View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by St Andrews Research Repository

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

Anna Selbmann[1], Volker B. Deecke[2], Ivan D. Fedutin[3], Olga A. Filatova[3], Patrick J. O. Miller[4], Jörundur Svavarsson[1], Filipa I. P. Samarra[5, 6]

[1] Faculty of Life and Environmental Sciences, University of Iceland, Reykjavík, Iceland
[2] Centre for National Parks and Protected Areas, University of Cumbria, Ambleside, United Kingdom
[3] Department of Vertebrate Zoology, Faculty of Biology, Moscow State University, Moscow, Russia
[4] Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, United Kingdom
[5] Marine and Freshwater Research Institute, Reykjavík, Iceland
[6] University of Iceland's Institute of Research Centers, Vestmannaeyjar, Iceland

Correspondence

Anna Selbmann, Faculty of Life and Environmental Sciences, University of Iceland, Sturlugata 7, 101 Reykjavík, Iceland
Email: selbmannanna@gmail.com

Abstract

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

KEYWORDS

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

1 INTRODUCTION

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

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

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

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

Before its collapse in the 1960s, the Atlanto-Scandian herring stock migrated between Iceland and Norway (Jakobsson & Østvedt, 1999). Killer whale catch locations from whalers indicate a strong association with herring occurrence, as well as a continuous distribution of killer whales between Iceland and Norway or migration between the two locations (Jonsgård & Lyshoel, 1970). The collapse of the Atlanto-Scandian herring stock led to a change in the herring distribution and resulted in the herring retreating closer to the coastal areas of Iceland and Norway (Jakobsson & Stefánsson, 1999; Kvamme et al., 2003). Comparisons of identification photographs collected in Iceland and Norway since the 1980s found no matches of killer whales between Iceland and Norway, indicating that little or no movement occurs between the populations (Foote, Similä, Víkingsson, & Stevick, 2010; Sigurjónsson et al., 1988). However, little dedicated photo-identification effort was invested in Iceland, hindering a full analysis of movements between the two regions. On the other hand, a small number of killer whales has been shown to undertake seasonal movements between Iceland and Shetland (Foote et al., 2010; Samarra & Foote, 2015), indicating that the movement patterns of Icelandic killer whales are not limited to Icelandic coastal waters. Updated comparisons of photo-identification catalogs from different regions of the North Atlantic have not been conducted yet, hindering our understanding of the connectivity of different killer whale populations in this ocean basin.

The acoustic behavior of Icelandic and Norwegian killer whales is very similar: both have high rates of echolocation and calling during feeding but are mostly silent when travelling (Samarra & Miller, 2015; Simon et al., 2007). Similarly, herring-eating killer whales in Shetland are highly vocal during feeding but whales in the same areas predating on seals are relatively quiet during hunting (Deecke et al., 2011). High frequency whistles have been recorded in Iceland, Norway, and Shetland (Samarra et al., 2010). The repertoires and time-frequency parameters of these whistles are similar between Iceland and Norway but different from those of the North Pacific (Samarra, Deecke, Simonis, & Miller, 2015). On the other hand, low frequency signals (<300 Hz) have been reported from killer whales in Iceland and Shetland but have not been found in recordings from Norway (Samarra, Deecke, & Miller, 2016). Similarly, the 'herding call', Icelandic call type I36, seems to play a particularly important role in the feeding strategy of Icelandic killer whales and has also been recorded in Shetland (call type NASh08), but not in Norway (Deecke et al., 2011; Samarra, 2015; Simon, Ugarte, Wahlberg, & Miller, 2006).

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

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

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

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

2 METHODS

2.1 Data collection

Acoustic recordings were made at different locations in Iceland, Norway, and Shetland (Figure 1) between 2005 and 2016 (Table 1). In order to use as many recordings as possible, acoustic data collected in various projects with different research priorities and recording set-ups were included (Table 1). In Iceland, killer whales are regularly seen during summer in Vestmannaeyjar, a spawning ground of the Icelandic summer-spawning (ISS) herring, and during winter in Breiðafjörður, an overwintering ground of ISS herring. In both areas, killer whales are often seen in large aggregations of 50-100 whales. Therefore, it can be difficult to discern isolated groups and establish group affiliation and social networks (Beck, Kuningas, Esteban, & Foote, 2012; Sigurjónsson et al., 1988; Tavares et al., 2017). Generally, recordings were made when whales were feeding on herring, which is also the behavior when these whales are most vocal (Samarra & Miller, 2015; Simon et al., 2007). The targeted prey could not be identified in all cases, but feeding on marine mammals was not observed. Identification photographs were collected during recordings in Iceland, except for recordings obtained from an Ecological Acoustic Recorder (EAR, Lammers, Brainard, Au, Mooney, & Wong. 2008), deployed in 2014 (22 February to 31 March) at ~30 m depth in Breiðafjörður.

In Norway, killer whales aggregated in fjords during the winter, where they were feeding on herring. While Norwegian killer whales are presumed to live in stable, moderately-sized matrilineal groups (Bisther & Vongraven, 1995), large aggregations were also frequently observed. The research focus in Norway was on individual tagged whales and their group. Photo-identification records of these focal groups were not always complete but group size was estimated and identification of pods was possible in most cases. During some Dtag deployments in Norway, animals were exposed to simulated sonar signals as part of a controlled exposure experiment (Miller et al., 2011). Only data prior to the start of sound transmissions were used from those deployments.

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

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

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

2.2 Acoustic analysis

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

2.3 Call classification and comparison

Calls from Iceland and Norway were classified based on visual and aural examination of spectrograms (Ford, 1987; Strager, 1995). The majority of killer whale calls are discrete. They have a distictive structure, are repetitive and can be classified into call types and subtypes (Ford, 1989). Aberrant calls are based on a discrete call type but are highly modified and variable calls cannot be arranged into clear categories (Ford, 1989). Features that appear readily discernible in spectrograms can usually be perceived acoustically (Wellard, Pitman, Durban & Erbe, 2020; Yurk et al. 2002; Sharpe, Castellote, Wade & Cornick, 2017). Classification was based on the shape of the call contour, the number of subunits (defined below), and to a lesser extent, call duration. Subtypes were assigned if a subunit was added or subtracted from a call, if a major change in a subunit occurred or if a HFC was present or absent (Strager 1995). Variability occurs in all call types and subtypes but certain categories are more variable than others (Ford, 1989). Call types were only divided into subtypes when the variation was discrete rather than graded. The entire dataset was classified by the first author and cross-validated by a second observer. If there was disagreement between the observers, both observers reviewed the classification and if no consensus could be reached the call was labelled as 'unknown'. At least three call examples were required to define a new type or subtype (Sharpe et al., 2017; Wellard et al., 2020).

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

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

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

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

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

2.4 Call measurements

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

All call categories were labelled single-component (if containing only a low-frequency component - LFC, i.e., monophonic or single-voiced) or two-component (if containing both a LFC and a high-frequency component - HFC, i.e., biphonic or two-voiced) and the number of subunits within each call category was counted. Various terminologies have been used to describe subunits of killer whale calls. The terms part, segment, component, or syllable have been used to refer to abrupt shifts in pulse repetition rate (Filatova, Ivkovich, Guzeev, Burdin, & Hoyt, 2017; Ford, 1991; Strager, 1993). Yurk et al. (2002) distinguished between elements (separating parts of a call marked by abrupt shifts) and segments (parts of a call separated by silent intervals). Shapiro, Tyack, and Seneff (2011) combined elements and segments under the term subunit. Following this definition, subunits were defined in the present study as parts of a call separated by abrupt shifts in pulse repetition rate of the LFC or separated by a very short silent interval (<0.2 s).

2.5 Statistical analysis

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

3 RESULTS

3.1 Call classification

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

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

3.2 Comparison of call types between locations

No call type matches were confirmed between Iceland and Norway. Eight call types were considered possible matches between Iceland and Norway. One of these call types was a match between Iceland and Shetland (I5.5, NAsh10, see below). All possible matches were composed of call types with very simple frequency contours and comprised a large number of calls but with much variability within each category. The graded nature of the variation within the categories precluded further division into subtypes. However, in every case only one or two calls included in each category showed similarities to call types from Norway, thus precluding confirmation of a match. In contrast, three call type matches between Iceland and Shetland were confirmed. Two of these matches had been previously described by Deecke et al. (2011): call type NASh08 was a match to Icelandic call type I36 described by Simon et al. (2006) (Figure 3) and NASh10 was a match to I5 described by Moore et al. (1988). In this study, we identified subtype I5.5 as the most likely match to NASh10, although further samples of calls from Shetland would be required to confirm this match unequivocally (Figure 4). In the increased sample size from Iceland analyzed in this study, we identified a further match between Iceland and Shetland: call type NASh13 matched call type I11.4 (Figure 5). All matches between Iceland and Shetland included killer whales that were observed feeding on herring in Shetland. Only two recordings with herring-eating killer whales were collected in Shetland, one in which the whales were silent and the other in which all call types were recorded during an approximately 29 min recording. Despite a large number of calls detected, overlapping calls and echolocation clicks resulted in a low number of high quality calls from this recording, making it unlikely that the whole group repertoire was captured (Deecke et al. 2011). Approximately 20 whales were present during this recording, including one whale that was photographically matched to Iceland (Deecke et al. 2011; Foote et al. 2010). There were no call type matches between Iceland and seal-hunting killer whales in Shetland, and there were also no matches between Shetland and Norway. None of the comparisons with previously established catalogs from Iceland and Norway yielded any additional confirmed matches. However, Icelandic call type I11.4, which matches call type NASh13 from Shetland, was considered a possible match to a Norwegian call type in the catalog of van Opzeeland et al. (2005). Overall, the visual and aural comparison of call type repertoires across different locations suggests that a small portion of call types is shared between Iceland and Shetland but no or very few call types are shared between either of these locations and Norway.

3.3 Quantitative analysis

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

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

Call measurements from Iceland and Norway were similar but with high variability in the data, illustrated by high coefficients of variation for all parameters (Table 3). Indeed, all frequency and time parameters measured in both locations overlapped in their distributions (Figure 6). Nevertheless, significant differences in the distributions of all parameters were found between Iceland and Norway (Kolmogorov-Smirnov tests: Start frequency D = 0.17; $p < 0.007$; end frequency D = 0.09; $p < 0.007$; mid frequency D = 0.18; $p < 0.007$; minimum frequency D = 0.17; $p < 0.007$; maximum frequency D = 0.15; $p < 0.007$; frequency range D = 0.15; $p < 0.007$; duration D = 0.24; $p < 0.007$). However, all parameters were correlated within each location (Pearson correlation: $p < 0.005$, see Table S3, Supplementary Material for details), except for the start and mid frequency in Iceland ($p = 0.89$). The low D-values indicate that the distributions are similar and a closer examination of the parameters' distributions showed that significant differences are likely caused by relatively small discrepancies, such as a shifted mode or median.

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

4 DISCUSSION

This study shows varying levels of call type repertoire similarities among Northeast Atlantic killer whales off Iceland, Norway, and Shetland. Call type comparisons yielded few matches suggesting divergence in repertoires, but general repertoire structure as well as call time and frequency parameters were similar. Call frequency parameters have been shown to be similar across oceans but to vary between ecotypes. For example, the calls of North Pacific transient killer whales have overall lower frequencies than North Pacific residents and North Atlantic killer whales (Icelandic and Norwegian populations; Filatova et al., 2015a; Foote & Nystuen, 2008). However, differences between North Pacific residents and North Atlantic killer whales were less pronounced, with significant frequency differences in the low frequency components but no significant differences in the high frequency components (Filatova et al., 2015a). Our results suggest that in the North Atlantic, time and frequency parameters are not clearly distinguishable between locations, at least for killer whales off Iceland and Norway.

A larger number of call types and subtypes were described in Iceland, which also had a larger sample size of recordings (Table 1), yet the ratio of call types to subtypes was very similar in both Iceland and Norway, indicating a similar level of structuring of the repertoires. The majority of Icelandic call types had two or more subunits, while most Norwegian call types only had one subunit. For this comparison, all call categories (types and subtypes) were included and call types, such as I43 (see Figure S2, Supplementary Material), which have a large number of subtypes with two or more subunits, may have led to an inflated number for Iceland. On the other hand, about 70% of Icelandic call types were single-component calls, while in Norway about half of the call types were composed of both a LFC and HFC. In Iceland, some call types are produced with and without a HFC (e.g., I53, Figure S3, Supplementary Material), suggesting that the HFC may be added to a call to provide additional information. The HFC appears to provide information on the direction of travel of the caller, thus two-component calls might serve as long-range cohesion signals (Filatova, Fedutin, Nagaylik, Burdin, & Hoyt, 2009; Miller, 2002, 2006). However, interpreting the role of this variation in broad repertoire structure and call complexity, such as the presence of a HFC, or number of subunits, is difficult at present given how little we know about their function. It has been suggested that killer whales may compose their calls from different subunits (Shapiro et al., 2011; Yurk, 2005). Investigating Norwegian killer whale calls, Shapiro et al. (2011) suggested that these subunits provide a simpler basic unit than an entire call and that assembling of calls from subunits is a way to increase repertoire size. However, subunits from Norwegian calls matched North Pacific resident and transient calls, indicating that each population of killer whales may use a portion of a universal inventory of subunits (Shapiro et al., 2011). Thus, the subunit approach may not permit sufficient distinction between populations. The presence of multiple call subunits in the Icelandic killer whale call repertoire suggests that at least some of the calls could also be built from subunits. The structure of call type I43 further supports this idea (Filatova et al., 2015b, Figure S2, Supplementary Material) and future investigation of these subunits could provide insight into repertoire complexity and whether Icelandic and Norwegian killer whale calls are built from the same subunits. Additionally, investigating behavioral context and group specificity of different call types and subtypes may provide insights into the function of some of the variation observed.

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

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

Eight call types included in this study were considered possible matches between Iceland and Norway, one of which was a confirmed match between Iceland and Shetland. Generally, these were call types with very simple frequency contours but large variability that precluded us from confirming a match. Even in entirely separated populations, there is a chance for similarity due to physical constraints of the sound production apparatus and random convergence (Filatova et al., 2016). Nevertheless, we cannot rule out the possibility that a larger sample size or a better understanding of within-population variation in call types would lead to future reassessments of these possible matches and increased call type matches between Icelandic and Norwegian killer whales. Likewise, future classifications using automated methods, such as ARTwarp (Deecke & Janik, 2006) could lead to different assignments of call types and subtypes as well as differences in matches between locations.

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

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

Lyshoel, 1970). Genetically, killer whales in both locations are also closely related (Foote et al., 2011) and show similar behaviors (Similä & Ugarte, 1993; Simon et al., 2007). Thus, some degree of call type sharing might have been expected. However, the consistent difference in the call type repertoires of the two populations found in this and previous studies suggests that if the populations were in contact in the past, they may not have been a single population with individuals ranging between the two locations. This hypothesis is supported by two factors. Firstly, killer whale call repertoires of some populations provide a measure of relatedness by matrilineal ancestry. In the North Pacific, resident killer whale groups that share call types are believed to share a common ancestral matrilineal heritage (Ford, 1991; Yurk et al., 2002). Both the call type repertoire and the structure of individual call types reflect relatedness (Deecke et al., 2010). Therefore, a lack of shared call types suggests a distant matrilineal relation. Secondly, killer whale call repertoires are thought to be highly conserved. The repertoires of North Pacific residents for example, have been shown to be stable for more than 30 years (Foote, Osborne, & Hoelzel, 2008; Ford, 1991). While killer whales in captive settings have been shown to change their repertoires over a few years when exposed to tankmates with unfamiliar call types (Crance et al., 2014), there is little evidence of fast changes in repertoires in the wild (Foote & Nystuen, 2008; Ford, 1991). Changes may occur in individual call types, such as duration (Wieland, Jones, & Renn, 2010), but call structure appears stable over decades (Deecke et al. 2000). In conjunction with the fact that killer whales are long-lived animals, with females having a life expectancy of 50-80 years (Olesiuk, Bigg, & Ellis, 1990), the consistent differences between repertoires of Icelandic and Norwegian killer whales are unlikely to have developed over a time frame of 50 to 60 years since the two populations were last thought to have been in contact. Further support for the suggestion that these populations may have been connected but not completely mixed in the past includes the existence of signals in Iceland that do not occur in Norway, such as the ‘herding call’ (Simon et al., 2006) and low-frequency sounds (Samarra et al., 2016). Nevertheless, recent changes in the distribution of the Norwegian spring-spawning herring stock, which is now found off east and northeast Iceland during the summer months (IESNS, 2018), could mean that the two populations may be in contact again. Indeed, North Atlantic herring can undergo changes in abundance and distribution (e.g., Óskarsson, Gudmundsdottir, & Sigurdsson, 2009), which are likely to influence the extent of connectivity over time between whales that specialize year-round or seasonally/opportunistically exploit this prey. We encourage continuing photo-identification and comparison of acoustic repertoires of whales found in different areas of the North Atlantic to better understand the connectivity of whales found in different locations.

ACKNOWLEDGEMENTS

We thank everyone involved in the fieldwork. Funding for data collection was provided by the BBC Natural History Unit, Fundação para a Ciência e a Tecnologia (grant number SFRH/BD/30303/2006), the Icelandic Research Fund (i. Rannsóknasjóður) through a START Postdoctoral Fellowship (grant number 120248042) and a Project Grant (grant number 163060-051), the National Geographic Global Exploration Fund (grant number GEFNE65-12), a Marie Curie International Incoming Fellowship (project number 297116), the Office of Naval Research (grant number N00014-08-1-0984), and a Russell Trust Award from the University of St. Andrews. All field research was carried out in compliance with local regulations and under permits by the Ministry of Fisheries or an institutional permit of the Marine and Freshwater Research Institute, Iceland. The Dtag data from Norway 2005 were collected in collaboration with A. D. Shapiro. All Dtag recordings made in Norway and those made in Iceland in 2009 were collected as part of the 3S research program on the behavioral effects of naval sonar on cetaceans. We thank Dr. I. van Opzeeland for providing spectrograms and audio files of call types from Norway for comparison. Previous drafts benefited from insightful comments by S. Parks and three anonymous reviewers, to which we are very thankful. Spectrograms for Shetland call types NaSH08, NaSH10, and NaSH13 (Figures 3-5) were generated from sound files used with permission by Aquatic Biology.

REFERENCES

Au, W. W. L., & Hastings, M. C. (2008). *Principles of marine bioacoustics*. New York, NY: Springer.

Baker, M. C., & Cunningham, M. A. (1985). The biology of bird-song dialects. *Behavioral and Brain Sciences*, 8, 85–133.

Barrett-Lennard, L. G., Ford, J. K. B., & Heise, K. A. (1996). The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour*, 51, 553–565.

Beck, S., Kuningas, S., Esteban, R., & Foote, A. D. (2012). The influence of ecology on sociality in the killer whale (*Orcinus orca*). *Behavioral Ecology*, 23, 246–253.

Bisther, A., & Vongraven, D. (1995). Studies of the social ecology of Norwegian killer whales (*Orcinus orca*). In A. S. Blix, L. Walløe, & Ø. Ulltang (Eds.), *Whales, seals, fish and man* (pp. 169–176). Amsterdam: Elsevier Science.

Van Cise, A. M., Mahaffy, S. D., Baird, R. W., Mooney, T. A., & Barlow, J. (2018). Song of my people: dialect differences among sympatric social groups of short-finned pilot whales in Hawai'i. *Behavioral Ecology and Sociobiology*, 72, 1–13.

Conner, D. A. (1982). Dialects versus geographic variation in mammalian vocalizations. *Animal Behaviour*, 30, 297–298.

Crance, J. L., Bowles, A. E., & Garver, A. (2014). Evidence for vocal learning in juvenile male killer whales, *Orcinus orca*, from an adventitious cross-socializing experiment. *Journal of Experimental Biology*, 217, 1229–1237.

Danishevskaya, A. Y., Filatova, O. A., Samarra, F. I. P., Miller, P. J. O., Ford, J. K. B., Yurk, H., … Hoyt, E. (2020). Crowd intelligence can discern between repertoires of killer whale ecotypes. *Bioacoustics*, 29, 15–27.

Deecke, V. B., Barrett-Lennard, L. G., Spong, P., & Ford, J. K. B. (2010). The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*). *Naturwissenschaften*, 97, 513–518.

Deecke, V. B., Ford, J. K. B., & Spong, P. (2000). Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. *Animal Behaviour*, 60, 629–638.

Deecke, V. B., & Janik, V. M. (2006). Automated categorization of bioacoustic signals: Avoiding perceptual pitfalls. *Journal of the Acoustical Society of America*, 119, 645–653.

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

Filatova, O. A., Burdin, A. M., & Hoyt, E. (2010). Horizontal transmission of vocal traditions in killer whale (*Orcinus orca*) dialects. *Biology Bulletin*, 37, 965–971.

Filatova, O. A., Burdin, A. M., & Hoyt, E. (2013). Is killer whale dialect evolution random? *Behavioural Processes*, 99, 34–41.

Filatova, O. A., Deecke, V. B., Ford, J. K. B., Matkin, C. O., Barrett-Lennard, L. G., Guzeev, … Hoyt, E. (2012). Call diversity in the North Pacific killer whale populations: Implications for dialect evolution and population history. *Animal Behaviour*, 83, 595–603.

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

Filatova, O. A., Fedutin, I. D., Nagaylik, M. M., Burdin, A. M., & Hoyt, E. (2009). Usage of monophonic and biphonic calls by free-ranging resident killer whales (*Orcinus orca*) in Kamchatka, Russian Far East. *Acta Ethologica*, 12, 37–44.

Filatova, O. A., Ivkovich, T. V., Guzeev, M. A., Burdin, A. M., & Hoyt, E. (2017). Social complexity and cultural transmission of dialects in killer whales. *Behaviour*, 154, 171–194.

Filatova, O. A., & Miller, P. J. O. (2015). An agent-based model of dialect evolution in killer whales. *Journal of Theoretical Biology*, 373, 82–91.

Filatova, O. A., Miller, P. J. O., Yurk, H., Samarra, F. I. P., Hoyt, E., Ford, J. K. B., …, Barrett-Lennard, L. G. (2015a). Killer whale call frequency is similar across the oceans, but varies across sympatric ecotypes. *Journal of the Acoustical Society of America*, 138, 251–257.

Filatova, O. A., Samarra, F. I. P., Barrett-Lennard, L. G., Miller, P. J. O., Ford, J. K. B., Yurk, H., … Hoyt, E. (2016). Physical constraints of cultural evolution of dialects in killer whales. *Journal of the Acoustical Society of America*, 140, 3755–3764.

Filatova, O. A., Samarra, F. I. P., Deecke, V. B., Ford, J. K. B., Miller, P. J. O., & Yurk, H. (2015b). Cultural evolution of killer whale calls: background, mechanisms and consequences. *Behaviour*, 152, 2001–2038.

Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L., Miller, P. J. O., & Hoelzel, A. R. (2006). Killer whales are capable of vocal learning. *Biology Letters*, 2, 509–512.

Foote, A. D., Newton, J., Piertney, S. B., Willerslev, E., & Gilbert, M. T. P. (2009). Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Molecular Ecology*, 18, 5207–5217.

Foote, A. D., & Nystuen, J. A. (2008). Variation in call pitch among killer whale ecotypes. *Journal of the Acoustical Society of America*, 123, 1747–1752.

Foote, A. D., Osborne, R. W., & Hoelzel, A. R. (2008). Temporal and contextual patterns of killer whale (*Orcinus orca*) call type production. *Ethology*, 114, 599–606.

Foote, A. D., Similä, T., Vikingsson, G. A., & Stevick, P. T. (2010). Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evolutionary Ecology*, 24, 803–814.

Foote, A. D., Vilstrup, J. T., de Stephanis, R., Verborgh, P., Abel Nielsen, S. C., Deaville, R., ... Piertney, S. B. (2011). Genetic differentiation among North Atlantic killer whale populations. *Molecular Ecology*, 20, 629–641.

Ford, J. K. B. (1987). *A catalgoue of underwater calls produced by killer whales (*Orcinus orca*) in British Columbia.* Canadian Data Report of Fisheries and Aquatic Sciences No. 633,165 pages.

Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, 67, 727–745.

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

Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S., & Balcomb, K. C. (1998). Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, 76, 1456–1471.

IESNS (2018). *International ecosystem survey in the Nordic Sea (IESNS) in May - June 2018* Working Document, 51 pages.

Jakobsson, J., & Østvedt, O. J. (1999). A review of joint investigations on the distribution of herring in the Norwegian and Iceland Seas 1950-1970. *Rit Fiskideildar*, 16, 209–238.

Jakobsson, J., & Stefánsson, G. (1999). Management of summer-spawning herring off Iceland. *ICES Journal of Marine Science*, 56, 827–833.

Johnson, M. P., & Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering*, 28, 3–12.

Jonsgård, Å., & Lyshoel, P. B. (1970). A contribution to the knowledge of the biology of the killer whale (*Orcinus orca*). *Nytt Magasin Zoologi*, 18, 41–48.

Krebs, J. R., & Kroodsma, D. E. (1980). Repertoires and geographical variation in bird song. *Advances in the Study of Behavior*, 11, 143–177.

Kvamme, C., Nøttestad, L., Fernö, A., Misund, O. A., Dommasnes, A., Axelsen, B. E., … Melle, W. (2003). Migration patterns in Norwegian spring-spawning herring: Why young fish swim away from the wintering area in late summer. *Marine Ecology Progress Series*, 247, 197–210.

Lammers, M. O., Brainard, R. E., Au, W. W. L., Mooney, T. A., & Wong, K. B. (2008). An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and other marine habitats. *Journal of the Acoustical Society of America*, 123, 1720–1728.

Miller, P., Antunes, R., Alves, A. C., Wensveen, P. J., Kvadsheim, P. H., Kleivane, L., ... Tyack, P. (2011). *The 3S experiments: studying the behavioural effects of naval sonar on killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*), and long-finned pilot whales (*Globicephala melas*) in Norwegian waters.* Scottish Oceans Institute Technial Report, SOI-2011-001, 290 pages.

Miller, P. J. O. (2002). Mixed-directionality of killer whale stereotyped calls: A direction of movement cue? *Behavioral Ecology and Sociobiology*, 52, 262–270.

Miller, P. J. O. (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology*, 192, 449–459.

Miller, P. J. O., & Bain, D. E. (2000). Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour*, 60, 617–628.

Mitani, J. C., Hunley, K. L., & Murdoch, M. E. (1999). Geographic variation in the calls of wild chimpanzees: A reassessment. *American Journal of Primatology*, 47, 133–151.

Moore, S. E., Francince, J. K., Bowles, A. E., & Ford, J. K. B. (1988). Analysis of calls of killer whales, *Orcinus orca*, from Iceland and Norway. *Rit Fiskideildar*, 11, 226–250.

Morin, P. A., Archer, F. I., Foote, A. D., Vilstrup, J., Allen, E. E., Wade, P., ... Harkins, T. (2010). Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Research*, 20, 908–916.

Murray, S. O., Mercado, E., & Roitblat, H. L. (1998). Characterizing the graded structure of false killer whale (*Pseudorca crassidens*) vocalizations. *Journal of the Acoustical Society of America*, 104, 1679–1688.

Nottebohm, F. (1969). The song of the chingolo, *Zonotrichia capensis*, in Argentina: description and evaluation of a system of dialect. *Condor*, 71, 299–315.

Olesiuk, P. F., Bigg, M. A., & Ellis, G. M. (1990). Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Reports of the International Whaling Commission*, 12, 209–243.

Van Opzeeland, I., Corkeron, P., Leyssen, T., Similä, T., & Van Parijs, S. (2005). Acoustic behaviour of Norwegian killer whales, *Orcinus orca*, during carousel and seiner foraging on spring-spawning herring. *Aquatic Mammals*, 31, 110–119.

Óskarsson, G. J., Gudmundsdottir, A., & Sigurdsson, T. (2009). Variation in spatial distribution and migration of Icelandic summer-spawning herring. *ICES Journal of Marine Science*, 66, 1762–1767.

Van Parijs, S. M., Leyssen, T., & Similä, T. (2004). Sounds produced by Norwegian killer whales, *Orcinus orca*, during capture. *Journal of the Acoustical Society of America*, 116, 557–560.

Pitman, R. L., & Ensor, P. (2003). Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management*, 5, 131–139.

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

Samarra, F. I. P., Deecke, V. B., & Miller, P. J. O. (2016). Low-frequency signals produced by Northeast Atlantic killer whales (*Orcinus orca*). *Journal of the Acoustical Society of America*, 139, 1149–1157.

Samarra, F. I. P., Deecke, V. B., Simonis, A. E., & Miller, P. J. O. (2015). Geographic variation in the time-frequency characteristics of high-frequency whistles produced by killer whales (*Orcinus orca*). *Marine Mammal Science*, 31, 688–706.

Samarra, F. I. P., Deecke, V. B., Vinding, K., Rasmussen, M. H., Swift, R. J., & Miller, P. J. O. (2010). Killer whales (*Orcinus orca*) produce ultrasonic whistles. *Journal of the Acoustical Society of America*, 128, 205–210.

Samarra, F. I. P., & Foote, A. (2015). Seasonal movements of killer whales between Iceland and Scotland. *Aquatic Biology*, 24, 75–79.

Samarra, F. I. P., & Miller, P. J. O. (2015). Prey-induced behavioural plasticity of herring-eating killer whales. *Marine Biology*, 162, 809–821.

Samarra, F. I. P., Tavares, S. B., Béesau, J., Deecke, V. B., Fennell, A., Miller, P. J. O., … Víkingsson, G. A. (2017). Movements and site fidelity of killer whales (*Orcinus orca*) relative to seasonal and long-term shifts in herring (*Clupea harengus*) distribution. *Marine Biology*, 164, 159.

Schevill, W. E., & Watkins, W. A. (1966). Sound structure and directionality in *Orcinus* (killer whale). *Zoologica*, 51, 71–76.

Selbmann, A., Deecke, V. B., Fedutin, I. D., Filatova, O. A., Miller, P. J. O., & Samarra, F. I. P. (2019). *A catalogue of pulsed calls produced by killer whales (*Orcinus orca*) in Iceland 2008-2016.* Report of the Marine and Freshwater Research Institute HV 2019-23, 93 pages.

Shamir, L., Yerby, C., Simpson, R., Benda-Beckmann, A. M. von, Tyack, P., Samarra, F., …

Wallin, J. (2014). Classification of large acoustic datasets using machine learning and crowdsourcing: Application to whale calls. *Journal of the Acoustical Society of America*, 135, 953–962.

Shapiro, A. D. (2008). *Orchestration: The movement and vocal behaviour of free-ranging Norwegian killer whales (*Orcinus orca*).* PhD Thesis,Massachusetts Institure of Technology and Woods Hole Oceanographic Institution, 310 pages.

Shapiro, A. D., Tyack, P. L., & Seneff, S. (2011). Comparing call-based versus subunit-based methods for categorizing Norwegian killer whale, *Orcinus orca*, vocalizations. *Animal Behaviour*, 81, 377–386.

Sharpe, D. L., Castellote, M., Wade, P. R., & Cornick, L. A. (2017). Call types of Bigg's killer whales (*Orcinus orca*) in western Alaska: using vocal dialects to assess population structure. *Bioacoustics*, 4622, 1–26.

Sigurjónsson, J., Lyrholm, T., Leatherwood, S., Jónsson, E., & Víkingsson, G. (1988). Photoidentification of killer whales, *Orcinus orca*, off Iceland, 1981 through 1986. *Rit Fiskideildar*, 11, 99–114.

Similä, T., Holst, J. C., & Christensen, I. (1996). Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 769–779.

Similä, T., & Ugarte, F. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology*, 71, 1494–1499.

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

Simon, M., Ugarte, F., Wahlberg, M., & Miller, L. E. E. A. (2006). Icelandic killer whales *Orcinus orca* use a pulsed call suitable for manipulating the schooling behaviour of herring *Clupea harengus*. *Bioacoustics*, 16, 57–74.

Slobodchikoff, C. N., Ackers, S. H., & Van Ert, M. (1998). Geographic variation in alarm calls of Gunnison's prairie dogs. *Journal of Mammalogy*, 79, 1265–1272.

Strager, H. (1993). *Catalogue of underwater calls from killer whales (*Orcinus orca*) in northern Norway* MSc Thesis,University of Aarhus, 80 pages.

Strager, H. (1995). Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway. *Canadian Journal of Zoology*, 73, 1037–1047.

Tavares, S. B., Samarra, F. I. P., & Miller, P. J. O. (2017). A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. *Behavioral Ecology*, 28, 500–514.

Thomsen, F., Franck, D., & Ford, J. K. B. (2001). Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Journal of the Acoustical Society of America*, 109, 1240–1246.

Watkins, W. A. (1968). The harmonic interval: Fact or artifact in spectral analysis of pulse trains. In T. N. Tavolga (Ed.), *Marine Bio-Acoustics Vol. 2* (pp. 15–43). New York , NY: Pergamon Press.

Weilgart, L., & Whitehead, H. (1997). Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology*, 40, 277–285.

Wellard, R., Erbe, C., Fouda, L., & Blewitt, M. (2015). Vocalisations of killer whales (*Orcinus orca*) in the Bremer Canyon, Western Australia. *PLoS One*, 10, e0136535.

Wellard, R., Pitman, R. L., Durban, J., & Erbe, C. (2020). Cold call: the acoustic repertoire of

Ross Sea killer whales (*Orcinus orca*, Type C) in McMurdo Sound, Antarctica. *Royal Society Open Science*, 7, 191228.

Wieland, M., Jones, A., & Renn, S. C. P. (2010). Changing durations of southern resident killer whale (*Orcinus orca*) discrete calls between two periods spanning 28 years. *Marine Mammal Science*, 26, 195–201.

Yurk, H. (2005). *Vocal culture and social stability in resident killer whales (*Orcinus orca*)* PhD Thesis,University of British Columbia, 114 pages.

Yurk, H., Barrett-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, 63, 1103–1119.

Table 1. Summary of recordings analyzed. No. days refers to the number of different recording events (days) when the data were collected. No. 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 it represents in brackets. Note that on some occasions different recording methods may have been used on the same day. Asterisks indicate 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, ±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, ±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, ±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, ±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, ±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, ±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, +0/-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, ±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, ±3 dB	96	03:50	4	2 (1.7%)
	Shetland	2009	Summer	“	96	11:14	7	118 (98.3%)

Table 2. Differences in complexity of killer whale calls from Iceland and Norway. Number of call types and subtypes with percentage in parentheses given for each category. Single-component refers to call types with only a low frequency component; two-component call 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%)

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

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

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

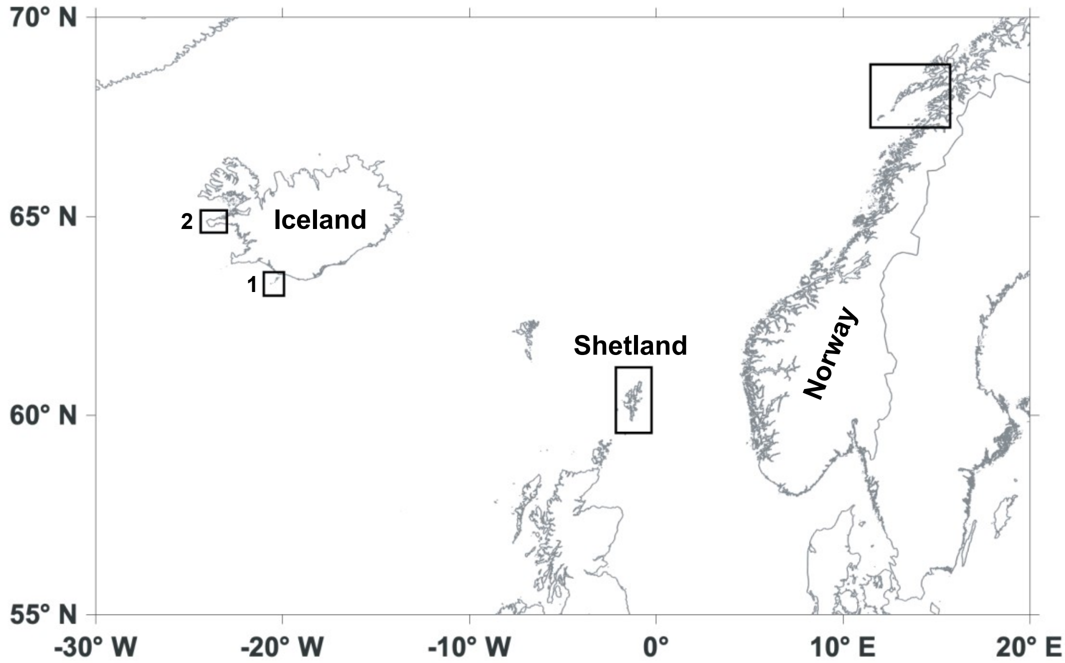

Figure 1. Map of the North Atlantic showing the study sites in Iceland (1 = Vestmannaeyjar, 2 = Breiðafjörður), Norway and Shetland.

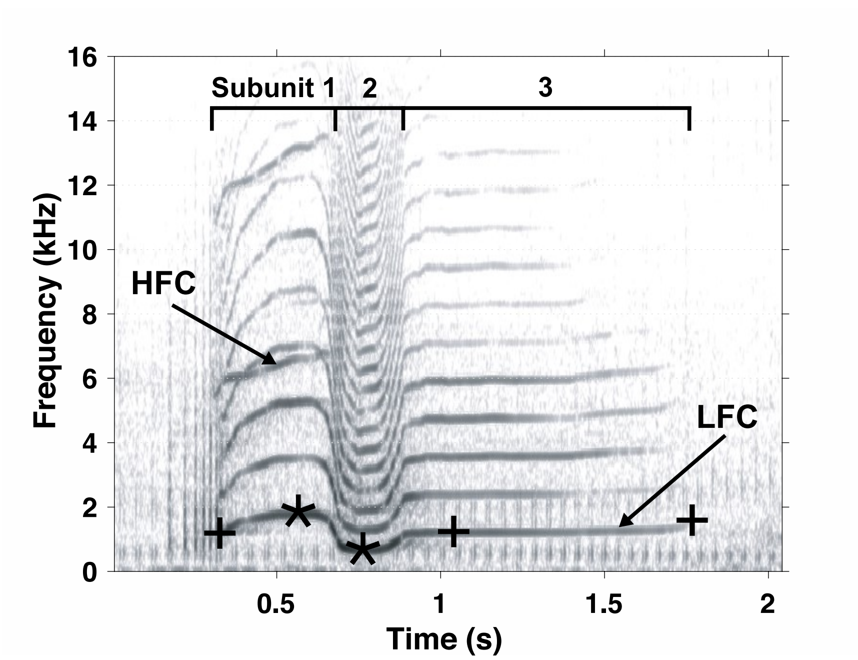

Figure 2. Spectrogram of an Icelandic killer whale call showing measurements taken for this study. Measurements were made of the start, mid and end frequency (crosses) and at the

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

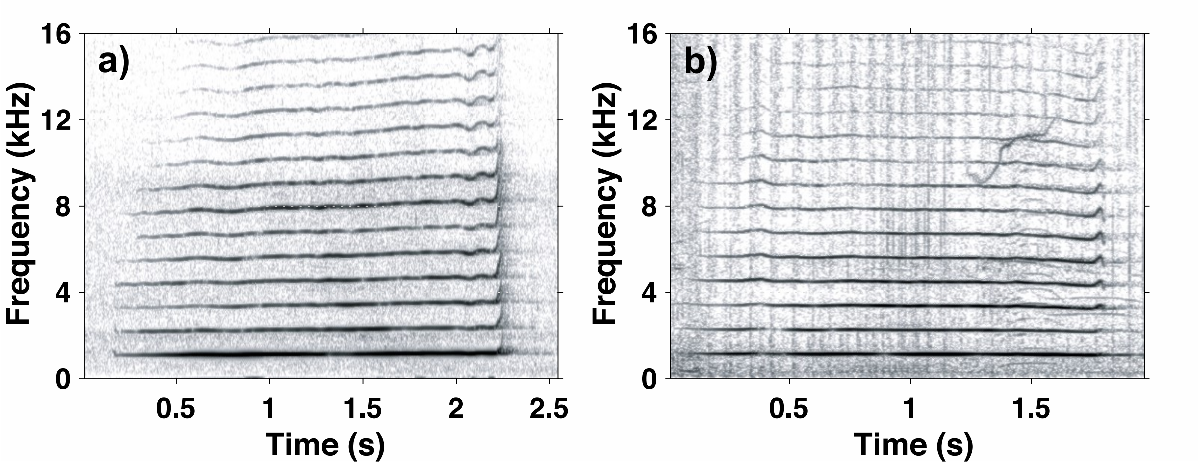

Figure 3. Matched call types I36 (a) and NASh08 (b; Deecke et al., 2011). Recordings were sampled at (a) 64 kHz and (b) 96 kHz Spectrogram parameters: Hann window; FFT size: (a) 2,048, (b) 4,096; 87.5% overlap; frequency resolution: (a) 31.25 Hz, (b) 23.44 Hz; time resolution: (a) 4.00 ms, (b) 5.33 ms.

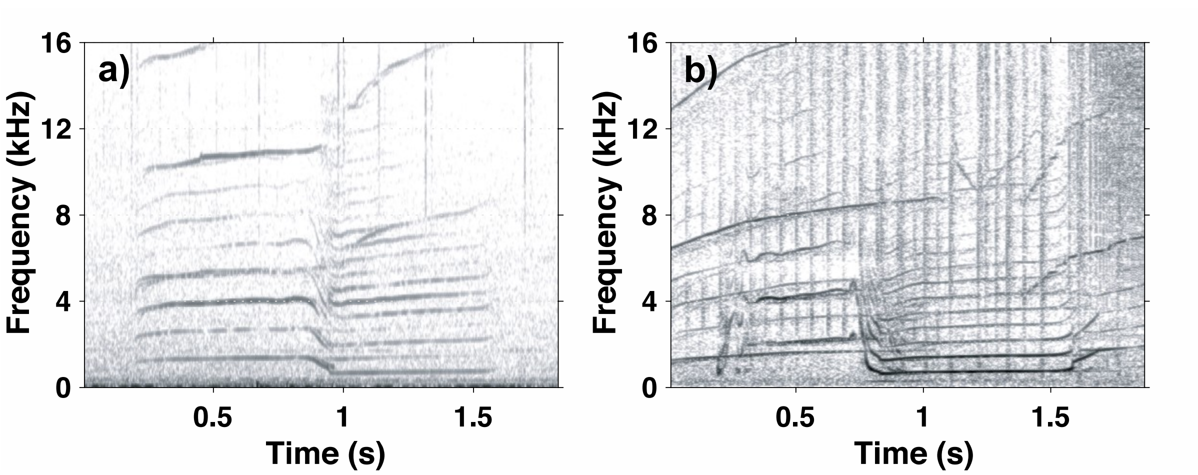

Figure 4. Matched call types I5.5 (a) and NASh10 (b; Deecke et al., 2011). Recordings were sampled at (a) 48 kHz and (b) 96 kHz. Spectrogram parameters: Hann window; FFT size: (a) 1,024, (b) 4,096; 87.5% overlap; frequency resolution: (a) 46.88 Hz, (b) 23.44 Hz; time resolution: (a) 2.67 ms, (b) 5.33 ms.

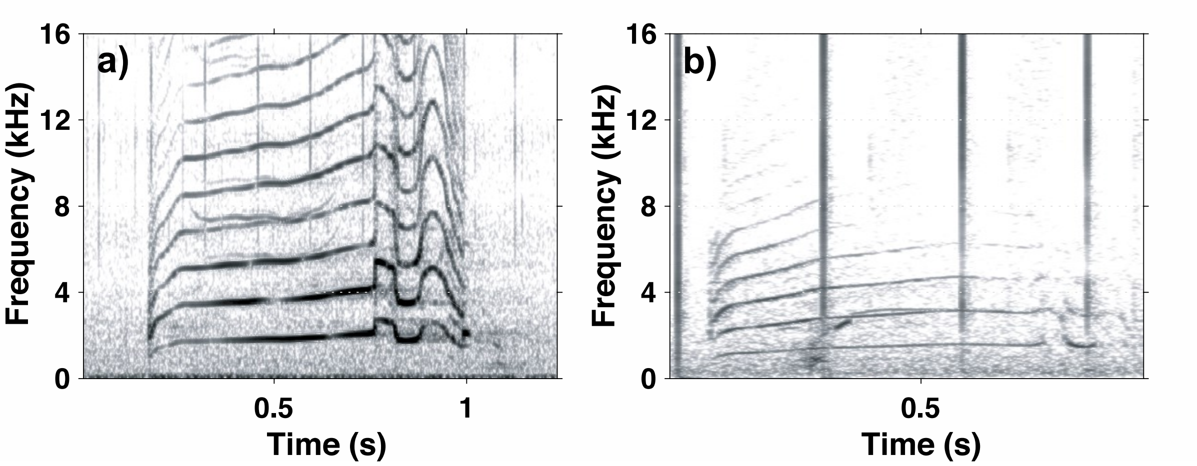

Figure 5. Matched call types I11.4 (a) and NASh13 (b; Deecke et al., 2011). Recordings were sampled at (a) 192 kHz and (b) 96 kHz. Spectrogram parameters: Hann window; FFT size: (a) and (b) 4,096; 87.5% overlap; frequency resolution: (a) 46.88 Hz, (b) 23.44Hz; time resolution: (a) 2.67 ms, (b) 5.33 ms.

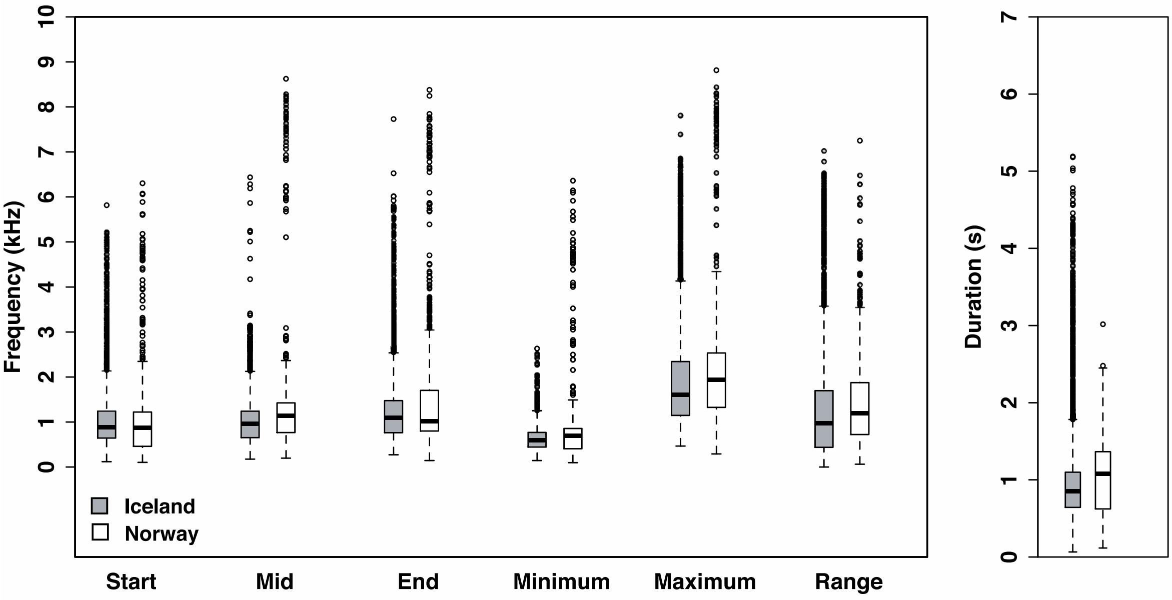

Figure 6. Boxplot showing the frequency variables (left panel) and duration (right panel) measured from killer whale calls in Iceland and Norway. Horizontal lines represent medians, boxes show interquartile ranges and whiskers indicate the values within 1.5 times the interquartile range. Outliers are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