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Selbmann, Anna ORCID: https://orcid.org/0000-0001-8687-7265 , Deecke, Volker B. ORCID: https://orcid.org/0000-0003-2781-5915 , Filatova, Olga A. ORCID: https://orcid.org/0000-0003-1533-4807 , Fedutin, Ivan D. ORCID: https://orcid.org/0000-0001-9558-0922 , Miller, Patrick J.O. ORCID: https://orcid.org/0000-0001-8028-9673 , Simon, Malene, Bowles, Ann E. ORCID: https://orcid.org/0000-0003-1980-6103 , Lyrholm, Thomas, Lacey, Claire ORCID: https://orcid.org/0000-0003-0541-8193 , Magnúsdóttir, Edda E. ORCID: https://orcid.org/0000-0001-8281-4232 , Maunder, William, Wensveen, Paul J. ORCID: https://orcid.org/0000-0002-9894-2543 , Svavarsson, Jörundur ORCID: https://orcid.org/0000-0003-1842-7515 and Samarra, Filipa I.P. ORCID: https://orcid.org/0000-0002-9909-0565 (2023) Call type repertoire of killer whales (Orcinus orca) in Iceland and its variation across regions. Marine Mammal Science, 39 (4). pp. 1136-1160.

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ARTICLE

Marine Mammal Science

Call type repertoire of killer whales (*Orcinus orca*) in Iceland and its variation across regions

Anna Selbmann[1] | Volker B. Deecke[2] | Olga A. Filatova[3] | Ivan D. Fedutin[3] | Patrick J. O. Miller[4] | Malene Simon[5] | Ann E. Bowles[6] | Thomas Lyrholm[7] | Claire Lacey[8] | Edda E. Magnúsdóttir[1] | William Maunder[9] | Paul J. Wensveen[1] | Jörundur Svavarsson[1] | Filipa I. P. Samarra[10]

[1]Faculty of Life and Environmental Sciences, University of Iceland, Reykjavík, Iceland

[2]Institute of Science and Environment, University of Cumbria, Ambleside, UK

[3]Department of Biology, University of Southern Denmark, Odense, Denmark

[4]Sea Mammal Research Unit, School of Biology, University of St Andrews, St Andrews, UK

[5]Greenland Climate Research Centre, Greenland Institute of Natural Resources, Nuuk, Greenland

[6]Hubbs-SeaWorld Research Institute, San Diego, California

[7]Swedish Museum of Natural History, Stockholm, Sweden

[8]Song of the Whale research team, Marine Conservation Research International, Kelvedon, UK

[9]Cardiff University, Cardiff, UK

[10]University of Iceland's Institute of Research Centres, Vestmannaeyjar, Iceland

Correspondence
Anna Selbmann, Faculty of Life and Environmental Sciences, University of Iceland, Sturlugata 7, 102 Reykjavík, Iceland.
Email: selbmann.anna@gmail.com

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Abstract

Killer whales (*Orcinus orca*) have group-specific call repertoires that can be used to track groups and populations using passive acoustic monitoring. To provide a detailed description of the Icelandic killer whale repertoire and its variation, we analyzed acoustic data collected in five locations between 1985 and 2016. Calls were classified manually, and CART and random forest analyses were employed to validate the manual classification. A total of 91 call categories (including call types and subtypes) were defined. Most call categories were recorded in more than one location, with the highest proportion shared between herring grounds in Vestmannaeyjar (South) and Breiðafjörður

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(West). However, both locations included call categories that were not recorded elsewhere in Iceland. Recordings from past herring wintering grounds in eastern Iceland included few call categories that matched other locations. Sample sizes from Reykjanes (Southwest) and Skjálfandi (North) were small and did not include unique call categories. The relative occurrence of call categories in Vestmannaeyjar changed little over a 14-year period (2002–2016), although shorter-term changes between years were observed that appeared to correlate to changes in individuals identified. This comparison of acoustic repertoires provides valuable information on the social structure and movement patterns of herring-eating killer whales around Iceland.

KEYWORDS
acoustic behavior, call repertoire, geographic variation, Northeast Atlantic, passive acoustic monitoring

1 | INTRODUCTION

Communication is a central aspect of animal behavior and understanding animal vocalizations can provide important insights into behavior, social structure, ecology, and evolution (Bradbury & Vehrencamp, 2011). For many marine mammal species, acoustic communication is particularly important as sound propagates farther and faster in water compared to air, and visibility is generally limited (Au & Hastings, 2008). Recent advances in technology have increased possibilities for underwater acoustic data collection, e.g., through passive acoustic monitoring (PAM). PAM provides many advantages: it is noninvasive, relatively inexpensive, and it can be applied in poor visibility (e.g., during night, high sea states). Thus, it enables long-term and year-round data collection in locations that are remote or difficult to survey, such as high latitude regions (Erbe, 2013; van Opzeeland et al., 2013; van Parijs et al., 2009). However, the first critical step in understanding vocal communication and using methods such as PAM, is to document the vocal repertoire, i.e., the sum of acoustic signals used by a species, as well as the variability within signal categories (Mellinger et al., 2007).

Killer whales (*Orcinus orca*) are highly vocal and most commonly produce pulsed calls (Ford, 1989). Pulsed calls (hereafter calls) are thought to play a key role in killer whale behavior, serving as contact signals, aiding group recognition, cohesion, and coordination of the spatial organization of the group (Ford, 1989; Miller, 2002). Killer whale calls are burst-pulse sounds consisting of rapidly repeated pulses, where the interpulse interval is so short that they appear tonal, as frequency-modulated sounds with several sidebands (Schevill & Watkins, 1966). They often have several components with abrupt changes in pitch and can contain two separately modulated frequency contours (Ford, 1987; Miller & Bain, 2000; Strager, 1995). The majority of killer whale calls are discrete, meaning that they have a distinctive structure, are repetitive and can be classified into call types and subtypes (Ford, 1989; Sharpe et al., 2019; Strager, 1995; van Opzeeland et al., 2005; Wellard et al., 2020; Yurk et al., 2002). The acoustic characteristics of killer whale calls appear as readily discernible features in spectrograms (Sharpe et al., 2019; Wellard et al., 2020; Yurk et al. 2002) and human observers have been shown to classify odontocete signals into biologically meaningful categories (Danishevskaya et al., 2020; Deecke et al., 1999; Deecke & Janik, 2006; Janik, 1999).

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Variation in the call repertoires of killer whales is observed between ecotypes, populations, social groups, or in different behavioral contexts. For example, in the Northeast Pacific, different ecotypes have been described, which have unique call repertoires (Ford et al., 1996). The fish-eating "resident" and mammal-eating "transient" (or "Bigg's") ecotypes use distinct call types that differ in structure (Deecke et al., 2005; Saulitis et al., 2005), and tonal frequency (Filatova et al., 2015; Foote & Nystuen, 2008). In the residents, call repertoires are linked to maternal relatedness, with closely related groups sharing more of their call repertoire than more distantly related groups (Deecke et al., 2010; Ford, 1991, Yurk et al., 2002). Transient killer whales, on the other hand, have a relatively small call repertoire that is shared more widely across social groups. Variation is only observed at the community level (Deecke, 2003; Sharpe et al., 2019).

The main purpose of diversity in group repertoires of killer whales is thought to be the transmission of group identity (Filatova et al., 2011; Ford, 1991; Miller & Bain, 2000). Group identity is important for killer whales in mate choice and survival. Genetic evidence indicates that mates are chosen from distantly related groups, with choice potentially based on dissimilar dialects to avoid inbreeding (Barrett-Lennard, 2000), contributing to evolutionary pressure to diversify the repertoire. Individual survival, on the other hand, is directly associated with group membership (Foster et al., 2012), creating the need to conform to the group and standardize the repertoire. These opposing selection pressures (diversifying and standardizing) are thought to lead to "the maximum diversity within the permitted range" (Filatova et al., 2012).

While most killer whale calls do not appear to be behavior-specific, the frequency of usage can be related to different behavioral or social contexts (Filatova et al., 2009, 2013; Ford, 1989; Weiß et al., 2006, 2007). However, relative call type occurrence appears to vary little between years and killer whale call repertoires have been shown to be stable over decades (Foote et al., 2008; Ford, 1991; Wellard et al., 2020). The stereotypy of killer whale calls, their long-term stability, and variations between ecotypes, populations, and social groups make these sounds very suitable for PAM methods, e.g., to study the spatial and temporal occurrence of different killer whale social groups (e.g., Yurk et al., 2010) and ecotypes (e.g., Myers et al., 2021; Rice et al., 2017; Riera et al., 2019). However, descriptions of the repertoires are lacking in several regions, including the Northeast Atlantic.

Acoustic studies across the region show that the call repertoire of killer whales from Iceland is distinct from Norway but has some overlap to Shetland, UK (Deecke et al., 2011; Moore et al., 1988; Selbmann et al., 2021), which supports the current understanding of the connectivity between these regions (Foote et al., 2010; Samarra & Foote, 2015; Sigurjónsson et al., 1988). However, finer-scale differences of the repertoire around Iceland remain unexplored. Icelandic killer whales exhibit variation in their movement patterns but understanding of the distributional range of the population and its substructure is still limited. Early studies consistently observed killer whales in herring (*Clupea harengus*) grounds (Sigurjónsson et al., 1988) and thus it was presumed that they were herring specialists, following the Icelandic summer-spawning herring stock (hereafter Icelandic herring). However, recent photo-identification studies have indicated that not all whales follow the herring year-round (Samarra et al., 2017). About half of the individuals identified were seen in both the herring wintering grounds in the west of Iceland and the spawning grounds in the south, but the other half were only sighted in either of the two locations. A few individuals seen only in the herring wintering grounds have been sighted repeatedly in Scotland during summer, where they appear to hunt seals (Foote et al., 2010; Samarra & Foote, 2015; Samarra et al., 2017). Movement and foraging patterns for the rest of the population remain unclear. In the 1980s and 1990s, the Icelandic herring wintering grounds were located to the east of Iceland, where killer whales were regularly sighted with herring (Foote et al., 2010; Sigurjónsson et al., 1988). Only a small proportion of whales identified there could be matched to sightings in the recent wintering grounds off western Iceland (Samarra et al., 2017). Occasional sightings of killer whales in north and southwest Iceland, outside herring grounds, are also reported, especially during winter and spring (Selbmann et al., 2022). The sporadic nature of these sightings makes photo-identification data from these areas scarce. To date, knowledge of the connectivity between different regions of Iceland is limited.

With an increasing number of deployments of PAM devices in the North Atlantic (e.g., Conservation of Arctic Flora and Fauna, 2020), a comprehensive description of the repertoires of killer whales in Icelandic waters and how they vary among locations could aid our understanding of the range and movement patterns of these whales. Here,

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we first use acoustic data collected over 32 years (1985–2016) in various locations around Iceland to provide a detailed description of the Icelandic killer whale call repertoire. We then investigate whether and how call repertoires differ between locations in Iceland and examine variation in the repertoire over a period of 14 years at one study site.

2 | METHODS

2.1 | Data collection

Data were collected in five locations around Iceland using a variety of recording methods (Table 1, Figure 1). Recordings were collected from boats that searched for whales and used boat-deployed hydrophones to record groups whenever possible, or using multisensor archival tags (Dtags, Johnson & Tyack, 2003) attached to whales, or moored hydrophones recording continuously or on a duty cycle (Table 1). The oldest set of recordings were collected in 1985–1987 in several small fjords in the east of Iceland (hereafter Eastfjords), then a wintering ground of Icelandic herring. The majority of calls analyzed from these recordings stem from one encounter with a large group of 60–80 individuals. In Vestmannaeyjar, a spawning ground of Icelandic herring in the south of Iceland, acoustic recordings were collected during eight summer field seasons (2002, 2008–2010, and 2013–2016). In Breiðafjörður, a current wintering ground of Icelandic herring in the west of Iceland, acoustic recordings were collected during two winter field seasons (2013–2014). Killer whales often gather in large aggregations of 50–100 whales in the herring grounds, which means that isolating groups and establishing group affiliations can be difficult (Sigurjónsson et al., 1988; Tavares et al., 2017). In all three locations, recordings were generally collected when whales were feeding on herring, as indicated from surface observations and photographs of herring floating at the surface or being taken by seabirds. Concurrent photo-identifications were available, except for recordings from Vestmannaeyjar in 2002 and 2016 and part of the moored hydrophone recordings from 2014 in Breiðafjörður. Individual identification data from Samarra et al. (2017) were used to estimate the number of whales present during recording days.

Two small samples of recordings were available from the southwest and the north of Iceland. A small sample of recordings was collected in 2004 southwest of the Reykjanes Peninsula in Southwest Iceland (hereafter Reykjanes) around two small groups of 1–10 killer whales. In northern Iceland, recordings from bottom-moored acoustic recorders (EARs; Lammers et al., 2008) were collected in Skjálfandi Bay (Magnúsdóttir et al., 2014, 2015). The EARs recorded for 1 min every 15 min (2008–2010) or 10 min every 15 min (2011). Identification photographs were not available for these two sets of recordings.

2.2 | Data processing and call categorization

Some recordings used here have been analyzed in previous studies for varying purposes. Most of the recordings from the Eastfjords (about 5 hr) had previously been analyzed and are the basis of a call catalog describing Icelandic call types I1–I35 (Moore et al., 1988). The recordings from Vestmannaeyjar collected in 2002 were previously analyzed for tail slaps and calling rates and led to the description of call type I36, the "herding call," which has been associated with feeding on herring (Simon et al., 2005, 2006, 2007). The 2008–2016 recordings from Vestmannaeyjar and the 2013–2014 recordings from Breiðafjörður were used to establish a call catalog (Selbmann et al., 2019). This data set was also used in a study comparing the repertoires of killer whales in Iceland, Norway, and Scotland (Selbmann et al., 2021). During the initial classification of the call types from Vestmannaeyjar and Breiðafjörður (Selbmann et al., 2019), comparisons to the catalog of Moore et al. (1988) were made whenever possible but comparability was limited as spectrograms of Moore et al. (1988) were only available in print without sound files. For the present study, parts of the original recordings were made available, making it possible to find examples from the

TABLE 1 Summary of acoustic recordings from Iceland that were inspected for killer whale calls. For details on recording methods in Vestmannaeyjar and Breiðafjörður see Selbmann et al. (2021). 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 (i.e., high perceived signal-to-noise ratio, little/no overlap with other sounds, clearly audible) calls extracted from the recordings. No. individuals ID indicates the mean number of whales identified per day from photographs collected alongside acoustic recordings.

Region	Year	Months	Sampling rate (kHz)	Duration (hh:mm)	Recording method	No. days	No. calls	No. individuals ID ± *SD* (min–max)
Eastfjords	1985	Oct	44.1	02:38	Single hydrophone (custom), Marantz PMD 360 recorder, frequency response: 0.05–15 kHz ±3 dB	3	46	11 ± 4 (7–14)
"	1986	Oct–Nov	44.1, 48	03:02	Single hydrophone (InterOcean T-902), Sony WM-D6C recorder, frequency response: 0.05–15 kHz ±3 dB	7	84	13 ± 12 (3–32)
"	1987	Oct	48	00:35	"	1	12	NA
Vestmannaeyjar	2002	Jun–Jul	48	15:29	Single hydrophone (Woods Hole Oceanographic Institute, frequency response flat within ±4 dB up to 20 kHz), Sony TCD-D8 digital audio tape recorder (flat frequency response 0.1–22 kHz)	13	234	NA
"	2008	Jun–Jul	96	15:52	4-element vertical array	7	5	10 ± 6 (4–20)
"	2009	Jul	96, 192	58:49	2- and 16-element towed arrays, 4-element vertical array, Dtags	15	2,912	21 ± 14 (4–45)
"	2010	Jul	48, 96	07:17	Single hydrophone, 2-element towed array	5	163	30 ± 22 (5–64)
"	2013	Jul	96	04:37	4-element vertical array	9	12	20 ± 16 (4–35)
"	2014	Jul	48, 96, 192	23:51	Single hydrophone, 2-element towed array	12	1,021	44 ± 25 (14–85)
"	2015	Jul	96, 192	54:46	Single hydrophone, 2-element towed array	18	899	24 ± 18 (4–72)
"	2016	Jul	96, 192	35:21	2-element towed array	12	994	NA
Reykjanes	2004	Jul	96	00:43	2-element towed array with Benthos AQ-4 hydrophones (Teledyne Benthos, Falmouth, MA) and preamplifiers (flat frequency response 0.01–15 kHz) connected to a National Instruments PCI-6013 data acquisition board and recorded directly to hard-disk	2	30	NA

(Continues)

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TABLE 1 (Continued)

Region	Year	Months	Sampling rate (kHz)	Duration (hh:mm)	Recording method	No. days	No. calls	No. individuals ID ± *SD* (min–max)
Skjálfandi	2008–2009	Sep–Feb	64	258:43	Ecological Acoustic Recorder (EAR, Lammers et al. 2008), frequency response: 1–28 kHz, ±1.5 dB	163	0	NA
"	2009	Apr–Nov	64	508:18	"	160	0	NA
"	2009–2010	Nov–May	64	292:18	"	184	13	NA
"	2010	May–Sep	64	223:35	"	141	0	NA
"	2011	Jan–Mar, Jul–Aug	16	1422:50	"	93	0	NA
Breiðafjörður	2013–2014	Feb–Mar	96, 240	23:33	Single hydrophone, 4-element vertical array, Dtags	24	1,515	42 ± 32 (1–159)
"	2014	Feb–Mar	64, 96, 192	442:44	Single hydrophone, 4-element vertical array, Dtags, Ecological Acoustic Recorder (EAR)	41	1,472	17 ± 15 (1–62)[a]

[a]Photo-identification not available for all days of EAR deployment.

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catalog in the recordings, create clearer spectrograms as well as sound clips, and compare those to calls from other recordings. Not all call categories described by Moore et al. (1988) were found in the available recordings from the Eastfjords. This is likely due to the strict call quality criteria applied in this study and because not all recordings used by Moore et al. (1988) were available. A comparison of previously established catalogs showed only one match: call type I67 (Selbmann et al., 2019) was a match to I13.1 (Moore et al., 1988).

Recordings were analyzed aurally and visually from spectrograms using Audacity versions 2.1.2 and 2.3.1 (https://audacityteam.org/) with a Hann window, FFT = 8,192 for 96, 192, and 240 kHz sampling rates and FFT = 4,096 for 44.1, 48, and 64 kHz sampling rates. Due to the many hours of recording time, the recordings from Skjálfandi were first scanned for possible killer whale calls using a frequency contour algorithm detecting tonal signals in the frequency range 2,000–8,000 Hz (FFT 512 and 2,048 for 64 and 16 kHz sampling rates, respectively, 75% overlap, Hamming window) in the software package Ishmael 1.0 (Mellinger, 2001; Mellinger et al., 2011). Subsequently, each file with a detection from the software was analyzed. Each call was marked and assigned a quality from 1 (poor) to 3 (high) based on the perceived signal-to-noise ratio, overlap with other sounds, and the clarity of the call. Only high-quality calls were extracted and used for further analysis.

Calls were classified based on visual and aural examination of spectrograms with specific attention to the shape of the call contour, the number of elements and segments, and to a lesser extent, call duration (Ford, 1987; Strager, 1995). Elements were defined as parts of a call separated by an abrupt shift in pulse repetition rate of the low-frequency component (Figure 2; Sharpe et al., 2019; Yurk et al., 2002). Segments separated parts of a call by a very short (<0.2 s) silent interval (Sharpe et al., 2019; Yurk et al., 2002). Subtypes were assigned if an element or segment was added/subtracted from a call, if a second frequency component was present/absent, or if a major change in an element occurred (Strager, 1995; see Figure 3 for examples). Variation occurs in all call types and some are more variable than others (Ford, 1989). A subtype was only created if the variation was discrete rather than graded. At least three occurrences of a call were required to define a new type or subtype (Sharpe et al., 2019; Wellard et al. 2020). The classification was performed by AS and cross-validated by FIPS.

2.3 | Validation of classification

The reliability of the classification was tested using two methods. First, observers with experience in cetacean acoustics were presented with a random subset of 60 pairs of calls. In an online questionnaire they were provided with the above definition of call type and subtype and presented the acoustic files and corresponding spectrograms. They were then asked to score each pair of calls as (1) different call types, (2) same call type but different subtypes, or (3) same call type and same subtype. Krippendorff's alpha was computed to test for observer agreement. The coefficient consists of a value between 0 and 1, with 1 indicating perfect agreement between observers and 0 absence of agreement (Hayes & Krippendorff, 2007). Second, classification and regression tree (CART) and random forest analyses were applied using the rpart and randomForest packages (Liaw & Wiener, 2002; Therneau & Atkinson, 2019) in R version 4.1.2 (R Core Team, 2021). CARTs and random forests are widely used in cetacean sound classification (Epp et al., 2022; Fournet et al., 2018; Garland et al., 2015; Rekdahl et al., 2013, 2017; Risch et al., 2013) and random forests have been successfully applied to killer whale calls (Sharpe et al., 2019). These analyses are robust to outliers, nonnormality, and nonindependent data and can handle correlated variables and small sample sizes (Breiman, 2001; Breiman et al., 1984). Following Sharpe et al. (2019), 13 metrics were measured for each call and used as predictor variables in the CART and random forest analyses: start and end frequency, sideband interval at the start, end, and the middle of the call, call duration, time to maximum frequency, time to maximum frequency proportion, frequency trend ratio, frequency range ratio, the number of elements and segments, and the presence/absence of a high-frequency component (Figure 2, Table S1). Sharpe et al. (2019) had measured 12 variables and recommended adding the middle sideband interval to improve the accuracy of the random forest. Measurements were taken from spectrograms (Hann window; FFT = 4,096, 2,048, or 1,024 for 240 and 192 kHz, 96 and 64 kHz, or 48 kHz sampling rates,

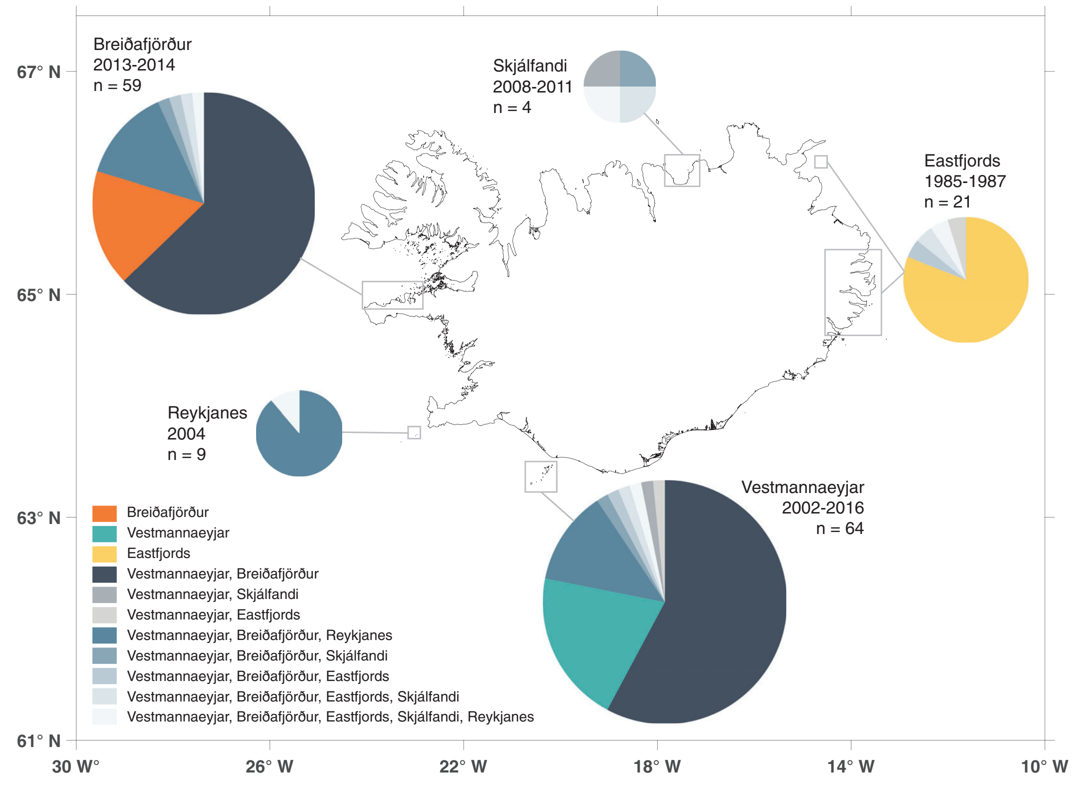

FIGURE 1 Map of Iceland showing the locations where acoustic recordings of killer whales were collected, including recording years. Pie charts show the patterns of call category matching between areas (n = number of call categories per location). Call categories occurring in only one location are indicated in yellow (Eastfjords), orange (Breiðafjörður), and turquoise (Vestmannaeyjar), while call categories occurring in multiple areas are indicated by varying shades of blue and gray. Pie chart size represents relative sample size (number of classified calls per location, log transformed due to very different sample sizes).

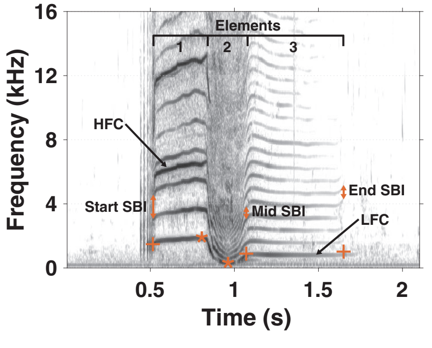

FIGURE 2 Spectrogram of an Icelandic killer whale call showing different metrics considered in the classification and measurements taken to obtain these metrics. Measurements taken on the low frequency component (LFC) were the start, mid, and end frequency (crosses) and maximum and minimum frequency (asterisks). Presence/absence of a high frequency component (HFC) was noted. Measurements of the sideband interval (SBI) were taken at the start, middle, and end of the call (double-ended arrows). Brackets indicate abrupt shifts in pulse repetition rate used to distinguish elements. Spectrogram parameters: Hann window; FFT size: 4,096; 87.5% overlap; frequency resolution: 46.88 Hz; time resolution: 2.67 ms.

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respectively; 87.5% overlap) using a custom routine in MATLAB R2017a (https://www.mathworks.com). Due to the large number of samples in some call categories, a maximum of 100 calls were measured for each category, resulting in a total of 1,999 calls measured. The CART used the Gini index to determine the "goodness of split" at each node (Breiman et al., 1984) and the terminal nodes were set to have a minimum sample of five, as most call categories had a sample larger than this. Cross-validation was applied before pruning to the tree with the smallest cross-validation error (Epp et al., 2022; Garland et al., 2015, Rekdahl et al., 2013, 2017). For the random forest, the number of preselected variables available for the split at each node was set to three, the number of trees grown was 1,000, and the decrease in the Gini index was used to assess the importance of each variable (Epp et al., 2022; Fournet et al., 2018; Garland et al., 2015; Sharpe et al., 2019). The random forest model was run five times and the final out-of-bag (OOB) error was obtained by averaging errors across all runs.

2.4 | Analysis of variation in call repertoire over time and between locations

Recordings at Vestmannaeyjar covered a time span of 14 years (2002–2016), providing the opportunity to investigate variation in call types recorded over time in this location and compare it to differences in repertoires between locations (Vestmannaeyjar and Breiðafjörður). Therefore, to examine variation in call type occurrence within and between locations over time, we investigated the relative call type production in the two locations (Vestmannaeyjar and Breiðafjörður) and across years within Vestmannaeyjar. We used two indices that have previously been applied in studies on killer whale call repertoires: (1) The similarity index (SI), which is an adaptation of Dice's coefficient of association (Ford, 1991; Yurk et al., 2002) and was calculated as:

$$\mathrm{SI} = \frac{2N_c}{R_1 + R_2}$$

where N_c is the total number of call categories shared between locations or years and R_1 and R_2 are the numbers of call categories at the two locations or in the two years. The index gives the proportion of call types shared, based on presence/absence. (2) The Whittaker Similarity index (WSI) furthermore considers the frequency of usage of different call categories (Crance et al., 2014) and was calculated as:

$$\mathrm{WSI} = \sum_{i=1}^{N} \min(p_{i,a}, p_{i,b})$$

where N is the total number of call categories, i is the individual call category, a and b are the locations or years being compared, and p is the proportion of the repertoire composed of a particular call, which is calculated as:

$$p_{i,a} = \frac{\text{calls of category } a \text{ produced in location/year } a}{\text{total calls in location/year } a}$$

Both indices produce values ranging from 0 to 1, with 1 indicating identical repertoires and 0 indicating fully distinct repertoires. A nonparametric Spearman rank correlation was applied to test for a linear relationship between locations (Vestmannaeyjar and Breiðafjörður) and between the two years with the longest time between them (2002 and 2016), due to the nonnormality of the distributions (Shapiro–Wilk normality tests: $p < .01$). All statistical analyses were performed using R version 4.1.2 (R Core Team, 2021). Call occurrence is expected to vary with the identity of groups being recorded or behavioral context (e.g., Filatova et al., 2009, 2013; Ford 1989, 1991); however, we did not have such data to investigate potential explanations for differences in call occurrence over time or between locations. Therefore, we provide only a general overview of the frequency with which different call categories were recorded at different locations or across time.

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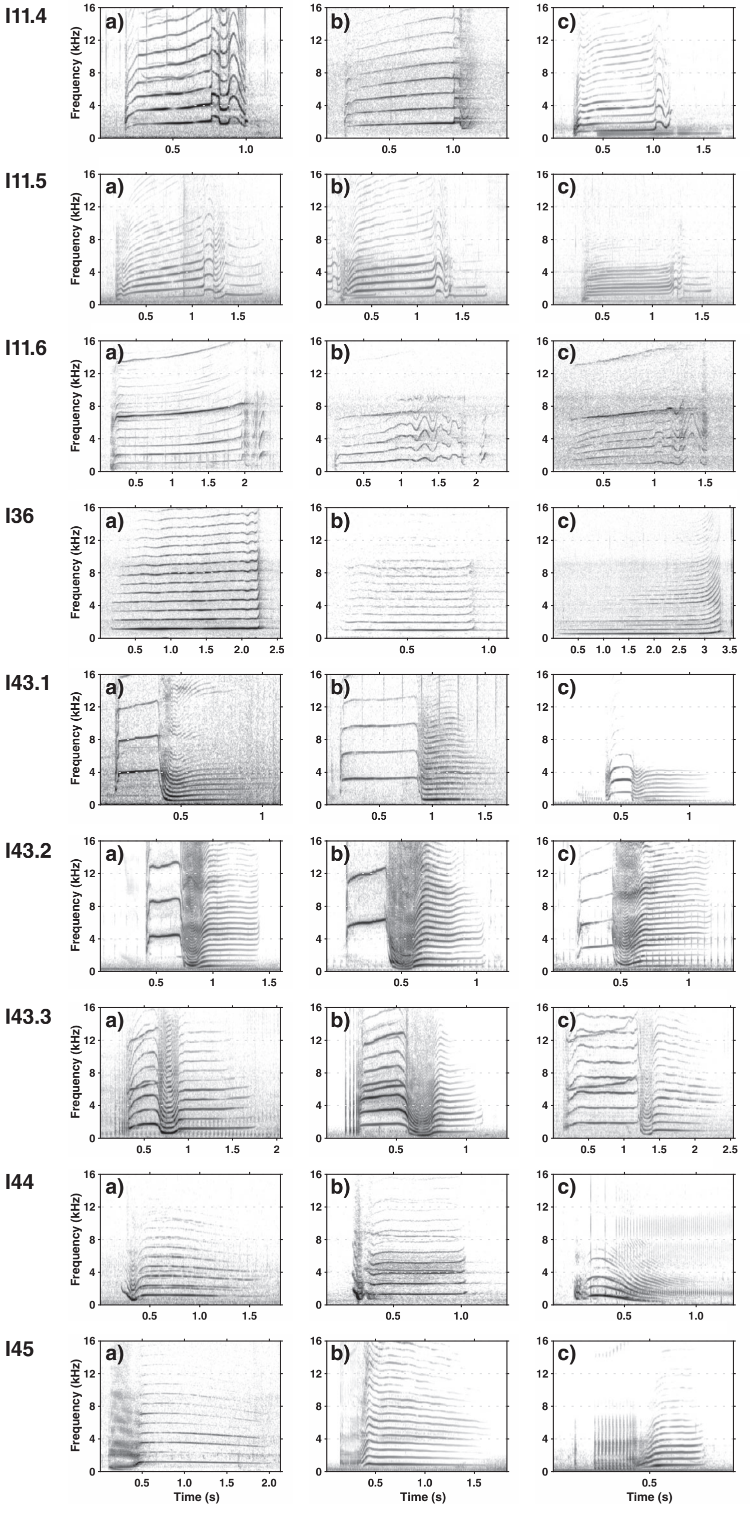

FIGURE 3 Legend on next page.

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3 | RESULTS

3.1 | Repertoire description and variation across regions

A total of 3,395 hr of recordings were used, and 9,412 high-quality calls were extracted (Table 1). The majority of recording time (92.4%) was from long-term EAR deployments in Breiðafjörður and Skjálfandi. In Skjálfandi, these recordings included very few killer whale calls.

Approximately 88% ($n = 8{,}321$) of all extracted calls were considered discrete and were manually classified. They were classified into 52 call types, 18 of which consisted of several subtypes (57 subtypes in total; Table S2). We use the term "call category" to include both call types and subtypes, where each call type and subtype is counted as one entity. In the case of call types that were composed of call subtypes we did not count the call type itself but only the number of subtypes. For example, call type I38, which has no subtypes, counts as one unique call category. On the other hand, call type I42, which is composed of subtypes I42.1, I42.2, and I42.3 counts as only three unique call categories. This approach allowed us to compare the number of shared categories across locations (rather than compare just the number of shared call types or just the number of subtypes). Therefore, a total of 91 call categories were classified from all the available recordings (see Table S2 for a complete list).

The classification success of the CART and random forest models was high. The CART correctly classified 84.8% (root node error: $n = 1899/1999$) of calls to the same category as the manual classification (Table S3) and the random forest model had a mean OOB error of 12.0% ± 0.2% across five trials (Table S4). These results improved only slightly when call subtypes were combined under their call type, i.e., call subtypes I11.4, I11.5, and I11.6, for example, were all combined under call type I11 (CART correctly classified 87.3%, random forest OOB error 9.4% ±0.1%). The most important variables in the random forest model, as indicated by the decrease in Gini index, were the sideband interval at the start, the frequency range, the sideband interval in the middle, and the duration of the call. Highest misclassification rates occurred for call categories with small sample sizes and few misclassification errors derived from the similarities between subtypes (Tables S3 and S4).

Agreement between the 11 observers and our classification was moderate (Krippendorff's alpha = 0.57). This result was driven primarily by distinguishing subtypes; when the data were subsampled to account only for comparisons of calls of different types or calls from the same type and subtype, interobserver agreement was very high (Krippendorff's alpha = 0.84). Due to time constraints, the interobserver test only included comparisons of two call samples. Finer distinctions (i.e., subtypes) often require a larger sample that provides more information, such as whether variation is graded or discrete and whether there are intermediates. This information was not present in the test and likely explains the moderate agreement on subtypes. As the CART and random forest analyses provided strong support for the initial classification and showed only minor improvements when call subtypes were combined under their call type, subsequent analyses were conducted including all call types and subtypes. Nevertheless, to ensure call classification at the subtype level was not driving the results, analyses were repeated with call subtypes combined under their call type (referred to as analysis at the call type level).

FIGURE 3 Three sample spectrograms of commonly recorded killer whale call categories in Iceland. Samples were selected to show the variation within each call category. Call categories I11.4, I36, I44, and I45 made up 38% of calls recorded. Subtypes I11.5 and I11.6 show examples where a subtype was created due to the addition of an element and the addition of a high frequency component. Call types I43.1 and I43.2 show a major change within an element that led to the creation of a subtype and I43.3 shows another example of the addition of a high frequency component. Recordings were sampled at 64 kHz (I11.4b, I11.6a-c, I36a-c, I45a, I53.1c), 96 kHz (I44b), and 192 kHz (I11.4b-c, I11.5a-c, I43.1a-c, I43.2a-c, I43.3a-c, I44a,c, I45b-c). Spectrogram parameters: Hann window, 87.5% overlap. For 64 kHz recordings: FFT size: 2,048, frequency resolution: 31.25 Hz, time resolution: 4.0 ms; for 96 kHz recordings: FFT size: 4,096, frequency resolution: 23.44 Hz, time resolution: 5.33 ms; for 192 kHz recordings: FFT size: 4,096, frequency resolution: 46.88 Hz, time resolution: 2.67 ms.

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The relative rate of occurrence varied considerably across call categories (Figure 4). The most common call categories were I45, I44, I11.4, and I36, comprising 13.5%, 8.5%, 8.0%, and 7.5% of recorded calls respectively. All other call categories represented <5% of recorded calls. All four commonly recorded call categories had a relatively simple call structure and/or included elements that made them easily recognizable (Figure 3). The two most common call types (I44 and I45) were highly variable but the graded nature of the variation within the categories precluded further division into subtypes. These call types included calls that may seem very different if viewed on their own but other examples fall between these extremes, which made it impossible to draw a line for division into subtypes. For example, call type I45 had a very simple structure, consisting of a short segment of clicks, followed by a downsweep contour, and showed considerable variation, e.g., in duration. This call type includes calls that have a duration of $\sim$1.5 s, while other examples last for <0.5 s (Figure 3, I45a and c). However, examination of all calls of this type showed no clear distinction of shorter or longer calls but a continuum of durations. Call type I44 is characterized by a distinctive start segment and was thus easy to recognize and classify. This call type also shows variation, with some calls having little frequency modulation and other calls having a distinct downsweep in fundamental frequency. Since it was not possible to distinguish clearly between these two variants, they were kept together but further sampling may lead to the definition of subtypes in the future. Call type I11.4 had a distinct ending with several frequency modulations. It was recorded in all locations. Call type I36, the herding call, was low in frequency, long in duration, and showed very little frequency modulation. It was noticeably more common in Breiðafjörður, despite the overall larger sample of calls from Vestmannaeyjar. Recordings from Vestmannaeyjar were only collected during daytime, while the sample from Breiðafjörður included many hours of recordings collected at night with the EAR when herding calls occurred more frequently (Richard et al., 2017).

Single-component call categories (containing only a low-frequency component, LFC, i.e., monophonic or single-voiced) were more common (68.1%, $n = 62$) than two-component call categories (containing both a LFC and a high-frequency component, HFC, i.e., biphonic or two-voiced, 31.9%, $n = 29$), but call types shared across locations showed no clear tendency to be predominantly single-component or two-component calls (Figure S1).

Most call categories (56%) were found at two or more locations but only one call category was recorded in all five locations (Figure 1, see Table S2 for a detailed list of call types and subtypes). The remaining 44% of call categories were unique to one of three locations: 19% were recorded only in the Eastfjords, 14% only in Vestmannaeyjar, and 11% only in Breiðafjörður. Both Skjálfandi and Reykjanes had very few call categories (four and nine, respectively) that were all found in at least one other location. These results remained similar at the call type level: 65% of call types were shared between two or more locations, while unique call types were found in the Eastfjords (17%), Breiðafjörður (10%), and Vestmannaeyjar (8%).

In Vestmannaeyjar and Breiðafjörður, the locations with most data, the majority of call categories were recorded in both locations, making up 77% and 83%, respectively, of the call categories recorded in each location. A total of 21 call categories were found in the Eastfjords, the majority of which (81.0%) were recorded only in the Eastfjords and in none of the other locations. Four call categories (19.0%) from the Eastfjords were also found in other locations: one in Vestmannaeyjar (I13.1/I67), one in Vestmannaeyjar and Breiðafjörður (I11.6), one in Vestmannaeyjar, Breiðafjörður, and Skjálfandi (I59.1), and one in all other locations (I11.4).

Photo-identification data were available for the locations and seasons where most of the acoustic data came from (Vestmannaeyjar 2008–2015, Breiðafjörður, except for recordings from the EAR, and the Eastfjords 1985–1986) and were used to investigate the possibility that the individuals recorded in different regions might be the same. A total of 431 individual whales were identified in days when acoustic data were collected, with a mean and standard deviation of 26 ± 24 (range 1–159) whales identified per recording day. Most whales were identified either only in Vestmannaeyjar, only in Breiðafjörður, or in both regions (see below). In the Eastfjords, 71 identified individuals were present during recordings but only one of those was also present in one recording day in Breiðafjörður in 2013.

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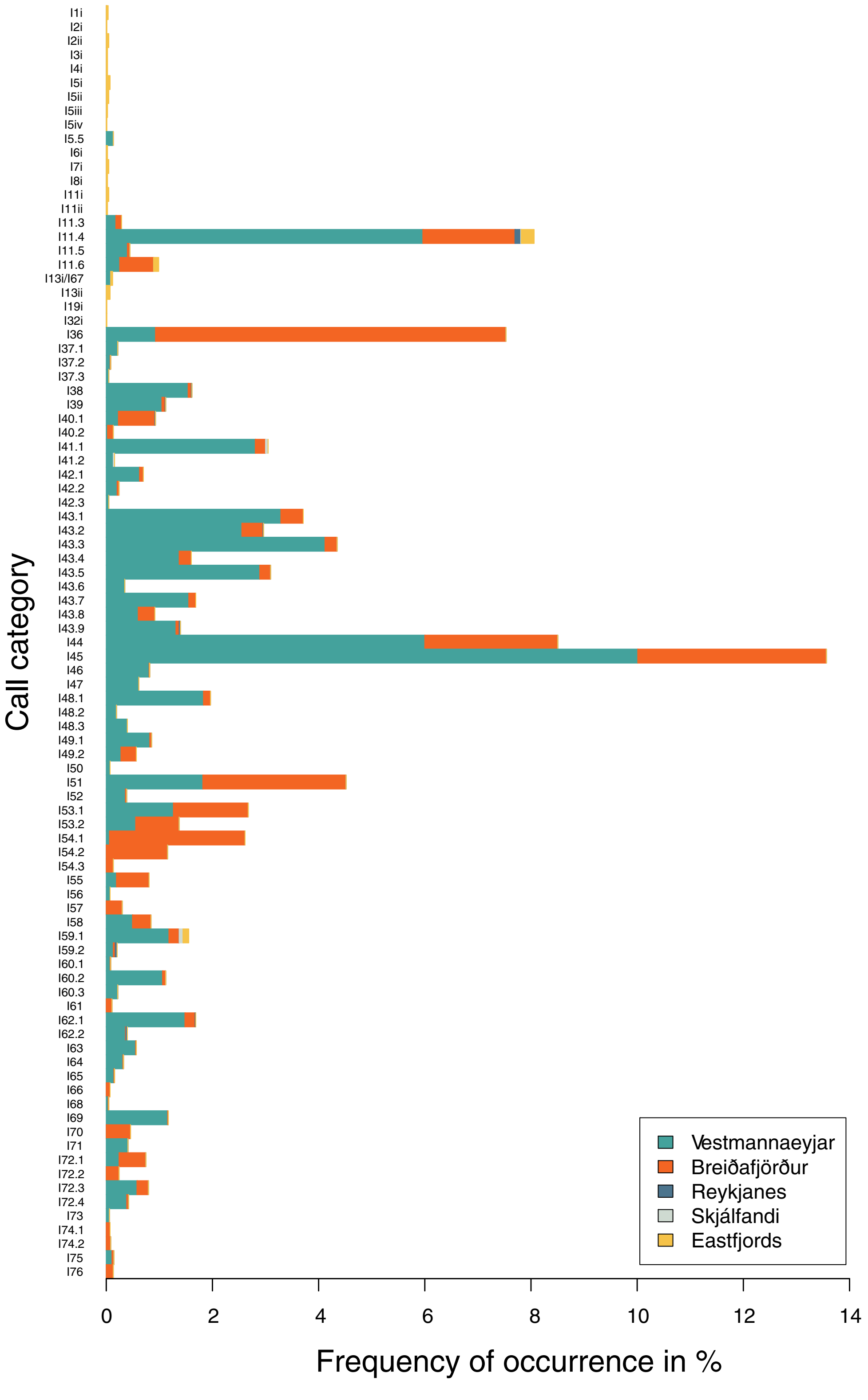

FIGURE 4 Relative rate of occurrence of different killer whale call categories in five locations around Iceland.

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3.2 | Comparison of call repertoires recorded in Vestmannaeyjar and Breiðafjörður

Vestmannaeyjar and Breiðafjörður had large sample sizes, allowing a more detailed analysis of variation between locations. Recordings in Vestmannaeyjar were collected on 91 days for a total of 216 hr and 2 min. The mean number of individual whales photo-identified per recording day (2008–2015) was 26 ± 21 (range 4–85). In Breiðafjörður, recordings were collected on 65 days and resulted in 466 hr and 17 min of recordings. A little over 430 hr came from an EAR deployment and thus included many hours without killer whale calls. Photo-identification data were available for 44 of the 65 recording days and a mean of 31 ± 29 (range 1–159) whales were identified per recording day. In total, 361 whales were identified; of these 141 (39.1%) were present during recording days in both locations, 129 (35.7%) were present only in Breiðafjörður and 91 (25.2%) only in Vestmannaeyjar.

From the acoustic recordings from Vestmannaeyjar, 5,588 calls were classified into 64 call categories. Of these, 15 call categories were only recorded in Vestmannaeyjar and not in Breiðafjörður. In Breiðafjörður, 2,612 calls were classified into 59 call categories, 10 of which were only recorded in Breiðafjörður and not in Vestmannaeyjar. In some cases, the unique call categories were one or more subtypes of a call type and other subtypes occurred in both locations. For example, I48.1 was recorded in both locations but the two other subtypes (I48.2 and I48.3) were only recorded in Vestmannaeyjar. Similarly, I54.1 was recorded in both locations but other subtypes (I54.2 and I54.3) were only recorded in Breiðafjörður (see Table S2 for details). Nevertheless, results remained similar at the call type level, with 37 call types in Vestmannaeyjar (7 of them unique to this location) and 36 call types in Breiðafjörður (6 of them unique to the location).

The SI for Vestmannaeyjar and Breiðafjörður was 0.80 (0.82 at call type level), indicating high similarity of the call categories present. However, the WSI was 0.46 (0.49 at call type level), showing that when the frequency of occurrence is considered, the two locations were less similar. These different patterns of relative production rate of call categories in the two locations can also be seen in Figure 4. In Breiðafjörður, a few call types dominated the repertoire, while the rest were recorded only rarely. In Vestmannaeyjar, the rate of occurrence of different call types was more evenly distributed. Thus, although a large proportion of call categories were recorded in both locations, they were not recorded at the same rates. Despite these differences, there was strong evidence that the relative occurrence of different call categories at both sites was positively correlated, although the correlation was weak (Spearman's correlation: $r_s = 0.30$, $p = .008$, $n_{\text{Vestmannaeyjar}} = 5{,}588$ calls, 216 hr, $n_{\text{Breiðafjörður}} = 2{,}612$ calls, 466 hr; Figure 5a).

3.3 | Comparison of call repertoires recorded in Vestmannaeyjar over time

A discovery curve (Figure 6; Figure S2 for analysis at call type level) indicated that the detection of new call categories in Vestmannaeyjar levelled off in 2016, suggesting good coverage of the repertoire at this location. However, it also showed a distinct increase in call categories recorded in 2014 ($n = 16$, 10 of which were new subtypes and 6 new call types). This corresponded with an increase in new individuals identified photographically ($n = 84$; Table S5). Individuals that were regularly sighted before 2014 continued to be detected but additional individuals not previously photographed were sighted from 2014 onwards (Figure S3 and Table S5), indicating that the increase in individuals and call categories does not represent a shift from one group to another. Similarly, call categories that were commonly recorded between 2008 and 2013 remained common in 2014–2016, and a different set of call categories was added in 2014–2016 (Figure S4).

Analysis of the long-term data set showed general stability in the repertoire with some variation between years (Table 2; Table S6 for analysis at call type level). The SI and WSI show a similar pattern of differences between years, but the WSI is overall more uniform. This shows that while there may be differences in the presence/absence of call categories, these are less pronounced when the frequency of occurrence is considered. The years 2008 and 2013 stand out as most different, which is likely due to the small sample sizes from these years (5 and 42 calls,

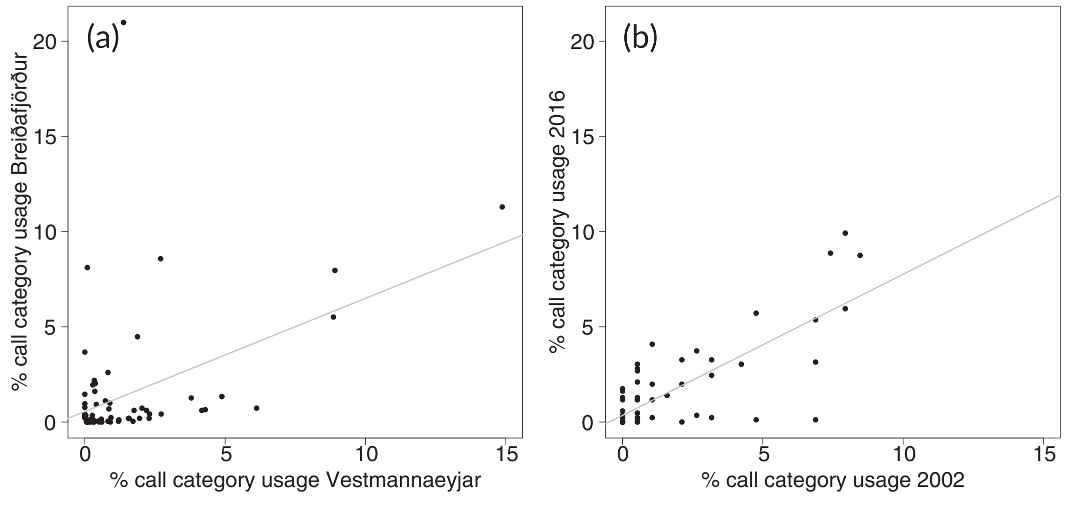

FIGURE 5 Relative production of call categories in a) Vestmannaeyjar compared to Breiðafjörður, b) Vestmannaeyjar in the year 2016 in comparison to 2002. Both were significantly positively correlated but the correlation was weaker between locations (Spearman's correlation: $r_s = 0.30$, $p = .008$) than between years (Spearman's correlation: $r_s = 0.71$, $p < .0001$). Each dot represents a call category (type or subtype).

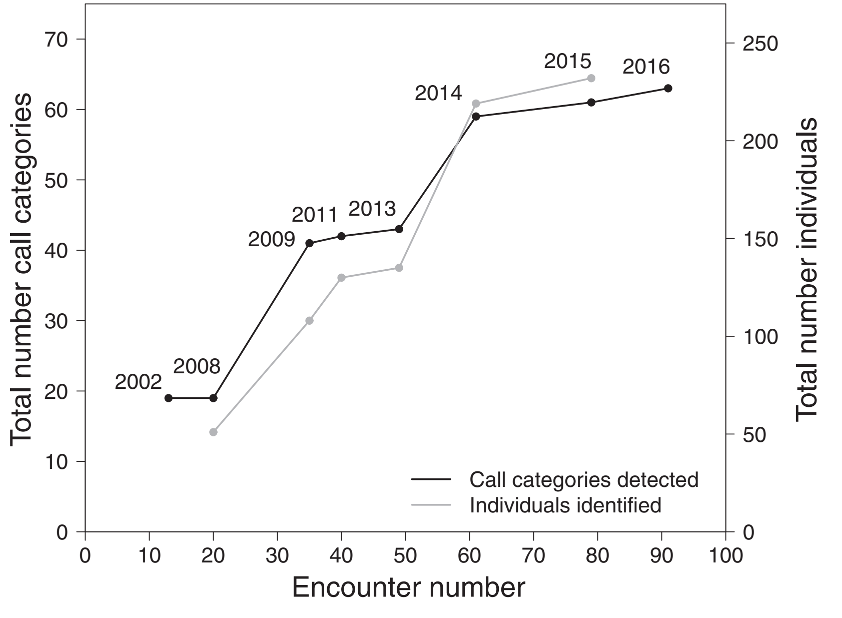

FIGURE 6 Discovery curve indicating the cumulative number of call categories recorded (black) and individual killer whales photo-identified during recordings (gray) in Vestmannaeyjar between 2002 and 2016.

respectively). The years with the highest similarity are 2014–2016, which are also similar to 2002. Indeed, there was strong evidence that the frequency of occurrence of different call categories in Vestmannaeyjar was positively correlated between 2002 and 2016 (Spearman's correlation: $r_s = 0.71$, $p < .001$, $n_{2002} = 189$ calls, 15 hr, $n_{2016} = 857$ calls, 35 hr, Figure 5b), suggesting similarity in the occurrence of call categories recorded in this region over time. A total of 49 call categories were recorded in 2002 and 2016 combined, of which 33 (67.3%) occurred in both years.

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TABLE 2 Comparison of the call repertoire of killer whales in Vestmannaeyjar between 2002 and 2016 based on the Similarity Index (SI) and Whittaker Similarity Index (WSI). Boxes are color-coded based on repertoire similarity in increments of 0.25 with darker shades showing the highest values of similarity.

Index	Year	2002	2008	2009	2010	2013	2014	2015	2016
SI	2002	1							
	2008	0.20	1						
	2009	0.56	0.15	1					
	2010	0.55	0.35	0.47	1				
	2013	0.14	0	0.24	0.24	1			
	2014	0.79	0.16	0.52	0.50	0.20	1		
	2015	0.75	0.17	0.58	0.51	0.24	0.81	1	
	2016	0.80	0.16	0.54	0.58	0.15	0.84	0.80	1
WSI	2002	1							
	2008	0.24	1						
	2009	0.42	0.28	1					
	2010	0.47	0.32	0.38	1				
	2013	0.08	0	0.07	0.20	1			
	2014	0.67	0.30	0.53	0.41	0.05	1		
	2015	0.55	0.30	0.41	0.51	0.24	0.51	1	
	2016	0.69	0.28	0.44	0.52	0.08	0.65	0.61	1

Figure 7 shows the relative production of each call category, further supporting that relative call category production was similar between these periods.

4 | DISCUSSION

4.1 | Variation in call repertoire across regions

Comparing killer whale call types and subtypes recorded in different locations around Iceland and spanning 32 years (1985–2016), we found a complex pattern of repertoire variation between regions. The majority of call categories recorded were shared between Vestmannaeyjar and Breiðafjörður, known Icelandic herring spawning and overwintering grounds that killer whales frequent seasonally to feed on herring. However, both locations also had a proportion of call categories that were not recorded elsewhere. Recordings from the Eastfjords, where Icelandic herring previously overwintered, included few call categories that matched other locations. The samples from Reykjanes and Skjálfandi were small, and it is unlikely that the full repertoire was captured at these locations, thus limiting conclusions that could be drawn. It is noteworthy that the sample from Skjálfandi in the north of Iceland matched call categories recorded around the country and that Reykjanes only included matches to Vestmannaeyjar and Breiðafjörður, except I11.4 which was recorded in all five locations.

These findings generally agree with what is currently known about the movement patterns of killer whales around Iceland. Photo-identification studies indicate that a minimum of 45% ($n = 146$) of the Icelandic killer whale population regularly moves between the herring spawning and wintering grounds in Vestmannaeyjar and Breiðafjörður, while 20% ($n = 64$) of individuals have only been sighted in Vestmannaeyjar, and 35% ($n = 117$) only in Breiðafjörður (Samarra et al., 2017). Similarly, in this study, we found that of all the call categories recorded, 54%

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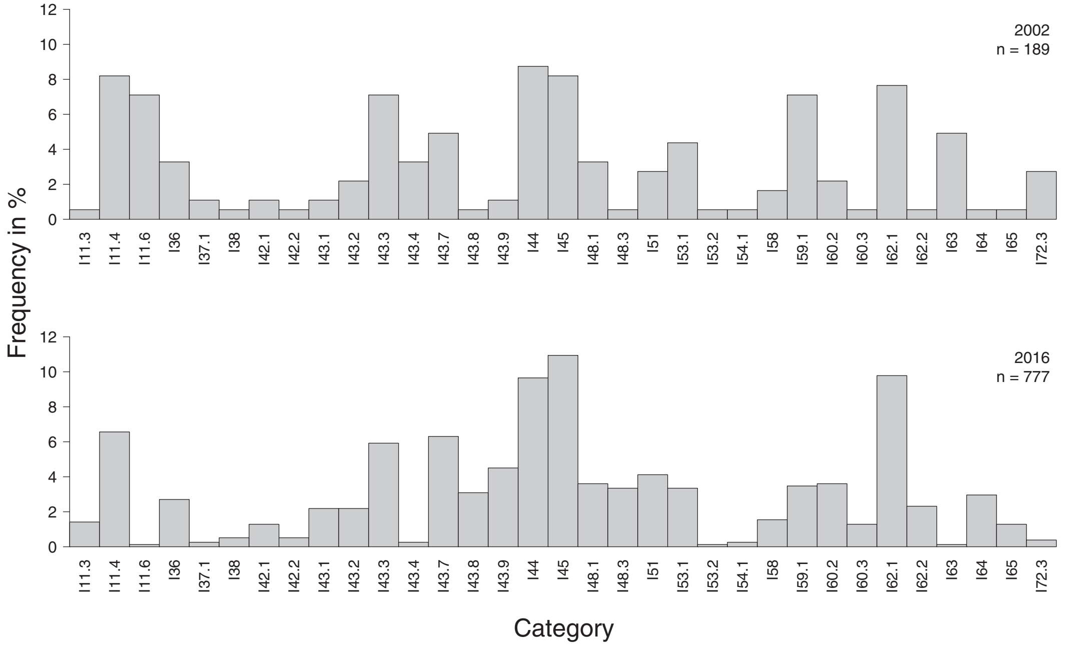

FIGURE 7 Relative frequency of occurrence (%) of call categories in Vestmannaeyjar in both 2002 (top) and 2016 (bottom). Note that only call categories occurring in both years ($n = 33$), and not the full repertoire recorded in each year, are displayed. The total number of call categories recorded was 36 in 2002 and 46 in 2016.

were found in both locations, 16% were only recorded in Vestmannaeyjar, and 11% only in Breiðafjörður. The SI for Vestmannaeyjar and Breiðafjörður was high, indicating similarity in the presence/absence of call categories but the WSI was lower, showing differences in the frequency of occurrence of these call categories. Likewise, the frequencies of occurrence of different call categories at the two locations were positively correlated (Figure 5). However, the correlation was weak, indicating some differences in the frequency of occurrence of shared call types and subtypes. The observed differences in call categories recorded in both locations and frequency of occurrence of different call categories support photo-identification studies showing differences in the individuals occurring in both areas (T. M. J. Marchon, personal communication, March 28, 2023). It could therefore be hypothesized that individuals or groups have different acoustic repertoires or that they use their repertoires differently in different social or environmental contexts. Future studies on group-specific repertoires would help elucidate these patterns.

Only 16 individuals (5%) from previous herring wintering grounds in eastern Iceland were photographically re-identified in current wintering grounds in Breiðafjörður (Samarra et al., 2017). Similarly, only four call categories (19%) recorded in the previous herring wintering grounds in the east of Iceland could be matched to other locations. Samarra et al. (2017) mention that the lack of photographic matches between past and current herring wintering grounds could have been due to a true difference in the individuals visiting both areas or due to missed detections resulting from the difficulty in matching individuals re-sighted over a time interval of up to 30 years. Assuming that individual killer whales in Iceland maintain their call type repertoire in the long-term, as observed in other areas (Foote et al., 2008; Ford, 1991), the lack of acoustic matches in this study suggests that both areas may indeed have been used by different individuals. An important caveat to this comparison is the limited sample size for the Eastfjords compared to Breiðafjörður which also could have resulted in the low number of acoustic matches.

Previous acoustic comparisons matched three call categories (I5.5, I11.4, and I36) between Iceland and Shetland (Deecke et al., 2011; Selbmann et al., 2021), and a part of the Icelandic killer whale population is known to regularly move between Breiðafjörður in Iceland and Scotland (Samarra & Foote, 2015; Samarra et al., 2017). Of the call types

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occurring in Iceland and Shetland, call type I11.4 was commonly recorded in this study and was found in all locations. Call type I36, the herding call, was only recorded in Vestmannaeyjar and Breiðafjörður, although a likely match was also found in lower quality calls from the Eastfjords that were not included in this study. Call type I5.5 was only recorded in Vestmannaeyjar and not in any of the other locations, which is interesting because movement between Vestmannaeyjar and Scotland has not been documented to date. However, only a few examples ($n = 11$) were recorded in Vestmannaeyjar, and it is possible that larger samples from other locations would include this call type. Other subtypes of this call type were also recorded in the Eastfjords. Individuals matched between Iceland and Scotland have only been sighted in the North, East/Southeast, or West of Iceland. Future photo-identification and acoustic recording comparisons using data collected from various regions in Iceland would be useful to further investigate the distribution range of whales traveling between both locations.

4.2 | Variation in call repertoire recorded over time

At the Vestmannaeyjar study site, long-term stability (2002–2016) and shorter-term changes (2008–2013 versus 2014–2016) in call repertoire were observed. Most of the call categories recorded in 2002 also occurred in 2016 and relative call occurrence changed little between 2002 and 2016 (Figures 5b and 7). However, some of the call categories that were recorded in 2002 were not present in 2008–2013 and occurred again in 2014–2016. This was accompanied by an increase of newly identified call categories in 2014 (Figure 6). The pattern of call occurrence indicates that call categories that were commonly recorded before 2014 remained common and that the new categories increased the total number of call categories recorded rather than replacing the existing repertoire.

This could be due to differences in sampling or differences in individuals present. While the time periods 2008–2013 and 2014–2016 have a similar sample size of calls included in the analysis (2,831 and 2,568 calls respectively), the sample from 2002 only included 189 classified calls. Most of the calls recorded in 2008–2013 were recorded from Dtags in 2009 ($n = 2{,}590$, see Table S7 and Figure S5). All calls from 2002 and 2014–2016 were recorded using single hydrophones, towed, and vertical hydrophone arrays. Dtag recordings are biased towards the tagged individual and its group (Johnson et al., 2009). Nevertheless, the Dtags were placed on four individuals each from a different social cluster (Tavares et al., 2017) and recordings included a total of 34 call categories, thus likely capturing a variety of individuals and groups. Furthermore, photo-identification data showed a distinct influx of new individuals. Individuals present varied between years but individuals that were regularly sighted before 2014 remained regular visitors to Vestmannaeyjar in 2014–2015. These results suggest that new individuals, that did not occur in this area in 2008–2013, arrived in 2014 and returned to the area in subsequent years. These variations in individuals present appear to be reflected in changes in call categories recorded.

Killer whale call repertoires have been shown to be stable over decades and relative call type occurrence also appears to vary little between years in other killer whale populations (Foote et al., 2008; Ford, 1991; Wellard et al., 2020). In our study, photo-identification data to determine whether the same individuals were sighted in 2002 and 2016 were not available. Nevertheless, Samarra et al. (2017) found high site fidelity to Vestmannaeyjar: the same individuals returned to the area in the summer months between 2008 and 2015. In addition, 27 individuals first identified in 1997–2007 in Vestmannaeyjar were resighted between 2008 and 2015, suggesting long-term site fidelity of at least some individuals to this area (Samarra et al., 2017). Assuming the stability in call type repertoire and usage in killer whales in Iceland follows the patterns described elsewhere, our results therefore suggest that individuals/groups return to this area in the long term. The movement patterns of this population are known to be varied; however, there is little knowledge about how movement patterns may change over time (Samarra et al., 2017). The results presented here highlight the value of long-term studies to fully capture the acoustic repertoire of this population, which can help understand long-term variation in site fidelity and movements even under conditions that limit on-water surveys.

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4.3 | Validation of the call classification

The CART and random forest analyses both showed high agreement with the initial manual classification, achieving results comparable to other cetacean studies. The CART correctly classified 84.8% of calls, which is similar to classification success in beluga (*Delphinapterus leucas*) and humpback whale (*Megaptera novaeangliae*) sounds (83%, Garland et al., 2015, and 70%–95%, Epp et al., 2022; Fournet et al., 2018; Rekdahl et al., 2013, 2017). The random forest model had an OOB error of 12%, which is higher than what has been previously reported in killer whales (4.4%, Sharpe et al., 2019), but this could be due to substantive differences in sample size between both studies ($n = 232$ in Sharpe et al., 2019 and $n = 1{,}999$ in this study). Compared to other cetaceans, the OOB error reported here was lower (17% for belugas and 15%–30% for humpback whales, Epp et al., 2022; Garland et al., 2015; Fournet et al., 2018; Rekdahl et al., 2013, 2017). The high agreement between the quantitative methods and the manual classification suggests the classification is reliable. To date, automated methods generally do not perform better than human observers in classifying odontocete sounds into biologically meaningful categories (Deecke et al., 1999; Deecke & Janik, 2006; Janik, 1999) but future work could benefit from clearer standards for killer whale call classification and standardized validation methods.

The interobserver reliability test indicated overall moderate agreement between observers when both call types and subtypes were considered. However, agreement was higher when differentiating at the call type level (i.e., distinguishing different call types or identifying calls of the same type and subtype) but lower on finer variations (i.e., when to differentiate between subtypes). These differences likely arose because some people are “splitters” and others “lumpers” and thus even experienced observers classify sounds differently (Oswald et al., 2022). A shortcoming of the interobserver reliability test was that observers were asked to directly compare between only two call samples, thus lacking information for finer distinctions (i.e., subtypes), such as whether variation is graded or discrete and whether there are intermediates. This was done to keep the task less time-intensive. However, interobserver tests that ask observers to classify a subset into as many categories as they think are appropriate have shown higher agreement rates compared to two-choice tests (e.g., Janik, 1999; Riesch & Deecke, 2011).

4.4 | Frequency of call occurrence

Four call types were more frequently recorded than the others, making up a total of 38% of calls recorded. The two most common call types (I44 and I45) were only recorded in Vestmannaeyjar and Breiðafjörður. A possible match to I45 was found in the recordings from the Eastfjords (I8i in the catalog by Moore et al., 1988) but could not be confirmed unequivocally. The other two commonly recorded call types (I11.4 and I36) were both previously found in Shetland as well (Deecke et al., 2011; Selbmann et al., 2021). Call type I11.4 was recorded in all locations and I36 was recorded in Vestmannaeyjar and Breiðafjörður.

All four call types are comparatively simple in structure. The herding call (I36) is known to be associated with feeding and may function in modifying prey behavior rather than strictly communication (Samarra, 2015; Simon et al., 2006). Since most of the recordings were collected in a feeding context, this likely explains why this call type was recorded frequently. However, the prevalence of I36 was mainly driven by its frequent occurrence in Breiðafjörður. Richard et al. (2017) found that the herding call was recorded more often at night. A large proportion of the recordings from Breiðafjörður was collected in the winter months using an EAR and thus included many hours of night-time recording, while recordings from Vestmannaeyjar were only collected during daytime and in summer. Therefore, the difference in the occurrence of I36 could be due to the timing of recordings.

Apart from Icelandic call type I36, killer whale call types are generally not restricted to specific behavioral contexts (Ford, 1991). However, the frequency of occurrence of specific call types may vary with behavior and social context (Filatova et al., 2009, 2013; Ford, 1989; van Opzeeland et al., 2005; Weiß et al., 2006). Northeast

Pacific resident killer whales, for example, appear to increase their matriline-specific calls after the birth of a calf (Weiß et al., 2006) or in the presence of more distantly related or unrelated groups (Weiß et al., 2007). Differences may also occur in the use of single-component and two-component calls. For example, Kamchatkan resident killer whales increase the use of two-component calls when several pods are present compared to single-pod encounters, when single-component calls dominate, indicating that two-component calls may be important family or pod markers (Filatova et al., 2009, 2013). Future work using recordings where behavioral context can be related to the sounds of an isolated group will be useful to better understand the nuances of call type usage in the Icelandic population.

4.5 | Call repertoire sharing and social structure

Varying levels of call repertoire sharing have been shown in other killer whale populations and differences in social organization could explain the different degrees of sharing in vocal patterns (Ford & Ellis, 1999). In the North Pacific, resident killer whales live in closed social groups with no immigration or emigration and closely related groups share more of their call repertoire than more distantly related groups (Bigg et al., 1990; Ford, 1991), while transients have a more widely shared repertoire and show dispersal of males and females from matrilines (Baird & Whitehead, 2000; Deecke, 2003).

Icelandic killer whales appear to live in a society without a clearly nested hierarchical structure (Tavares et al., 2017), although more data are necessary to clearly understand the population's social structure. Associations between individuals are nonrandom but a few strong social bonds exist, and associations are not assorted by the different movement patterns of individuals (Tavares et al., 2017). An early study based on the recordings from the Eastfjords suggested group-specific repertoires in Icelandic killer whales (Moore et al., 1988). This suggestion was likely based on the pattern observed in the Pacific Northwest, the only point of comparison available at the time, and the available data set was small. Even using the longer-term photographic identifications and acoustic recordings available to us now, we have not found the evidence needed to characterize group-specific repertoires or dialects in the Icelandic population. However, our study does suggest some repertoire differences between regions known to be visited by different whales. Thus, even though we do not know which individuals were recorded, this study supports the existence of a certain degree of differentiation of call repertoires among groups in Iceland. Further work using recordings from known individuals and combined with a better understanding of the population's social structure will be necessary to understand the relationship between social organization and acoustic repertoires in Icelandic killer whales.

4.6 | Conclusions

This study contributes to our knowledge of killer whale call repertoires around Iceland and will be useful in PAM applications. Despite sample sizes from different regions varying greatly, the results highlight regional variation in killer whale call repertoires, which can help us understand movement patterns and distribution ranges of these whales. Some limitations of this study could be addressed in the future. Continued acoustic monitoring effort is needed, in particular in less-studied areas, as well as offshore, to better understand regional variation in call repertoires in Icelandic waters. Furthermore, it remains unclear whether group-specific repertoires exist in Icelandic killer whales. This is mainly due to their apparent nonhierarchical social structure and the fact that the whales are often encountered in large feeding aggregations, which makes it difficult to assign social units and to obtain recordings from isolated groups. Further research into group-specificity of Icelandic killer whale calls, call usage and how these might differ from populations with different social association patterns would aid our understanding of drivers of variation in killer whale call repertoires.

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AUTHOR CONTRIBUTIONS

Anna Selbmann: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; validation; visualization; writing - original draft; writing - review & editing. **Volker B. Deecke:** Funding acquisition; investigation; methodology; resources; writing – review and editing. **Olga Filatova:** Funding acquisition; investigation; resources; writing – review and editing. **Ivan D. Fedutin:** Investigation; resources; writing – review and editing. **Patrick Miller:** Funding acquisition; investigation; resources; writing – review and editing. **Malene Simon:** Funding acquisition; investigation; resources; writing – review and editing. **Ann E Bowles:** Investigation; resources; writing – review and editing. **Thomas Lyrholm:** Investigation; resources; writing – review and editing. **Claire Lacey:** Funding acquisition; investigation; resources; writing – review and editing. **Edda Elísabet Magnúsdóttir:** Data curation; funding acquisition; investigation; resources; writing – review and editing. **William Maunder:** Data curation; investigation; writing – review and editing. **Paul Wensveen:** Funding acquisition; supervision; writing – review and editing. **Jörundur Svavarsson:** Funding acquisition; supervision; writing – review and editing. **Filipa Samarra:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – original draft; writing – review and editing.

ORCID

Anna Selbmann https://orcid.org/0000-0001-8687-7265
Volker B. Deecke https://orcid.org/0000-0003-2781-5915
Olga A. Filatova https://orcid.org/0000-0003-1533-4807
Ivan D. Fedutin https://orcid.org/0000-0001-9558-0922
Patrick J. O. Miller https://orcid.org/0000-0001-8028-9673
Ann E. Bowles https://orcid.org/0000-0003-1980-6103
Claire Lacey https://orcid.org/0000-0003-0541-8193
Edda E. Magnúsdóttir https://orcid.org/0000-0001-8281-4232

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Paul J. Wensveen https://orcid.org/0000-0002-9894-2543
Jörundur Svavarsson https://orcid.org/0000-0003-1842-7515
Filipa I. P. Samarra https://orcid.org/0000-0002-9909-0565

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