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Killer whale call frequency is similar across the oceans, but varies across sympatric ecotypes

Olga A. Filatova[a)]
Department of Vertebrate Zoology, Faculty of Biology, Moscow State University, Moscow 119991, Russia

Patrick J. O. Miller
Sea Mammal Research Unit, Scottish Oceans Institute, University of St. Andrews, St. Andrews, Fife KY16 8LB, Scotland

Harald Yurk
JASCO Applied Sciences Ltd., 2305-4464 Markham Street, Victoria, British Columbia V8Z 7X8, Canada

Filipa I. P. Samarra
Marine Research Institute, Skulagata 4, Reykjavik 121, Iceland

Erich Hoyt
Whale and Dolphin Conservation, Park House, Allington Park, Bridport, Dorset DT6 5DD, United Kingdom

John K. B. Ford
Pacific Biological Station, Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, British Columbia V9T 1K6, Canada

Craig O. Matkin
North Gulf Oceanic Society, Homer, Alaska 99603, USA

Lance G. Barrett-Lennard
Vancouver Aquarium Marine Science Centre, Vancouver, British Columbia V6B 3X8, Canada

Killer whale populations may differ in genetics, morphology, ecology, and behavior. In the North Pacific, two sympatric populations ("resident" and "transient") specialize on different prey (fish and marine mammals) and retain reproductive isolation. In the eastern North Atlantic, whales from the same populations have been observed feeding on both fish and marine mammals. Fish-eating North Pacific "residents" are more genetically related to eastern North Atlantic killer whales than to sympatric mammal-eating "transients." In this paper, a comparison of frequency variables in killer whale calls recorded from four North Pacific resident, two North Pacific transient, and two eastern North Atlantic populations is reported to assess which factors drive the large-scale changes in call structure. Both low-frequency and high-frequency components of North Pacific transient killer whale calls have significantly lower frequencies than those of the North Pacific resident and North Atlantic populations. The difference in frequencies could be related to ecological specialization or to the phylogenetic history of these populations. North Pacific transient killer whales may have genetically inherited predisposition toward lower frequencies that may shape their learned repertoires. © 2015 Acoustical Society of America. [http://dx.doi.org/10.1121/1.4922704]

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I. INTRODUCTION

Killer whale pods produce stereotyped calls that form specific dialects, unique for each pod within a population (Ford, 1991; Strager, 1995; Yurk *et al*., 2002; Filatova *et al*., 2007). These calls are socially learned and change with time through a process of cultural transmission, leading to divergence (or, in some cases, convergence) of group repertoires (Ford, 1991; Deecke *et al*., 2000; Miller and Bain, 2000; Yurk *et al*., 2002; Filatova *et al*., 2013). Temporal changes in call structure should also cause the gradual divergence of population repertoires. Other communication systems based on learned acoustic signals, such as bird song and human language, display both dialect variation within populations and geographic variation between distant populations or subpopulations (Krebs and Kroodsma, 1980; Jablonski and Aiello, 1998).

In killer whales, geographic variation of stereotyped calls has received less attention than the study of group-specific repertoires. Those few comparative studies report different call repertoires but overall similarity in acoustic features across populations (Awbrey, 1982; Moore *et al*., 1988; Stenersen and Similä, 2004). Foote and Nystuen (2008) found some call pitch variation across eastern North Pacific ecotypes, while Filatova *et al*. (2012) showed that call repertoire similarity was not directly correlated with geographic distance in resident-type North Pacific populations.

a)Electronic mail: alazor@rambler.ru

Comparing acoustic repertoires across populations has gained importance in light of the uncertain systematic status of killer whales as a single species. Several studies have pointed to the existence of reproductively isolated ecotypes inhabiting the same or adjacent habitats (Bigg *et al*., 1990; Ford *et al*., 1998; Pitman and Ensor, 2003). For example, three ecotypes were discovered in the North Pacific (Ford *et al*., 1998): "Residents" that specialize on fish live mainly in coastal waters and usually travel in large stable social units of maternally related animals (Ford *et al*., 2000; Ivkovich *et al*., 2010); "transients" or Bigg's killer whales that hunt primarily marine mammals and typically travel in smaller, more fluid social groups (Baird and Dill, 1996; Ford *et al*., 1998); and "offshores" that appear to feed on sharks (Ford *et al*., 2011) and occur away from shore travelling in large groups (50+) with an unknown social structure. There have been multiple suggestions to recognize resident and transient killer whales as different species based on morphological, behavioral, and genetic divergence (Baird *et al*., 1988; Reeves *et al*., 2004; Morin *et al*., 2010).

Transient killer whales also differ from residents in their calling behavior, being considerably less vocal and producing calls only in specific behavioral contexts (Deecke *et al*., 2005). Furthermore, Foote and Nystuen (2008) showed that transient killer whale calls were characterized by significantly lower acoustic frequencies compared to calls of resident and offshore killer whales. However, only calls from one transient population were investigated in that study, so it is not clear if the acoustic differences reflect true ecotype differences or whether the observed spectral composition of calls was specific to this mammal-eating population.

Ecological variation and population structure in eastern North Atlantic killer whales are less understood than these aspects are for whales in the North Pacific. In the eastern North Atlantic, there is evidence for two partially sympatric populations that may specialize on different prey types (Foote *et al*., 2011). Feeding on either fish or marine mammals is observed in the area, but it is not clear if any groups specialize on specific prey or switch between prey types (Beck *et al*., 2012).

Genetic studies using mitochondrial deoxyribonucleic acid (DNA) sequences have shown that North Pacific residents are more closely related to eastern North Atlantic killer whales than to sympatric North Pacific transients (Morin *et al*., 2010; Moura *et al*., 2015). However, behavioral observations suggest that while hunting on seals, North Atlantic killer whales demonstrate behavioral features, such as group size (Beck *et al*., 2012) and vocal activity (Deecke *et al*., 2011), which are similar to North Pacific transients, despite being genetically closer to North Pacific residents. The similarity in behavior and vocal activity between the North Pacific transients and North Atlantic killer whales may be due to convergent foraging strategies, but it is not known whether ecological specialization might also lead to convergence in call structure.

Given the genetic similarity between allopatric North Pacific resident and eastern North Atlantic killer whales and the divergence of sympatric North Pacific transients, a comparison of the structure of stereotyped calls produced by these different ecotypes and populations could provide new insights into how and why killer whales use learned behaviors, such as vocalizations. In this paper, we report on a wide-scale comparison of frequency variables in killer whale calls recorded from several North Pacific resident and transient populations, and from two populations from the eastern North Atlantic, to assess which factors drive the large-scale changes in call structure. We explore whether call structure is more similar in geographically or genetically close populations, and whether call structure in the populations with presumably mixed foraging strategies (eastern North Atlantic) is intermediate between specialized fish- and mammal-eating populations.

II. METHODS

A. Data collection

Acoustic recordings used for this study were collected over various field projects by means of a variety of equipment. However, all recordings were made at a sampling rate of 44.1 kHz or higher, enabling systematic evaluation of call features <22.05 kHz. Figure 1 shows the geographical locations of recordings used for this study.

Recordings of the Northern resident, Southern resident, West Coast transient, and Alaskan resident killer whale populations were taken from existing long-term recording databases. Recordings of Southern residents were made from 1980 to 2009, Northern residents from 1988 to 1999, and Alaskan residents from 1984 to 2008.

Calls from Kamchatkan residents were recorded between 2000 and 2014 off the southeastern coast of Kamchatka peninsula as a part of the Far East Russia Orca Project.

False Pass transients were recorded between 2003 and 2008 in False Pass (eastern Aleutian Islands) as part of a project conducted by the North Gulf Oceanic Society.

Calls from Icelandic killer whales were obtained between 2008 and 2014 using both digital acoustic recording tags (Dtags; Johnson and Tyack, 2003) and various other
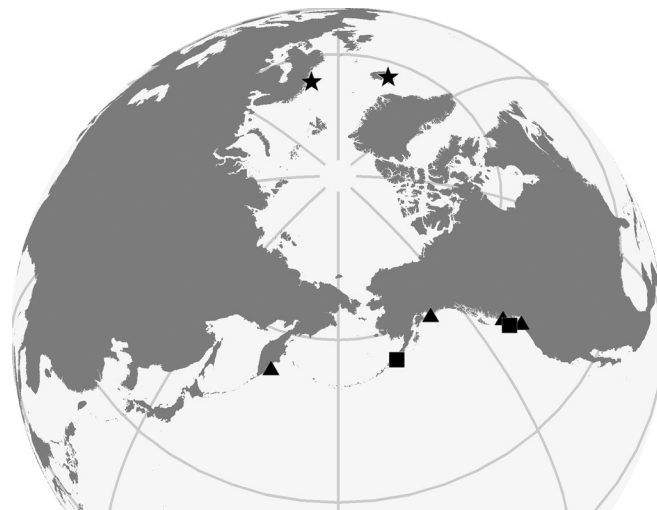

FIG. 1. Locations of recordings used for this study: triangles represent North Pacific residents, rectangles represent North Pacific transients, and stars represent eastern North Atlantic killer whales.

recording systems at two main locations: One near Grundarfjörður on the Snæfellsnes Peninsula (West Iceland), the other near Vestmannaeyjar off the southern coast of Iceland.

Calls from Norwegian killer whales were obtained between 2005 and 2009 using Dtags in the northern Norwegian Vestfjord fjord system and off Vesterållen.

Calls from four North Pacific resident populations and the West Coast transient population were classified according to existing catalogues (Ford, 1987; Yurk *et al*., 2002; Filatova *et al*., 2004). For the False Pass transient population, call categorization was performed based on audible characteristics of calls and visual inspection of spectrographic features. For Icelandic and Norwegian killer whales, we have modified and updated existing classifications (Strager, 1995; Shapiro, 2008; Duc, 2011). The herding calls of Icelandic killer whales (Simon *et al*., 2006) were not included in the analysis.

Two calls from each call type or subtype were used for the analysis. If a call type had no subtypes, two samples from that call type were used; for call types that were produced as discrete subtypes, we used two samples from each subtype. When possible, the pairs of call samples from the same type/subtype were selected from different encounters and different years to cover the presumed variation in the call structure. For calls that did not fall into discrete subtypes but showed apparent group-specific variations (e.g., N12; see Ford, 1991), two calls from opposite extremes of the structural continuum were selected.

Norwegian killer whales are known to produce compound calls, which consist of combinations of other stereotyped calls produced in stable sequences (Strager, 1995; Shapiro *et al*., 2011). Treating every stable sequence as a separate type would produce pseudo-replication through the increased presence of calls used as parts of stable sequences (as they will be measured twice—as a separate call and as a part of a stable sequence). Thus, we only measured those stable sequences that contained calls or syllables not observed occurring separately.

In total, 630 call samples were used for the analysis (Table I).

B. Acoustic and statistical analysis

To capture the frequency parameters over the whole call duration, we extracted call contours following the method described in Filatova *et al*. (2012). The extracted contours represented a set of frequency measurements of each call's fundamental frequency spaced 0.01 s apart. Many stereotyped calls contain an overlapping high-frequency component (HFC), comprising two-voiced, or biphonic, calls. For these two-voiced calls, we extracted the contours of both the low-frequency components (LFCs) and HFCs.

For each frequency contour, we calculated the median frequency and interquartile interval over all its points. We normalized the interquartile interval by dividing it by the median for each contour. We compared the median values and normalized interquartile intervals calculated from extracted frequency contours across three killer whale assemblages: eastern North Atlantic (Norwegian and Icelandic populations), North Pacific resident (Kamchatkan, Alaskan, Northern, and Southern resident populations) and North Pacific transient (West Coast transient and False Pass transient populations) using the Mann-Whitney test with Bonferroni correction (i.e., the significance values were divided by the number of pairwise comparisons). For two-voiced calls, we compared LFCs and HFCs separately.

III. RESULTS

The median frequency of the fundamental frequency contour of both LFCs and HFCs of calls varied across ecotypes (Fig. 2). The frequency of the LFC of all three ecotypes differed significantly, but the difference between North Pacific transient killer whales and the other two groupings was considerably more pronounced than between North Pacific resident and eastern North Atlantic killer whales (Mann-Whitney test with Bonferroni correction: transient vs eastern North Atlantic $W = 4062$, $p < 0.0001$; transient vs resident $W = 7561$, $p < 0.001$; resident vs eastern North Atlantic $W = 28\,504$, $p < 0.05$). The frequency of the HFC differed significantly between North Pacific transient killer whales and the other two groupings, but not between North Pacific resident and eastern North Atlantic killer whales (transient vs eastern North Atlantic $W = 265$, $p < 0.0001$; transient vs resident $W = 821$, $p < 0.0001$; resident vs eastern North Atlantic $W = 5522$, $p = 0.45$).

The normalized interquartile range of the fundamental frequency contour of the LFC did not have any significant differences across ecotypes (Fig. 3). The interquartile range of the fundamental frequency contour of the HFC was significantly different only between North Pacific resident and eastern North Atlantic killer whales (Mann-Whitney test with Bonferroni correction: $W = 5181$, $p < 0.001$). The

TABLE I. Number of call samples from each population used for the analysis.

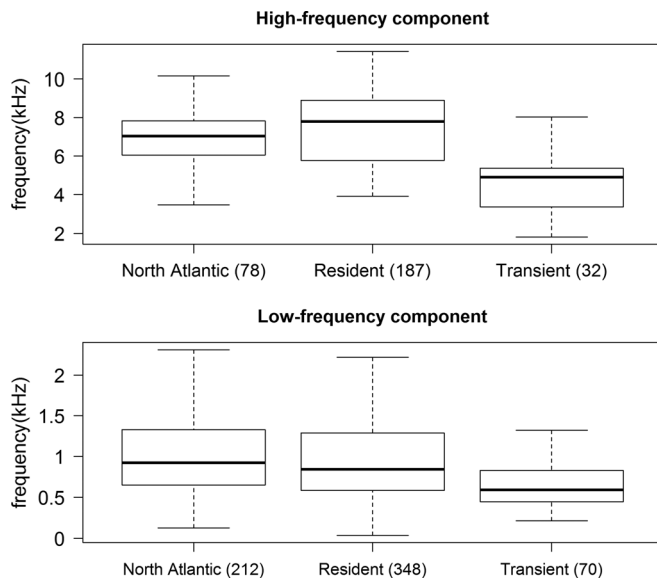| Population	Area	Ecotype	Number of calls	Number of calls with HFC
Iceland	Eastern North Atlantic	Unknown	140	42
Norway	Eastern North Atlantic	Unknown	72	36
Kamchatka	Western North Pacific	Resident	102	55
Alaska	Eastern North Pacific	Resident	88	42
Northern resident	Eastern North Pacific	Resident	96	62
Southern resident	Eastern North Pacific	Resident	62	28
West Coast transient	Eastern North Pacific	Transient	36	12
False Pass transient	Eastern North Pacific	Transient	34	20

FIG. 2. Median fundamental frequency of LFCs and HFCs of killer whale calls from eastern North Atlantic, North Pacific resident, and transient populations. Sample size is shown in parentheses.

differences in all other comparisons were non-significant (Fig. 3).

To visualize the differences in frequency profiles across populations, we plotted the histograms of all measured frequency points from the fundamental frequency contours (rather than median values used for the statistical analysis) for each population. The frequency profiles were unique for every ecotype, but again the transients were the most divergent group (Fig. 4). North Pacific resident and eastern North Atlantic killer whales typically had the major histogram peak between 500 Hz and 1 kHz, except for Southern resident killer whales that had that peak between 1 and 1.5 kHz. Transient killer whales had a peak either well below 500 Hz (False Pass transients) or close to 500 Hz (West Coast
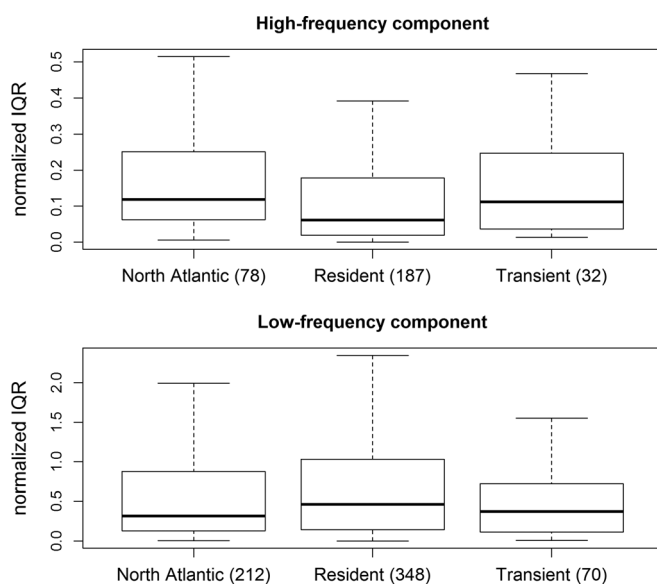

FIG. 3. Differences in interquartile range of LFCs and HFCs of killer whale calls from eastern North Atlantic, North Pacific resident, and transient populations. Sample size is shown in parentheses.

transients). The second peak, corresponding to the fundamental contour in the HFC, showed variability among populations. In the calls from the eastern North Atlantic and North Pacific resident killer whales, the peak usually occurred between 5 and 9 kHz. In transient killer whales, there was no clear peak for measured frequency points in the HFC, and measured values ranged from 2 to 8 kHz. In contrast to measured values from HFCs from the eastern North Atlantic and North Pacific resident killer whales, no extracted points from HFCs of transients had values > 8.5 kHz. In the eastern North Atlantic and North Pacific resident killer whales, measured values from HFCs ranged up to at least 10 kHz (Southern residents) and often even up to >15 kHz (Icelandic, Norwegian, and Kamchatkan populations, Fig. 4).

IV. DISCUSSION

Our results demonstrate that both LFCs and HFCs of North Pacific transient killer whale calls have significantly lower frequencies than those of the North Pacific resident and eastern North Atlantic populations. The range of frequency modulation within calls, quantified as the interquartile range of fundamental frequency points, did not show the same pattern with little consistent variation across the ecotypes. This indicates that although calls cover a similar range of frequencies, the calls produced by transients are shifted to a lower frequency. Two possible reasons may explain our findings: The difference in frequencies could be related to ecological specialization or to the phylogenetic history of these populations.

Similar to our study, Foote and Nystuen (2008) found that the minimum frequency of West Coast transient calls was significantly lower than that of Southern resident calls. They explained the higher frequency of resident calls as an adaptation to avoid the low-frequency hearing range of their salmonid prey. However, the overlapping HFC of resident calls was also significantly higher than in transients, though both of them were far beyond salmon's hearing range.

Lower frequencies of both LFCs and HFCs in North Pacific transients may be an adaptation to a different active space than prey hearing range. Lower frequencies attenuate slower underwater and may propagate over longer ranges, so the lower-frequency calls potentially may be heard at greater distances, though the difference in attenuation is not large: ~ 0.07 dB per km for 2 vs 1 kHz and 0.59 dB per km for 10 vs 5 kHz (Tables of Physical and Chemical Constants, 2008). However, the hearing sensitivity for killer whales may drop significantly at frequencies < 2 kHz (Szymanski *et al.*, 1999), which would mean the shift to the lower frequencies would also decrease the detectability of the calls over distance. The reported audiograms in Szymanski *et al.* (1999) represent hearing of a North Pacific resident killer whale and a North Atlantic killer whale. Audiograms of transient killer whales are unavailable, but the overall sensitivity range (shape of the hearing curve) is likely similar to that of fish-eating killer whales. The tested hearing of the two killer whales showed threshold decreases between 2 kHz vs 1 kHz of ~ 33 dB, and between 10 kHz vs 5 kHz of ~ 13 dB (Szymanski *et al.*, 1999).
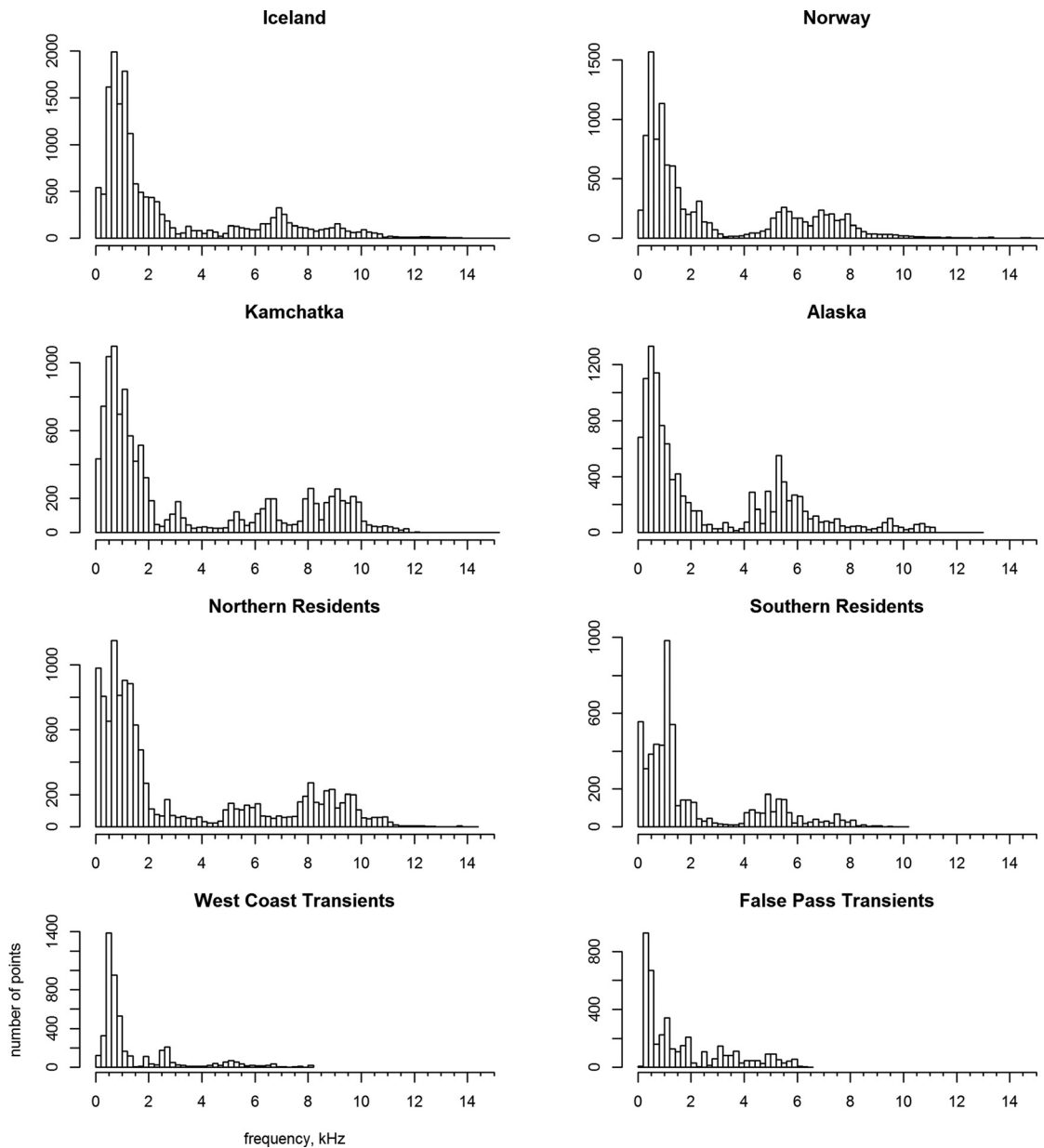
FIG. 4. Histograms of all fundamental frequency points extracted from spectrogram contours of calls from eight killer whale populations.

Frequencies <1 kHz were not tested in this study, but Hall and Johnson (1972) reported a 13 dB increase in hearing sensitivity for a resident killer whale for 500 Hz vs the value reported for 1 kHz in Szymanski et al. (1999). Transients could be more sensitive to lower frequencies, which would correlate with their use of passive listening as a strategy to detect prey (Deecke et al., 2005). Alternatively, the use of lower frequencies by transients may actually be an adaptation to a smaller active space to avoid being detected by their prey. Resident calls with the lower fundamental frequency have lower source levels (Miller, 2006), which may be also the case for transient calls. Testing of hearing sensitivities and source level measurements of calls, as well as estimates of active space of transient calls, would be useful to test these hypotheses.

We found that the median fundamental frequency of the calls from Icelandic and Norwegian killer whales was similar to that of the North Pacific residents and significantly different from transients. The foraging specialization

of Icelandic and Norwegian killer whales remains unclear. Both populations are thought to prey primarily upon Atlantic herring (Sigurjónsson et al., 1988; Similä et al., 1996), but may consume other fish species (Vester and Hammerschmidt, 2013); however, there are also reports of killer whales hunting marine mammals both from Iceland and Norway. It is not known whether killer whales regularly switch from fish to marine mammals in the eastern North Atlantic. Vongraven and Bisther (2014) have reported that some identified whales have been seen preying on both seals and herring, but it is based on only seven observations, three of which were of a single pod (K1).

Foote et al. (2009) reported two ecotypes in the North Atlantic—one generalist and one specialist, but a later study (Foote et al., 2012) showed that the higher ^{15}N variation in "generalist" type was, in fact, due to pooling of muscle, tooth, and bone collagen samples, assuming the same turnover rates for different tissues. Study of skin samples from the same

areas (Foote *et al.*, 2012) showed much lower variation, suggesting that killer whales were mostly feeding on fish. However, the possibility that killer whales in these areas may sometimes hunt marine mammals cannot be ruled out because the turnover rate for stable isotopes in odontocete skin is estimated to be around several weeks (Browning *et al.*, 2014). Some killer whales observed hunting on marine mammals near the Shetland Islands were socially connected to those feeding on herring in Iceland, so, at least population-level specialization is unlikely (Beck *et al.*, 2012). Generally, our knowledge of North Atlantic killer whale ecology is too limited to draw conclusions regarding its relationship to the frequency of stereotyped calls. However, the fact that eastern North Atlantic and North Pacific resident killer whales have similar frequency profiles, despite being somewhat different in ecology (residents being mostly salmon-feeding specialists; Ford, 1998; Ford and Ellis, 2006; Hanson *et al.*, 2010) suggests that variations in frequency profiles are more likely to be related to population history than to ecology.

The phylogenetic history of killer whale populations and ecotypes is not yet clear. Some authors suggest that the North Pacific resident and transient ecotypes evolved separately, and their sympatry arises from secondary contact (Foote *et al.*, 2011); others argue that the divergence between ecotypes occurred locally in sympatry (Moura *et al.*, 2015). In any case, transient killer whales are the most divergent group based on mitochondrial DNA among all killer whale populations examined to date, including North Atlantic and Southern Ocean populations (Morin *et al.*, 2010; Moura *et al.*, 2015). The date of divergence between transients and all other killer whales is estimated to be about 700,000 years ago (Morin *et al.*, 2010).

Therefore, eastern North Atlantic killer whales are more genetically related to North Pacific residents than they both are to North Pacific transients. Killer whale calls are learned rather than genetically inherited, so, it is possible that calls of transients have diverged from repertoires of other populations due to the random drift in call parameters. However, if the repertoire were totally learned, drift would have likely occurred between North Pacific residents and eastern North Atlantic killer whales as well. There is some indication of a connection between the North Pacific offshore ecotype and a population off Newfoundland ∼11 000 years ago, but North Pacific resident and eastern North Atlantic populations appear to be separated by at least several thousand years (Foote *et al.*, 2011).

The rate of cultural change in killer whale dialects is unknown, but some studies suggest that detectable changes may occur over the span of several decades (Deecke *et al.*, 2000; Wieland *et al.*, 2010). Thus, several thousand years of separation should lead to completely different repertoires through random drift. However, the frequency profiles of different North Pacific resident and eastern North Atlantic populations are similar (Fig. 4), suggesting some inherited predisposition or ecological forcing toward particular frequencies.

Though killer whale stereotyped calls are learned, some structural characteristics appear to be inherent species-specific traits, such as production of calls with an overlapping HFC which is found in all studied populations (Moore *et al.*, 1988; Ford, 1991; Strager, 1995; Yurk *et al.*, 2002; Filatova *et al.*, 2007), or production of calls with rapid, up-down frequency modulations emitted in high arousal ("excitement") situations by North Pacific residents and transients (Ford, 1989; Rehn *et al.*, 2011) and captive Icelandic whales (Graham and Noonan, 2010).

In bird song—another example of a learned communication system—the range of signals that can be learned is limited by genetically inherited predispositions (Lachlan and Feldman, 2003). Many songbirds learn their songs from fathers or neighboring males, but despite some variation, their song remains species-specific and retains a certain structure (Slater, 1989). Similarly to bird song, preference for specific frequencies may be an inherent species-specific trait of killer whale acoustic repertoires.

Therefore, the difference in preferred frequencies between North Pacific transients and other killer whale populations may reflect their genetically inherited predisposition toward different call parameters, shaped by feedback from ecological interaction with prey. Further research on the acoustic repertoires of other transient populations is required to clarify the stability and scope of these frequency differences.

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