit occurred or if a HFC was present or  
249 absent (Strager 1995). Variability occurs in all call types and subtypes but certain categories  
250 are more variable than others (Ford, 1989). Call types were only divided into subtypes when  
251 the variation was discrete rather than graded. The entire dataset was classified by the first  
252 author and cross-validated by a second observer. If there was disagreement between the  
253 observers, both observers reviewed the classification and if no consensus could be reached  
254 the call was labelled as ‘unknown’. At least three call examples were required to define a new  
255 type or subtype (Sharpe et al., 2017; Wellard et al., 2020).

256         The Norwegian call types were matched to previously published catalogs (Moore et  
257 al., 1988; van Opzeeland, Corkeron, Leyssen, Similä, & van Parijs, 2005; van Parijs,  
258 Leyssen, & Similä, 2004; Shapiro, 2008; Strager, 1993). Similarities to the catalogs of Moore  
259 et al. (1988), Strager (1993), van Parijs et al. (2004), and van Opzeeland et al. (2005) were  
260 noted but only a limited comparison was possible, due to issues with quality of the  
261 spectrogram images or unavailability of samples of call types. Strager (1993) defined the first  
262 34 call types, van Opzeeland et al. (2005) added call types N35 to N63, and Shapiro (2008)  
263 added call types N64 to N103. Newly defined types were numbered N104 onwards (see  
264 Figure S1, Supplementary Material).

265         The only previously published catalog of calls from Iceland is that of Moore et al.  
266 (1988), who classified call types I1 to I35 based on a few hours of recordings from East

267 Iceland. This was followed by a description of call type I36, the ‘herding call’ by Simon et al.  
268 (2006). Comparisons to the catalog of Moore et al. (1988) were made whenever possible and  
269 call types that could not be compared or that were different from previously described call  
270 types were labelled from I37 onwards.

271 Call types from Shetland were established by Deecke et al. (2011), consisting of six  
272 call types and two subtypes from seal-hunting killer whales and seven call types of killer  
273 whales feeding on herring.

274 Each call type and subtype from each location was compared by visual and aural  
275 inspection. A match between call types was defined as showing high similarity with a  
276 complete or nearly complete match in frequency contour shape, including similar aural  
277 qualities. Call types that showed some degree of similarity but are not complete matches were  
278 labelled possible matches, e.g., if a part of the contour is not totally matched, or if the match  
279 was only to one or a few examples of a highly variable call type. All call types showed some  
280 variability but certain call types were more variable than others. Therefore all available  
281 examples within each call type were considered in the comparison. In addition, comparisons  
282 were also undertaken whenever possible to previously published catalogs from each region  
283 (Iceland: Moore et al., 1988; Norway: Moore et al., 1988; van Opzeeland et al., 2005; van  
284 Parijs et al., 2004; Shaprio, 2008; Strager, 1993). This ensured that as many call types from  
285 each region as possible were included in our comparison of Northeast Atlantic killer whale  
286 call type repertoires.

287

## 288 2.4 Call measurements

289 To compare the call type repertoires recorded in different locations quantitatively, duration,  
290 start, end, mid, maximum, and minimum frequency of the fundamental frequency of the low  
291 frequency component were measured for each call (Figure 2). These parameters were chosen

292 based on a review of the published literature with the aim to select commonly used  
293 parameters to maximize comparability between studies. If some or all points were only  
294 clearly visible in higher harmonics, measurements were taken from the clearest harmonic and  
295 divided by its number to obtain the fundamental frequency (Watkins, 1968). The aim of this  
296 quantitative analysis was not to measure calls in detail for quantitative classification, but  
297 rather to test for general patterns that differed between the two populations. Therefore, calls  
298 were measured over their entire duration and not divided into subunits. In some call types,  
299 where a short pause separated two subunits, the pause was included in the duration  
300 measurements (e.g., N72.2, I44). Due to variation in call quality, not all parameters were  
301 measured from all calls. The measurements were made using a custom routine in MATLAB  
302 R2017a (The MathWorks, Natick, USA). This routine displays a spectrogram (Hann window;  
303 FFT = 4,096, 2,048 or 1,024 for 240 and 192 kHz, 96 and 64 kHz or 48 kHz sampling rates  
304 respectively; 87.5% overlap) of the call and a crosshair cursor is placed on the relevant points  
305 to take the measurements. Call parameters were only extracted if they were clearly visible in  
306 the spectrogram. The precision of the measurements is in the order of 50-100 Hz and 50-100  
307 ms.

308 All call categories were labelled single-component (if containing only a low-  
309 frequency component - LFC, i.e., monophonic or single-voiced) or two-component (if  
310 containing both a LFC and a high-frequency component - HFC, i.e., biphonic or two-voiced)  
311 and the number of subunits within each call category was counted. Various terminologies  
312 have been used to describe subunits of killer whale calls. The terms part, segment,  
313 component, or syllable have been used to refer to abrupt shifts in pulse repetition rate  
314 (Filatova, Ivkovich, Guzeev, Burdin, & Hoyt, 2017; Ford, 1991; Strager, 1993). Yurk et al.  
315 (2002) distinguished between elements (separating parts of a call marked by abrupt shifts)  
316 and segments (parts of a call separated by silent intervals). Shapiro, Tyack, and Seneff (2011)

317 combined elements and segments under the term subunit. Following this definition, subunits  
318 were defined in the present study as parts of a call separated by abrupt shifts in pulse  
319 repetition rate of the LFC or separated by a very short silent interval ( $<0.2$  s).

320

## 321 2.5 Statistical analysis

322 To test for differences in parameter distributions among locations, Kolmogorov-Smirnov  
323 tests were used, due to the nonnormality of all distributions (Shapiro-Wilk normality tests:  $p$   
324  $< 0.01$ ). The significance level was adjusted using a Bonferroni correction for multiple  
325 comparisons ( $0.05/7 = 0.007$ ). In addition, a multivariate approach was applied by using a  
326 discriminant function analysis (DFA) to investigate differences in discrete calls between  
327 locations. All measured time and frequency parameters were included but only calls for  
328 which all measurements could be taken were used. Location was used as the grouping  
329 variable. The jackknife cross-validation of the `lda` function of the MASS Package 7.3-35 in  
330 RStudio 1.1.456 for Mac OS was applied to test classification success based on the DFA.

331

## 332 **3 RESULTS**

333

### 334 3.1 Call classification

335 A total of 666 hr and 50 min of recordings were collected around Iceland on 138 days in  
336 2008–2010 and 2013–2016. Off Norway, 48 hr and 52 min were collected on 12 days in  
337 2005, 2006, 2008, and 2009 and around Shetland 15 hr and 4 min on 11 days in 2008 and  
338 2009. The larger collection of recordings from Iceland is mainly due to 432 hr of recordings  
339 collected using an EAR over 38 days in the winter of 2014. The mean $\pm$ SD number of whales  
340 photo-identified per recording day was  $31\pm 28$  (range 1-159),  $25\pm 23$  (range 7-75), and  $9\pm 7$   
341 (range 4-20) for Iceland, Norway, and Shetland, respectively (see table S1, Supplementary

342 Material). A total of 439 individual whales were photo-identified during days when  
343 recordings were collected in Iceland and 62 in Shetland (Table S1, Supplementary Material).  
344 Most individuals were present in multiple recording sessions. Around Iceland, individual  
345 whales were identified on a mean of  $9 \pm 9$  (range 1-44) different recording days, around  
346 Shetland on a mean of  $1 \pm 1$  (range 1-5) days (table S1, Supplementary Material). The number  
347 of whales identified and the number of repeat days are minimum estimates as it is possible  
348 that some individuals were missed. Off Norway, a total of 9 different identified groups and 4  
349 unidentified groups were recorded on a mean of  $1 \pm 1$  (range 1-3) days. From the acoustic  
350 recordings, 8,993 high quality calls were extracted from Iceland and 3,215 from Norway.  
351 Deecke et al. (2011) had previously processed the recordings from Shetland and extracted  
352 120 discrete calls, which were used in this study. Approximately 89% ( $n = 8,011$ ) of the  
353 extracted calls from Iceland were discrete and were classified. About 10% ( $n = 890$ ) were  
354 variable and 1% ( $n = 92$ ) were aberrant calls. Discrete calls were assigned to 43 call types, 15  
355 of which had 31 subtypes resulting in 74 call categories (see Selbmann et al., 2019 for the full  
356 catalog and Table S2, Supplementary Material for a summary). Of the Norwegian calls  
357 approximately 95% ( $n = 3,059$ ) were discrete, 4% ( $n = 133$ ) variable and 1% ( $n = 23$ )  
358 aberrant. Norwegian discrete calls were assigned to 32 types, 9 of which had 22 subtypes  
359 resulting in 54 call categories. Most call categories from Norway (75.9%) could be matched  
360 to previous catalogs and only types N104 to N110 were newly described here (see Figure S1,  
361 Supplementary Material).

362

### 363 3.2 Comparison of call types between locations

364 No call type matches were confirmed between Iceland and Norway. Eight call types were  
365 considered possible matches between Iceland and Norway. One of these call types was a  
366 match between Iceland and Shetland (I5.5, NAsh10, see below). All possible matches were

367 composed of call types with very simple frequency contours and comprised a large number of  
368 calls but with much variability within each category. The graded nature of the variation  
369 within the categories precluded further division into subtypes. However, in every case only  
370 one or two calls included in each category showed similarities to call types from Norway,  
371 thus precluding confirmation of a match. In contrast, three call type matches between Iceland  
372 and Shetland were confirmed. Two of these matches had been previously described by  
373 Deecke et al. (2011): call type NASH08 was a match to Icelandic call type I36 described by  
374 Simon et al. (2006) (Figure 3) and NASH10 was a match to I5 described by Moore et al.  
375 (1988). In this study, we identified subtype I5.5 as the most likely match to NASH10,  
376 although further samples of calls from Shetland would be required to confirm this match  
377 unequivocally (Figure 4). In the increased sample size from Iceland analyzed in this study,  
378 we identified a further match between Iceland and Shetland: call type NASH13 matched call  
379 type I11.4 (Figure 5). All matches between Iceland and Shetland included killer whales that  
380 were observed feeding on herring in Shetland. Only two recordings with herring-eating killer  
381 whales were collected in Shetland, one in which the whales were silent and the other in which  
382 all call types were recorded during an approximately 29 min recording. Despite a large  
383 number of calls detected, overlapping calls and echolocation clicks resulted in a low number  
384 of high quality calls from this recording, making it unlikely that the whole group repertoire  
385 was captured (Deecke et al. 2011). Approximately 20 whales were present during this  
386 recording, including one whale that was photographically matched to Iceland (Deecke et al.  
387 2011; Foote et al. 2010). There were no call type matches between Iceland and seal-hunting  
388 killer whales in Shetland, and there were also no matches between Shetland and Norway.  
389 None of the comparisons with previously established catalogs from Iceland and Norway  
390 yielded any additional confirmed matches. However, Icelandic call type I11.4, which matches  
391 call type NASH13 from Shetland, was considered a possible match to a Norwegian call type



392 in the catalog of van Opzeeland et al. (2005). Overall, the visual and aural comparison of call  
393 type repertoires across different locations suggests that a small portion of call types is shared  
394 between Iceland and Shetland but no or very few call types are shared between either of these  
395 locations and Norway.

396

### 397 3.3 Quantitative analysis

398 Measurements were taken of 5,752 calls ( $n_{\text{Iceland}} = 4,037$ ,  $n_{\text{Norway}} = 1,715$ ) and used for the  
399 multivariate comparison between the Icelandic and Norwegian repertoire. Only 24 calls from  
400 Shetland were of sufficient quality to measure all time and frequency parameters and this  
401 small sample size precluded us from including calls from Shetland in further analyses.

402 The level of complexity within each call type differed between the two locations  
403 (Table 2). In Iceland the proportion of two-component calls is smaller (32%) than in Norway,  
404 where approximately half (52%) the calls are composed of both a LFC and a HFC (Table 2).  
405 However, the majority of Icelandic calls (76%) had two or more subunits, while most  
406 Norwegian calls (87%) had only one or two subunits (Table 2).

407 Call measurements from Iceland and Norway were similar but with high variability in  
408 the data, illustrated by high coefficients of variation for all parameters (Table 3). Indeed, all  
409 frequency and time parameters measured in both locations overlapped in their distributions  
410 (Figure 6). Nevertheless, significant differences in the distributions of all parameters were  
411 found between Iceland and Norway (Kolmogorov-Smirnov tests: Start frequency  $D = 0.17$ ;  $p$   
412  $< 0.007$ ; end frequency  $D = 0.09$ ;  $p < 0.007$ ; mid frequency  $D = 0.18$ ;  $p < 0.007$ ; minimum  
413 frequency  $D = 0.17$ ;  $p < 0.007$ ; maximum frequency  $D = 0.15$ ;  $p < 0.007$ ; frequency range  $D$   
414  $= 0.15$ ;  $p < 0.007$ ; duration  $D = 0.24$ ;  $p < 0.007$ ). However, all parameters were correlated  
415 within each location (Pearson correlation:  $p < 0.005$ , see Table S3, Supplementary Material  
416 for details), except for the start and mid frequency in Iceland ( $p = 0.89$ ). The low D-values

417 indicate that the distributions are similar and a closer examination of the parameters'  
418 distributions showed that significant differences are likely caused by relatively small  
419 discrepancies, such as a shifted mode or median.

420         Despite some differences in the parameter comparison, the DFA showed little  
421 discrimination between the two locations. Using the entire data set the proportion of correctly  
422 classified calls was 71%. However, only 6% of Norwegian calls were classified correctly in  
423 comparison to 98% of Icelandic calls. This result probably reflects the larger sample size  
424 from Iceland. Thus, we used a random subsample of calls from Iceland to obtain equal  
425 sample sizes ( $n = 1,715$  calls from each location). The correctly classified proportion of calls  
426 was 55%, with 51% of Icelandic and 61% of Norwegian calls classified correctly. Therefore,  
427 the DFA suggests low distinction in the time and frequency variables of calls recorded in  
428 both locations.

429

#### 430 **4 DISCUSSION**

431 This study shows varying levels of call type repertoire similarities among Northeast Atlantic  
432 killer whales off Iceland, Norway, and Shetland. Call type comparisons yielded few matches  
433 suggesting divergence in repertoires, but general repertoire structure as well as call time and  
434 frequency parameters were similar. Call frequency parameters have been shown to be similar  
435 across oceans but to vary between ecotypes. For example, the calls of North Pacific transient  
436 killer whales have overall lower frequencies than North Pacific residents and North Atlantic  
437 killer whales (Icelandic and Norwegian populations; Filatova et al., 2015a; Foote & Nystuen,  
438 2008). However, differences between North Pacific residents and North Atlantic killer whales  
439 were less pronounced, with significant frequency differences in the low frequency  
440 components but no significant differences in the high frequency components (Filatova et al.,

441 2015a). Our results suggest that in the North Atlantic, time and frequency parameters are not  
442 clearly distinguishable between locations, at least for killer whales off Iceland and Norway.

443 A larger number of call types and subtypes were described in Iceland, which also had  
444 a larger sample size of recordings (Table 1), yet the ratio of call types to subtypes was very  
445 similar in both Iceland and Norway, indicating a similar level of structuring of the  
446 repertoires. The majority of Icelandic call types had two or more subunits, while most  
447 Norwegian call types only had one subunit. For this comparison, all call categories (types and  
448 subtypes) were included and call types, such as I43 (see Figure S2, Supplementary Material),  
449 which have a large number of subtypes with two or more subunits, may have led to an  
450 inflated number for Iceland. On the other hand, about 70% of Icelandic call types were  
451 single-component calls, while in Norway about half of the call types were composed of both  
452 a LFC and HFC. In Iceland, some call types are produced with and without a HFC (e.g., I53,  
453 Figure S3, Supplementary Material), suggesting that the HFC may be added to a call to  
454 provide additional information. The HFC appears to provide information on the direction of  
455 travel of the caller, thus two-component calls might serve as long-range cohesion signals  
456 (Filatova, Fedutin, Nagaylik, Burdin, & Hoyt, 2009; Miller, 2002, 2006). However,  
457 interpreting the role of this variation in broad repertoire structure and call complexity, such as  
458 the presence of a HFC, or number of subunits, is difficult at present given how little we know  
459 about their function. It has been suggested that killer whales may compose their calls from  
460 different subunits (Shapiro et al., 2011; Yurk, 2005). Investigating Norwegian killer whale  
461 calls, Shapiro et al. (2011) suggested that these subunits provide a simpler basic unit than an  
462 entire call and that assembling of calls from subunits is a way to increase repertoire size.  
463 However, subunits from Norwegian calls matched North Pacific resident and transient calls,  
464 indicating that each population of killer whales may use a portion of a universal inventory of  
465 subunits (Shapiro et al., 2011). Thus, the subunit approach may not permit sufficient

466 distinction between populations. The presence of multiple call subunits in the Icelandic killer  
467 whale call repertoire suggests that at least some of the calls could also be built from subunits.  
468 The structure of call type I43 further supports this idea (Filatova et al., 2015b, Figure S2,  
469 Supplementary Material) and future investigation of these subunits could provide insight into  
470 repertoire complexity and whether Icelandic and Norwegian killer whale calls are built from  
471 the same subunits. Additionally, investigating behavioral context and group specificity of  
472 different call types and subtypes may provide insights into the function of some of the  
473 variation observed.

474         Using a large sample of recordings, particularly for Iceland, this study supports  
475 varying levels of call type sharing among Northeast Atlantic killer whales. The confirmation  
476 of some call type matches between Iceland and Shetland, but no matches between Shetland  
477 and Norway, supports current knowledge on movement patterns of these populations. A  
478 comparison of photo-identified individuals found no matches between Norway and Shetland,  
479 but some matches between Iceland and Shetland (Foote et al., 2010). Indeed, a fraction of the  
480 Icelandic killer whale population has been confirmed seasonally moving between Iceland and  
481 Scotland (Samarra & Foote, 2015; Samarra et al., 2017). However, only one individual  
482 known to travel between Iceland and Scotland was confirmed present during both recordings  
483 from Iceland and recordings from Shetland used in this study (see Supplementary Material).  
484 All other individuals known to travel between Iceland and Scotland were only recorded in  
485 one location (either Iceland or Shetland). A lack of call type matches between Iceland and  
486 Norway supports previous studies that found no photographic matches between Iceland and  
487 Norway (Foote et al., 2010) and no shared call types between Iceland and Norway, using a  
488 smaller sample of calls (Moore et al., 1988). However, the most recent photographic datasets  
489 collected in both Iceland and Norway have not been compared yet and this ongoing work  
490 might shed light into the present-day connectivity between these populations.

491 Danishevskaya et al. (2020) found that human observers distinguished Icelandic and  
492 Norwegian killer whale calls but clustered them with those of North Pacific residents. To date  
493 only one study indicates a link between Icelandic and Norwegian killer whale call repertoires:  
494 Strager (1995) found two matches between call types recorded off Norway and those  
495 recorded off East Iceland by Moore et al. (1988). Neither of those call types was recorded in  
496 our study. The coverage of Icelandic call types is presumed to be high in our study. We used  
497 a large data set, collected in seven seasons over an eight-year period in two different  
498 locations and described 43 call types and 31 subtypes. A total of 439 whales were present  
499 during these recordings with a mean of 31 individuals per recording day. The majority of  
500 whales that we have identified in Iceland based on photo-identification were present during  
501 recording days, thus while we did not necessarily attempt to capture the acoustic repertoire of  
502 all animal present, it is possible many of these whales were recorded. While individual  
503 whales were present on more than one day, repeat sightings were generally low. Our sample  
504 from Norway was limited in area coverage and number of individuals recorded. However,  
505 data were collected in four seasons over a five year period and a total of 13 different pods  
506 were present during our recordings, with a mean of 25 individuals per day and low numbers  
507 of repeats. Furthermore, we included all available previous descriptions of Norwegian killer  
508 whale calls (Moore et al., 1988; van Opzeeland et al., 2005; van Parijs et al., 2004; Shapiro,  
509 2008; Strager, 1993) and the previous Icelandic study (Moore et al., 1988) in our comparison  
510 in order to provide the most comprehensive comparison possible.

511 Eight call types included in this study were considered possible matches between  
512 Iceland and Norway, one of which was a confirmed match between Iceland and Shetland.  
513 Generally, these were call types with very simple frequency contours but large variability that  
514 precluded us from confirming a match. Even in entirely separated populations, there is a  
515 chance for similarity due to physical constraints of the sound production apparatus and

516 random convergence (Filatova et al., 2016). Nevertheless, we cannot rule out the possibility  
517 that a larger sample size or a better understanding of within-population variation in call types  
518 would lead to future reassessments of these possible matches and increased call type matches  
519 between Icelandic and Norwegian killer whales. Likewise, future classifications using  
520 automated methods, such as ARTwarp (Deecke & Janik, 2006) could lead to different  
521 assignments of call types and subtypes as well as differences in matches between locations.

522         The data included in this study came from a variety of research projects with varying  
523 research priorities. Data collected in Iceland were collected using a variety of recording  
524 systems including towed and vertical hydrophone arrays, single hydrophones, a moored  
525 recorder and Dtags. Data in Norway and Shetland were recorded using Dtags and a towed  
526 array, respectively. Towed arrays, single hydrophones and moored recorders should provide  
527 the best methods to record vocalizations of groups of whales as they are usually placed at  
528 some distance to the animals and thus have less bias towards particular individuals. Dtag  
529 recordings may have individual bias. As the hydrophone is placed on the animal, the majority  
530 of calls are likely to stem from this individual or others close by (Johnson, de Soto, &  
531 Madsen, 2009). Depending on the exact location of the tag on the animal, flow noise can  
532 mask sounds and the body of the animal can act as a shield, attenuating sounds from the  
533 opposite side of the animal (Benda-Beckmann, Wensveen, Samarra, Beerens, & Miller, 2016;  
534 Madsen et al., 2006). However, the majority of the recordings used here were collected when  
535 the whales were feeding and often large numbers of whales were present. Therefore, all  
536 recording methods are likely to have captured a variety of individuals present, even though  
537 we cannot exclude some bias towards the tagged individual or others in its proximity for the  
538 Dtag recordings.

539         Killer whales in Iceland and Norway were thought to have been in contact until as  
540 recently as the 1960s, with a uniform distribution across the Northeast Atlantic (Jonsgård &

541 Lyshoel, 1970). Genetically, killer whales in both locations are also closely related (Foote et  
542 al., 2011) and show similar behaviors (Similä & Ugarte, 1993; Simon et al., 2007). Thus,  
543 some degree of call type sharing might have been expected. However, the consistent  
544 difference in the call type repertoires of the two populations found in this and previous  
545 studies suggests that if the populations were in contact in the past, they may not have been a  
546 single population with individuals ranging between the two locations. This hypothesis is  
547 supported by two factors. Firstly, killer whale call repertoires of some populations provide a  
548 measure of relatedness by matrilineal ancestry. In the North Pacific, resident killer whale  
549 groups that share call types are believed to share a common ancestral matrilineal heritage  
550 (Ford, 1991; Yurk et al., 2002). Both the call type repertoire and the structure of individual  
551 call types reflect relatedness (Deecke et al., 2010). Therefore, a lack of shared call types  
552 suggests a distant matrilineal relation. Secondly, killer whale call repertoires are thought to be  
553 highly conserved. The repertoires of North Pacific residents for example, have been shown to  
554 be stable for more than 30 years (Foote, Osborne, & Hoelzel, 2008; Ford, 1991). While killer  
555 whales in captive settings have been shown to change their repertoires over a few years when  
556 exposed to tankmates with unfamiliar call types (Crance et al., 2014), there is little evidence  
557 of fast changes in repertoires in the wild (Foote & Nystuen, 2008; Ford, 1991). Changes may  
558 occur in individual call types, such as duration (Wieland, Jones, & Renn, 2010), but call  
559 structure appears stable over decades (Deecke et al. 2000). In conjunction with the fact that  
560 killer whales are long-lived animals, with females having a life expectancy of 50-80 years  
561 (Olesiuk, Bigg, & Ellis, 1990), the consistent differences between repertoires of Icelandic and  
562 Norwegian killer whales are unlikely to have developed over a time frame of 50 to 60 years  
563 since the two populations were last thought to have been in contact. Further support for the  
564 suggestion that these populations may have been connected but not completely mixed in the  
565 past includes the existence of signals in Iceland that do not occur in Norway, such as the

566 'herding call' (Simon et al., 2006) and low-frequency sounds (Samarra et al., 2016).  
567 Nevertheless, recent changes in the distribution of the Norwegian spring-spawning herring  
568 stock, which is now found off east and northeast Iceland during the summer months (IESNS,  
569 2018), could mean that the two populations may be in contact again. Indeed, North Atlantic  
570 herring can undergo changes in abundance and distribution (e.g., Óskarsson,  
571 Gudmundsdottir, & Sigurdsson, 2009), which are likely to influence the extent of  
572 connectivity over time between whales that specialize year-round or  
573 seasonally/opportunistically exploit this prey. We encourage continuing photo-identification  
574 and comparison of acoustic repertoires of whales found in different areas of the North  
575 Atlantic to better understand the connectivity of whales found in different locations.  
576  
577



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596

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833 **Table 1.** Summary of recordings analyzed. No. days refers to the number of different recording events (days) when the data were collected. No.  
834 calls refers to the number of high-quality calls extracted from the recordings, with the percentage of the total high-quality calls per location that  
835 it represents in brackets. Note that on some occasions different recording methods may have been used on the same day. Asterisks indicate  
836 recordings that were part of the sonar exposure experiment study and recording duration is limited to preexposure data.

Location	Region	Year	Season	Recording equipment	Sampling rate (kHz)	Recording duration (hh:mm)	No. days	No. calls
Norway	Vestfjord	2005	Winter	Dtag (flat frequency response: 0.6–45 kHz; Johnson & Tyack 2003)	96	19:37	5	2,110 (65.6%)
	Vestfjord*	2006	Winter	“	96	07:53	4	638 (19.8%)
	Vestfjord*	2008	Spring	“	192	03:46	1	1 (<0.1%)
	off Vesterålen*	2009	Spring	“	192	04:14	1	429 (13.3%)
	off Vesterålen	2009	Spring	“	96	13:21	1	37 (1.2%)
Iceland	Vestmannaeyjar	2008	Summer	4-element vertical hydrophone array (High Tech Inc. 94-SSQ with pre-amplifiers; High Tech Instruments, Long Beach, MS)	96	15:52	7	5 (0.1%)

			connected to an Edirol FA-101 soundcard (Roland Corporation US, Los Angeles, CA) and recording onto a laptop using PAMGUARD (Gillespie et al., 2008)				
Vestmannaeyjar	2009	Summer	Dtag	192	12:17	3	2,477 (27.5%)
Vestmannaeyjar	2009	Summer	“	96	04:12	1	359 (4.0%)
Vestmannaeyjar	2009	Summer	4-element vertical hydrophone array (High Tech Inc. 94-SSQ with pre-amplifiers; High Tech Instruments, Long Beach, MS) connected to an Edirol FA-101 soundcard (Roland Corporation US, Los Angeles, CA) and recording onto a laptop using PAMGUARD (Gillespie et al., 2008), frequency response: 0.02–40 kHz, +0/-2 dB	192	29:47	13	54 (0.6%)
Vestmannaeyjar	2009	Summer	16-element towed hydrophone array, recording onto an Alesis ADAT-HD24 XR	96	03:41	2	0

			(Alesis, Cumberland, RI, USA), frequency response 0.022–44 kHz, $\pm 0.5$ dB (Miller & Tyack 1998)					
Vestmannaeyjar	2009	Summer	2-element towed array with Benthos AQ-4 hydrophones (Teledyne Benthos, Falmouth, MA, USA) and Magrec HP-02 (Magrec Ltd., Lifton, UK) pre-amplifiers recording onto a Marantz PMD671 (Marantz America LLC, Mahwah, NJ, USA), frequency response: 0.1–40 kHz, $\pm 3$ dB	96	08:52	2	22 (0.2%)	
Vestmannaeyjar	2010	Summer	“	96	05:02	4	119 (1.3%)	
Vestmannaeyjar	2010	Summer	Single hydrophone (HTI-94-SSQ, High Tech Inc. Long Beach, MS, USA, with pre-amplifiers) recording onto a laptop using Adobe Audition 2.0	96	00:20	2	30 (0.3%)	
Vestmannaeyjar	2010	Summer	“	48	01:55	2	14 (0.2%)	

Vestmannaeyjar	2013	Summer	4-element vertical array hydrophone (High Tech Inc. 94-SSQ with pre-amplifiers; High Tech Instruments, Long Beach, MS) connected to a Roland R-44 recorder (Roland Corporation US, Los Angeles, CA, USA), frequency response: 0.02–30 kHz, +0/-3 dB	96	04:37	4	12 (0.1%)
Vestmannaeyjar	2014	Summer	2-element towed hydrophone array with Benthos AQ-4 hydrophones (Teledyne Benthos, Falmouth, MA, USA) and Magrec HP-02 (Magrec Ltd., Lifton, UK) pre-amplifiers recording onto a Sound Devices 702 (Sound Devices LLC, Reedsburg, WI, USA), frequency response 0.1–40 kHz, ±3 dB	192	12:02	6	660 (7.3%)
Vestmannaeyjar	2014	Summer	“	48	06:15	4	280 (3.1%)

Vestmannaeyjar	2014	Summer	Single hydrophone (HTI-94-SSQ, High Tech Inc. Long Beach, MS, USA, with pre-amplifiers) recording onto a M-Audio Microtrack II (M-Audio, Cumberland, RI, USA), flat frequency response: 0.002–30 kHz	96	05:34	4	81 (0.9%)
Vestmannaeyjar	2015	Summer	2-element towed hydrophone array with Benthos AQ-4 hydrophones (Teledyne Benthos, Falmouth, MA, USA) and Magrec HP-02 (Magrec Ltd., Lifton, UK) pre-amplifiers recording onto a Sound Devices 702 (Sound Devices LLC, Reedsburg, WI, USA), frequency response 0.1–40 kHz, $\pm 3$ dB	192	52:43	18	844 (9.4%)
Vestmannaeyjar	2015	Summer	2-element towed array with Benthos AQ-4 hydrophones (Teledyne Benthos, Falmouth, MA, USA) and Magrec HP-02 (Magrec Ltd., Lifton, UK) pre-amplifiers recording onto a Marantz PMD671 (Marantz America	96	01:36	1	55 (0.6%)



			LLC, Mahwah, NJ, USA), frequency response 0.1–40 kHz, $\pm 3$ dB					
Vestmannaeyjar	2015	Summer	Single hydrophone (HTI-94-SSQ, High Tech Inc. Long Beach, MS, USA, with pre-amplifiers) recording onto a M-Audio Microtrack II (M-Audio, Cumberland, RI, USA), flat frequency response: 0.002–30 kHz	96	00:27	1	0	
Vestmannaeyjar	2016	Summer	2-element towed hydrophone array with Benthos AQ-4 hydrophones (Teledyne Benthos, Falmouth, MA, USA) and Magrec HP-02 (Magrec Ltd., Lifton, UK) pre-amplifiers recording onto a Sound Devices 702 (Sound Devices LLC, Reedsburg, WI, USA), frequency response 0.1–40 kHz, $\pm 3$ dB	192	22:57	8	559 (6.2%)	
Vestmannaeyjar	2016	Summer	2-element towed hydrophone array with Benthos AQ-4 hydrophones (Teledyne	96	12:24	4	435 (4.8%)	

			Benthos, Falmouth, MA, USA) and Magrec HP-02 (Magrec Ltd., Lifton, UK) pre-amplifiers recording onto a Marantz PMD671 (Marantz America LLC, Mahwah, NJ, USA), frequency response 0.1–40 kHz, $\pm 3$ dB				
Breiðafjörður	2013	Winter	Dtag	240	05:33	3	250 (2.8%)
Breiðafjörður	2013	Winter	4-element vertical hydrophone array (High Tech Inc. 94-SSQ with pre-amplifiers; High Tech Instruments, Long Beach, MS) connected to a Roland R-44 recorder (Roland Corporation US, Los Angeles, CA, USA), frequency response: 0.02–30 kHz, $\pm 3$ dB	96	10:37	13	605 (6.7%)
Breiðafjörður	2013	Winter	Single hydrophone (HTI-94-SSQ, High Tech Inc. Long Beach, MS, USA, with pre-amplifiers) recording onto a M-Audio	96	07:23	14	660 (7.3%)

			Microtrack II (M-Audio, Cumberland, RI, USA), flat frequency response: 0.002–30 kHz					
Breiðafjörður	2014	Winter	Dtag	192	04:37	1	31 (0.3%)	
Breiðafjörður	2014	Winter	4-element vertical hydrophone array (High Tech Inc. 94-SSQ with pre-amplifiers; High Tech Instruments, Long Beach, MS) connected to a Roland R-44 recorder (Roland Corporation US, Los Angeles, CA, USA), frequency response: 0.02–30 kHz, +0/-3 dB	96	02:54	6	15 (0.2%)	
Breiðafjörður	2014	Winter	Single hydrophone (HTI-94-SSQ, High Tech Inc. Long Beach, MS, USA, with pre-amplifiers) recording onto a M-Audio Microtrack II (M-Audio, Cumberland, RI, USA), flat frequency response: 0.002–30 kHz	96	03:03	7	85 (0.9%)	

	Breiðafjörður	2014	Winter	EAR (Lammers et al. 2008), recording for 5 min every 10 min, frequency response 1–28 kHz, $\pm 1.5$ dB	64	432:10	38	1,341 (14.9%)
Scotland	Shetland	2008	Summer	2-element towed hydrophone array with Benthos AQ-4 hydrophones (Teledyne Benthos, Falmouth, MA, USA) and Magrec HP-02 (Magrec Ltd., Lifton, UK) pre-amplifiers recording onto a Marantz PMD671 (Marantz America LLC, Mahwah, NJ, USA), frequency response 0.1–40 kHz, $\pm 3$ dB	96	03:50	4	2 (1.7%)
	Shetland	2009	Summer	“	96	11:14	7	118 (98.3%)

838 **Table 2.** Differences in complexity of killer whale calls from Iceland and Norway. Number  
 839 of call types and subtypes with percentage in parentheses given for each category. Single-  
 840 component refers to call types with only a low frequency component; two-component call  
 841 types have both a low and high frequency component.

Location	Single- component	Two- component	Number of subunits				
			1	2	3	4	5
Iceland	50 (68%)	24 (32%)	18 (24%)	40 (54%)	14 (19%)	2 (3%)	-
Norway	26 (48%)	28 (52%)	31 (57%)	16 (30%)	5 (9%)	1 (2%)	1 (2%)

842

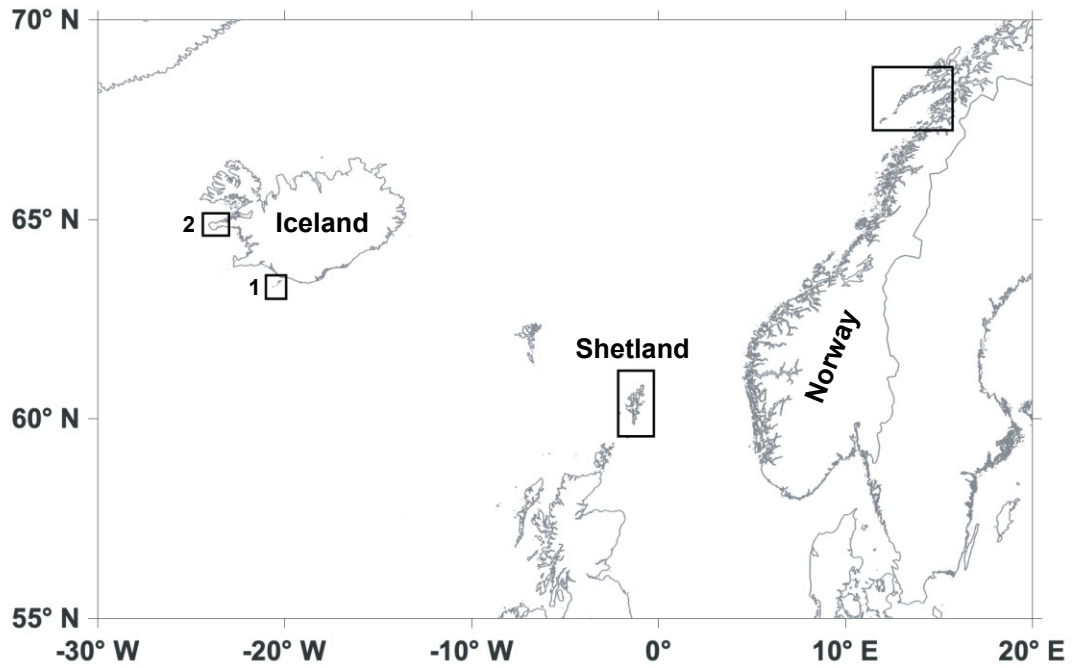
843

844 **Table 3.** Descriptive statistics of killer whale calls from Iceland and Norway. Sample sizes  
 845 are indicated for each location in brackets. The values presented are the mean  $\pm$  standard  
 846 deviation with the coefficient of variation as a percentage in parentheses and minimum and  
 847 maximum values in brackets. Frequency range was calculated as the difference between the  
 848 maximum and minimum frequency.

Location	Iceland (n = 4,037)	Norway (n = 1,715)
Start frequency (kHz)	1.1 $\pm$ 0.7 (64.4%) [0.1-5.8]	1.0 $\pm$ 0.8 (79.2%) [0.1-6.3]
End frequency (kHz)	1.3 $\pm$ 0.8 (60.8%) [0.3-7.7]	1.5 $\pm$ 1.3 (85.8%) [0.1-12.2]

Mid frequency (kHz)	1.0 ± 0.5 (50.8%) [0.2-6.4]	1.3 ± 1.1 (86.5%) [0.2-8.6]
Minimum frequency (kHz)	0.6 ± 0.3 (42.1%) [0.1-2.6]	0.7 ± 0.7 (89.8%) [0.1-6.4]
Maximum frequency (kHz)	1.9 ± 1.2 (60.8%) [0.5-7.8]	2.1 ± 1.2 (59.4%) [0.3-12.2]
Frequency range (kHz)	1.3 ± 1.2 (93.1%) [0-7.0]	1.3 ± 0.9 (64.3%) [0.1-7.3]
Duration (s)	1.0 ± 0.6 (63.9%) [0.1-5.2]	1.1 ± 0.5 (44.2%) [0.1-3.0]

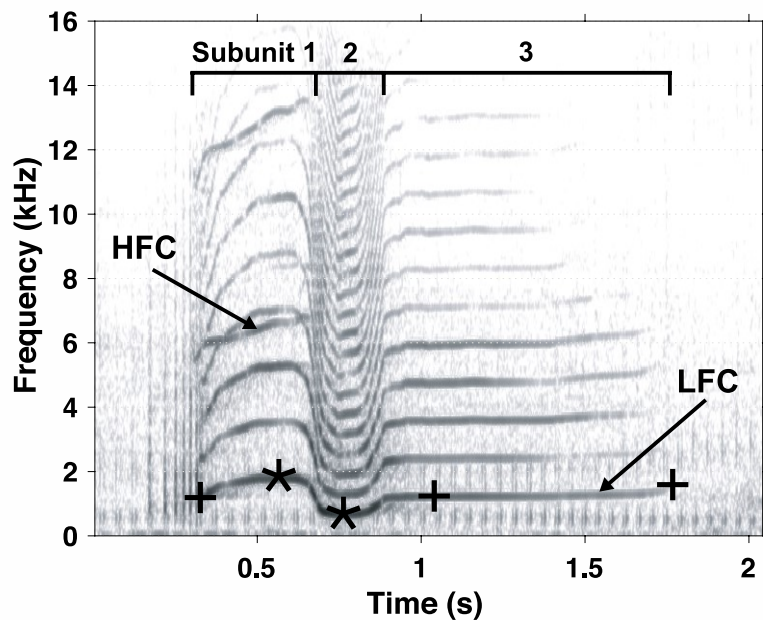
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850

851 **Figure 1.** Map of the North Atlantic showing the study sites in Iceland (1 = Vestmannaeyjar,  
 852 2 = Breiðafjörður), Norway and Shetland.

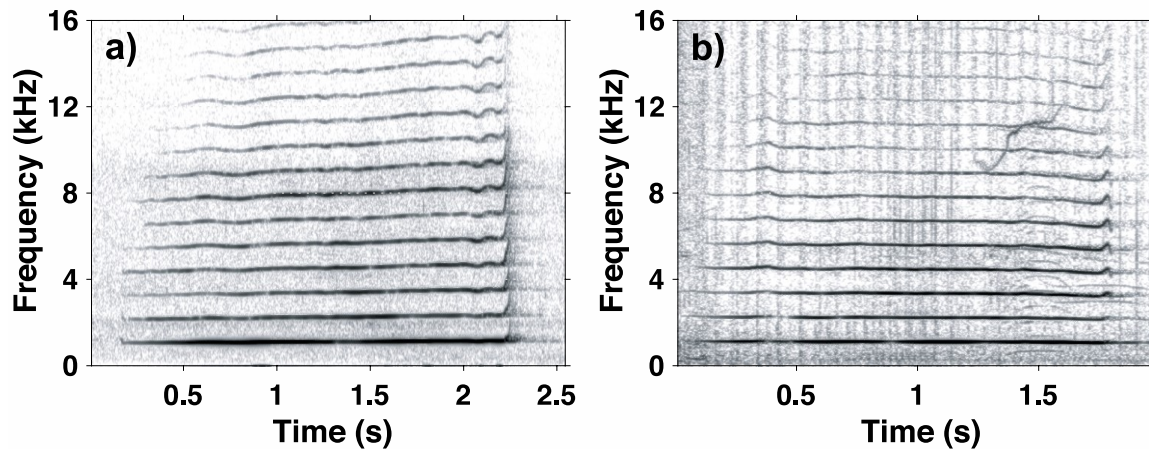
853



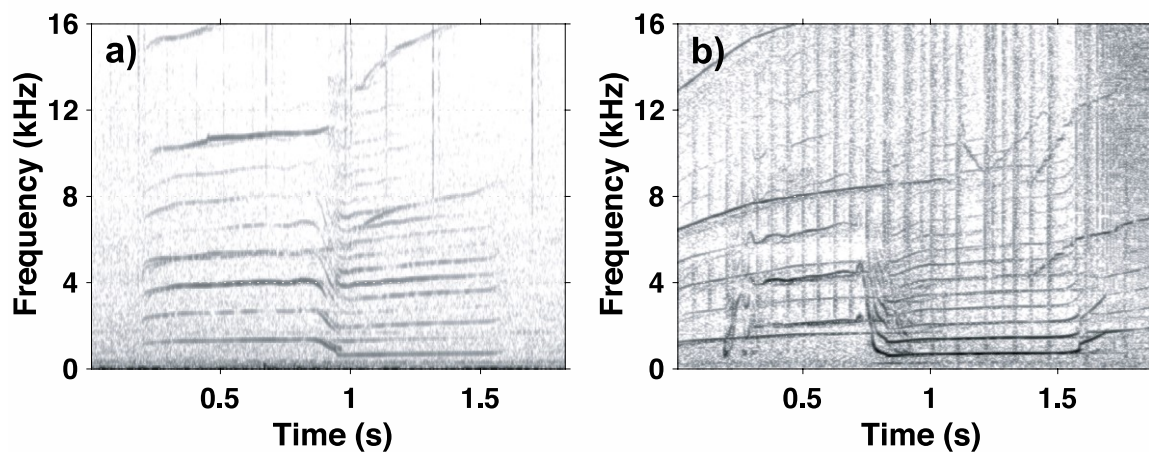
854

855 **Figure 2.** Spectrogram of an Icelandic killer whale call showing measurements taken for this  
 856 study. Measurements were made of the start, mid and end frequency (crosses) and at the

857 maximum and minimum frequency (asterisks) of the low frequency component (LFC). The  
858 high frequency component (HFC) was not measured. Recording sampled at 192 kHz.  
859 Spectrogram parameters: Hann window; FFT size: 4,096; 87.5% overlap; frequency resolution:  
860 46.88 Hz; time resolution: 2.67 ms.  
861



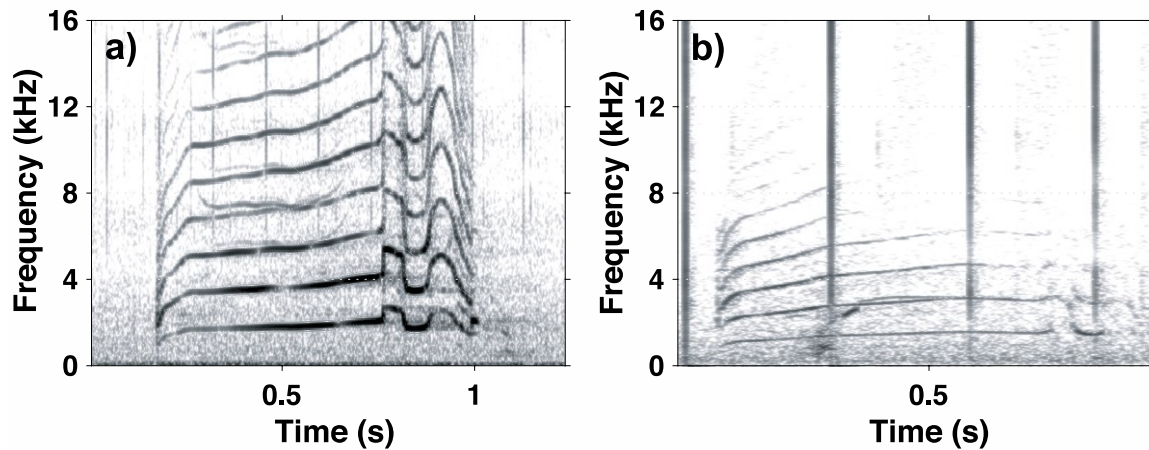
862  
863 **Figure 3.** Matched call types I36 (a) and NASH08 (b; Deecke et al., 2011). Recordings were  
864 sampled at (a) 64 kHz and (b) 96 kHz Spectrogram parameters: Hann window; FFT size: (a)  
865 2,048, (b) 4,096; 87.5% overlap; frequency resolution: (a) 31.25 Hz, (b) 23.44 Hz; time  
866 resolution: (a) 4.00 ms, (b) 5.33 ms.  
867



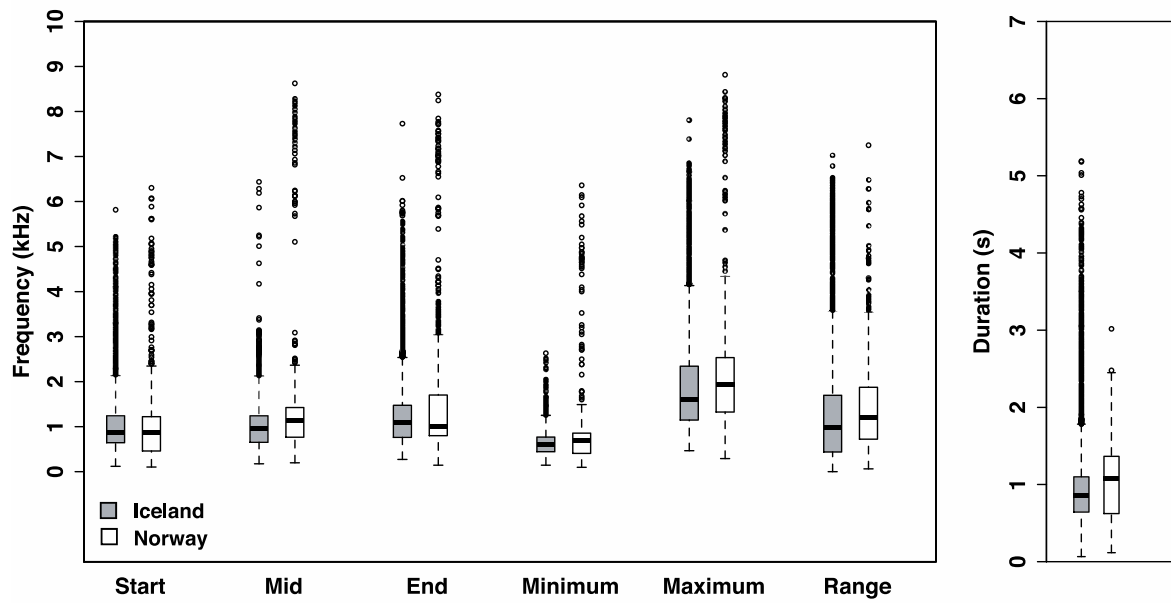
868



869 **Figure 4.** Matched call types I5.5 (a) and NASH10 (b; Deecke et al., 2011). Recordings were  
870 sampled at (a) 48 kHz and (b) 96 kHz. Spectrogram parameters: Hann window; FFT size: (a)  
871 1,024, (b) 4,096; 87.5% overlap; frequency resolution: (a) 46.88 Hz, (b) 23.44 Hz; time  
872 resolution: (a) 2.67 ms, (b) 5.33 ms.  
873



874  
875 **Figure 5.** Matched call types I11.4 (a) and NASH13 (b; Deecke et al., 2011). Recordings were  
876 sampled at (a) 192 kHz and (b) 96 kHz. Spectrogram parameters: Hann window; FFT size: (a)  
877 and (b) 4,096; 87.5% overlap; frequency resolution: (a) 46.88 Hz, (b) 23.44Hz; time resolution:  
878 (a) 2.67 ms, (b) 5.33 ms.  
879



880

881 **Figure 6.** Boxplot showing the frequency variables (left panel) and duration (right panel)  
 882 measured from killer whale calls in Iceland and Norway. Horizontal lines represent medians,  
 883 boxes show interquartile ranges and whiskers indicate the values within 1.5 times the  
 884 interquartile range. Outliers are shown as single points.

885