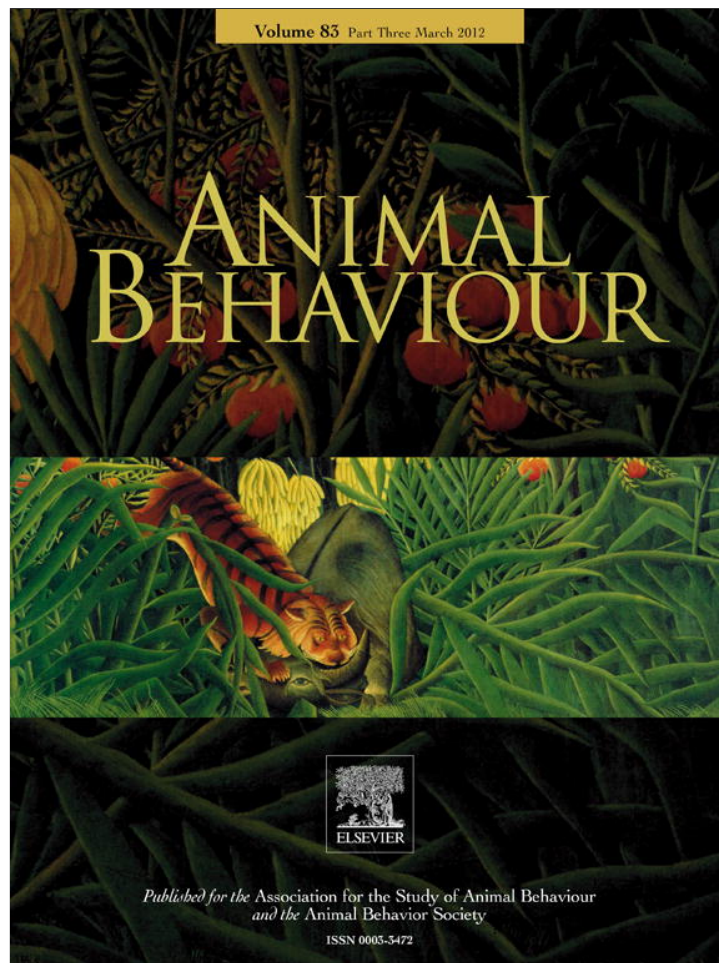


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Call diversity in the North Pacific killer whale populations: implications for dialect evolution and population history

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Although killer whale, *Orcinus orca*, dialects have been studied in detail in several populations, little attempt has been made to compare dialect characteristics between populations. In this study we investigated geographical variation in monophonic and biphonic calls among four resident populations from the North Pacific Ocean: Northern and Southern residents from British Columbia and Washington State, southern Alaska residents, and eastern Kamchatka residents. We tested predictions generated by the hypothesis that call variation across populations is the result of an accumulation of random errors and innovation by vertical cultural transmission. Call frequency contours were extracted and compared using a dynamic time-warping algorithm. We found that the diversity of monophonic calls was substantially higher than that of biphonic calls for all populations. Repertoire diversity appeared to be related to population size: in larger populations, monophonic calls were more diverse and biphonic calls less diverse. We suggest that the evolution of both monophonic and biphonic calls is caused by an interaction between stochastic processes and directional selection, but the relative effect of directional selection is greater for biphonic calls. Our analysis revealed no direct correlation between call repertoire similarity and geographical distance. Call diversity within predefined call categories, types and subtypes, showed a high degree of correspondence between populations. Our results indicate that dialect evolution is a complex process influenced by an interaction among directional selection, horizontal transmission and founder effects. We suggest several scenarios for how this might have arisen and the implications of these scenarios for call evolution and population history.

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Vocal variation among groups of animals may occur at different levels. Differences in vocalizations between neighbouring groups of potentially interbreeding individuals are called dialects, whereas differences in acoustic repertoires over long distances and between populations that normally do not interbreed are referred to as geographical variation (Conner 1982). Dialects are common in birds (Baker & Cunningham 1985), but rare in mammals, being mostly limited to cetaceans (e.g. Ford 1991; Rendell & Whitehead 2003), bats (e.g. Boughman 1997; Esser & Schubert 1998; Yoshino

et al. 2008) and humans (e.g. Labov 2001). In contrast, geographical variation in vocal repertoires is common among both bird and mammalian populations (e.g. Krebs & Kroodsma 1980; Slobodchikoff et al. 1998; Mitani et al. 1999).

Killer whales, *Orcinus orca*, are widely distributed throughout the world's oceans (Forney & Wade 2007). Different populations display substantial variation in diet, behaviour, morphology and genetics (Ford et al. 1998; Pitman & Ensor 2003; Foote et al. 2009; Morin et al. 2010). Rather than being genetically coded, the vocal repertoire of killer whales is thought to be learned (Bowles et al. 1988; Ford 1991; Deecke et al. 2000; Foote et al. 2006), which leads to formation of dialects between neighbouring groups in some populations and geographical variation between distant populations.

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As a species, killer whales feed on a wide variety of prey, but different populations often show a high degree of dietary specialization (Ford et al. 1998; Saulitis et al. 2000; Ford & Ellis 2006). In several regions, sympatric populations show little or no dietary overlap and represent different ecotypes (Ford et al. 1998; Saulitis et al. 2000; Pitman & Ensor 2003). Three killer whale ecotypes have been described from the North Pacific and these differ in social structure, morphology, genetics and behaviour: residents specialize on fish and live in large stable social units (Ford & Ellis 2006; Ivkovich et al. 2010), transients hunt primarily marine mammals and live in smaller more fluid social groups (Baird & Dill 1996; Ford et al. 1998), and offshores are probably fish specialists (Ford et al. 2011) and live in large groups with an unknown social structure.

Dialects have been described for several resident killer whale populations from the North Pacific (Ford 1991; Yurk et al. 2002; Filatova et al. 2007) and for killer whales from the northeastern Atlantic (Strager 1995). Resident killer whales from the North Pacific have a complex nested social structure comprising (1) matriline containing a matriarch and all her descendants, which always travel together; (2) pods containing a set of matrilines that associate frequently and use a common repertoire of stereotyped calls, which represents the vocal dialect of the pod; (3) acoustically distinct clans composed of pods that share some calls in their repertoire; and (4) populations or communities containing one or more associating clans (Ford 1991; Ford 2002; Ivkovich et al. 2010).

Several distinct populations of resident killer whales have been identified in the North Pacific: Northern and Southern residents from British Columbia and Washington State, and southern Alaska residents in the northeastern Pacific (Matkin et al. 1999; Ford 2002), eastern Kamchatka residents in the northwestern Pacific (Ivkovich et al. 2010) and a number of less studied putative populations around the Aleutian and Kuril Islands and in the Bering and Okhotsk seas. To date, genetic and other research on these populations (Barrett-Lennard 2000; Hoelzel et al. 2002) has not provided detailed information about historical relationships among them.

It has been suggested that repertoires of stereotyped calls may serve as a marker of maternal relatedness. Divergence between vocal repertoires of killer whale pods is thought to happen gradually as pods grow bigger and matrilines spend less and less time together (Ford 1991). Vocal learning involves a series of call mistakes and innovations, which gradually make vocal repertoires diverge. For these reasons, Ford (1991) suggested a direct relationship between the maternal ancestry of different pods within clans and the degree of similarity of their vocal repertoires: the more distant the common maternal ancestry between pods, the fewer calls shared within their repertoires. This prediction was confirmed by Deecke et al. (2010), who showed that the similarity of one call type across matrilines was correlated with matriarch relatedness in spite of the biparental inheritance of nuclear DNA.

These findings suggest that populations with more recent common maternal ancestry should have more similar repertoires as

well. Although killer whale dialects have been described in detail within several populations, few studies have examined vocal variation between killer whale populations. Yurk (2005) compared distribution of call syllables among populations and showed that distinct lower frequency syllables were shared between clans but differed between populations, whereas upper frequency syllables varied between clans of the same population. Foote & Nystuen (2008) showed that the frequency parameters of calls varied across ecotypes (resident, transient and offshore). In this study, we investigated the variation of whole frequency contours across the three North Pacific resident killer whale populations.

Comparing killer whale acoustic repertoires is complicated by the fact that killer whale sounds are not structurally homogeneous. They comprise three distinct structural categories, common to all killer whale populations studied to date: whistles, echolocation clicks and pulsed calls. Most pulsed calls are highly stereotyped and can be easily divided into call types (Ford 1991) with varying degrees of variability within types. Many call types have an overlapping, independently modulated, high-frequency component (Fig. 1); this phenomenon is usually referred to as 'biphonation' (Wilden et al. 1998; Fitch et al. 2002) or, when two independent sources are responsible, 'two-voiced calling' (Zollinger et al. 2008). Since the mechanism responsible for this pattern in killer whales is unknown, we use the former term in this paper.

Biphonic sounds have been described in mammals as diverse as canids (Wilden et al. 1998; Riede et al. 2000; Volodin & Volodina 2002), primates (Fischer et al. 2001; Brown et al. 2003; Riede et al. 2004) and cetaceans (Tyson et al. 2007). While the functional significance of biphonation in calls is not readily understood, its presence in the vocalizations of different species suggests a potentially important communicative role. Proposed functions include the enhancement of individual recognition (Aubin et al. 2000; Fitch et al. 2002; Volodina et al. 2006) or honest signalling of physical condition (Fitch et al. 2002). For killer whales, it has been suggested that differences in the directionality of the low- and high-frequency components in biphonic calls can provide information on the orientation of a caller relative to a listener (Miller 2002). Differences in usage of biphonic and monophonic calls in diverse social contexts suggest that they may have distinct functions in killer whale communication, with biphonic calls functioning mostly as group identifiers and monophonic calls serving as short-range contact signals (Filatova et al. 2009). Moreover, biphonic and monophonic calls show substantial differences in source levels (Miller 2006) and structure (Filatova et al. 2007), which suggests that they should be considered two distinct structural categories.

In this study, we examined geographical variation in monophonic and biphonic calls among four resident populations from the North Pacific Ocean: Northern and Southern residents of British Columbia and Washington State, southern Alaska residents, and eastern Kamchatka residents (Fig. 2). We tested predictions generated by the hypothesis that call variation across populations is

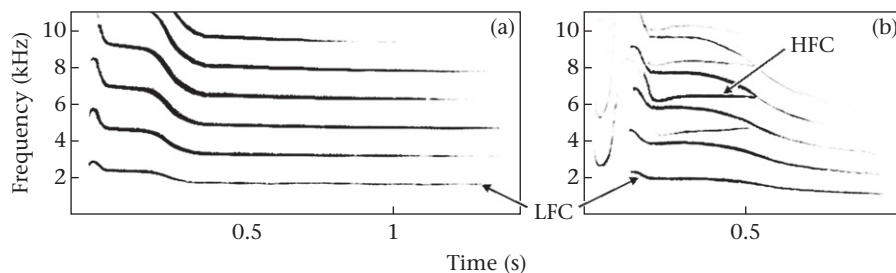


Figure 1. Spectrograms of a (a) monophonic and (b) biphonic call. Note the low-frequency component (LFC) with multiple harmonics in both sounds and the high-frequency component (HFC), which is not a harmonic of the LFC, in the biphonic call.

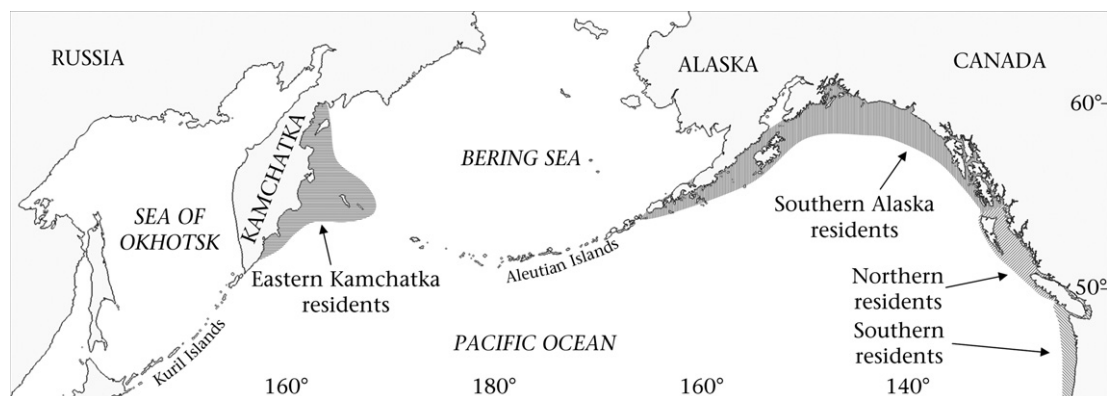


Figure 2. Map of the North Pacific Ocean showing the home ranges of the resident killer whale populations investigated in this study.

the result of an accumulation of random errors and innovations by vertical cultural transmission. First, we compared the diversity of monophonic and biphonic calls within these populations. Second, we compared the similarity of monophonic and biphonic calls between each pair of populations. Finally, we measured call diversity within predefined call categories, types and subtypes, and examined whether call diversity within these categories differed across populations.

METHODS

The Study Populations

Southern resident killer whales (referred to below as SR) inhabit the coastal waters of southern British Columbia and Washington State. The core area of this population comprises the waters off southern Vancouver Island, but they sometimes range south as far as Monterey Bay, California. The population consists of the single acoustic clan J-clan (Ford 1991), which comprised 86 individuals in 2010 (Ellifrit et al. 2011).

Northern resident killer whales (referred to below as NR) inhabit the coastal waters of central British Columbia to southeastern Alaska (approximately 48–58°N). The population comprises three acoustic clans: A-clan, G-clan and R-clan (Ford 1991).

Southern Alaska resident killer whales (referred to below as AR) range from southeastern Alaska to Kodiak Island (Matkin et al. 1999) and possibly into the Aleutian Islands and the Bering Sea (Allen & Angliss 2010). This population includes two acoustic clans: AB-clan and AD-clan (Yurk et al. 2002).

Eastern Kamchatka resident killer whales (referred to below as KR) are encountered along the eastern coast of Kamchatka peninsula from Avacha Gulf to Karaginsky Gulf and east to the Commander Islands. This population comprises three acoustic clans: Avacha clan, K19 clan and K20 clan (Filatova et al. 2007).

Some overlap exists in the ranges of the northeastern Pacific populations: SR overlap with NR in the waters off Vancouver Island, and NR overlap with AR in southeastern Alaska (Ford et al. 2000). Despite this overlap, members of different populations do not associate (Ford et al. 2000) or interbreed (Barrett-Lennard 2000).

Data Collection

Sound recordings used for this study were taken from existing long-term databases. Recordings of Southern residents were made from 1980 to 2009, Northern residents from 1988 to 1999, southern Alaska residents from 1984 to 2008, and eastern Kamchatka residents from 2000 to 2009. All recording systems had a flat frequency

response from at least 0.1 to 7 kHz, although in most cases this extended up to 20 kHz. We only included recordings that had sufficient frequency bandwidth and signal-to-noise ratio to display all call features clearly.

The recordings were made from small (4–9 m) boats. Photographs were taken during all recording sessions and compared to identification catalogues to confirm pod and population identity, as described in Bigg et al. (1990).

During designated field work for this study, whales were approached following procedures to minimize disturbance. To take photographs, the boat approached at slow speed at approximately 45° to the whale's course when they were travelling and left the group immediately after the photographs of all group members were obtained. To make sound recordings, we moved the boat 200–300 m ahead of the animals and waited until they passed us. If the whales were feeding or milling, we stayed at a distance of 100–300 m from them to avoid disturbing their natural behaviour. When the animals showed strong avoidance behaviour (e.g. change in the direction of movement away from the boat), we stopped our activities and kept a distance of at least 500 m from the group.

Acoustic and Statistical Analysis

We classified most calls according to existing catalogues (Ford 1987; Yurk et al. 2002; Filatova et al. 2004). For Alaska and Kamchatka, however, some call types were split and others were added according to the results of more recent studies (see Filatova et al. 2007; Yurk et al. 2010). Two calls from each type/subtype were used for the analysis, with some exclusion of rare call types for which we were not able to obtain at least two call samples of adequate quality. If a call type had no subtypes, two samples from this call type were used. For call types that fell into 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 the opposite ends of the structural continuum were selected. In total, 348 samples of 174 call types/subtypes were used for the analysis: 34 SR monophonic, 28 SR biphonic, 34 NR monophonic, 62 NR biphonic, 48 AR monophonic, 40 AR biphonic, 46 KR monophonic, 56 KR biphonic. Because our primary interest was call evolution, rare calls were of equal interest to common calls, and we did not weight call similarities by the frequency with which each call occurred.

Call contours were extracted using a custom-made MATLAB (The Mathworks, Inc., Natick, MA, U.S.A.) routine for manually

tracking frequency contours of each frequency component (available online at www.russianorca.org/sound_pro.htm). After the operator selected enough points to track all modulations of the contour from the fundamental frequency and harmonics, the algorithm performed the generalization of frequency points by dividing them by the band number and joined them into a set of frequency measurements of the fundamental frequency, which were then smoothed and interpolated to produce a vector of frequency measurements with the sampling interval 0.01 s (Fig. 3). For biphonic calls, contours were extracted from both the low- and the high-frequency components. Calls were identified as biphonic if they contained the overlapping high-frequency component (Fig. 1).

Similarity of calls was measured using dynamic time warping. Dynamic time warping is an algorithm developed for the automated recognition of human speech that allows limited compression and expansion of the time axis of a signal to maximize frequency overlap with a reference signal (e.g. Itakura 1975). For this study, we used a modified version of the warping algorithm of Deecke & Janik (2006). Percentage similarity of contours was calculated by dividing the smaller frequency value by the larger value at each point and multiplying by 100:

$$S(i) = \min[M(i), N(i)]/\max[M(i), N(i)] \times 100$$

where M is the reference contour and N the input contour. From the resulting similarity matrix, a cost matrix was constructed that kept a running tab on the similarities of the elements making up the curves while adding up these costs to give a final number called the 'similarity' between the contours. In our algorithm, each element of the cost matrix was obtained by comparing the weighted sum of similarity values from two columns and two rows distant from the weighted diagonal.

Because the algorithm of Deecke & Janik (2006) only allows expansion or compression of the time axis by a factor of three, the algorithm cannot be used to compare calls that differ in length by more than a factor of three. In this case, their similarity is considered 0%. This constraint biased the results in comparisons where many short or long contours were present in the repertoire of one population but not the other. To avoid this, we developed an additional algorithm that stretched the shorter contour through interpolation to make it one point longer than a third of the longer contour.

For each pair of contours within each sample set, we measured their relative similarity in frequency using this dynamic time-warping algorithm. By generating all possible pairwise comparisons between call samples from sample sets, we used N samples to generate $0.5 \times N \times (N - 1)$ comparisons. Since the correlation structure of this data set was unknown, we assumed that all data

points generated with the same sample were correlated. To achieve independence between the analysis units, we calculated the mean similarity for each call sample and used it as the unit of analysis for the further comparison.

For the measurements of intrapopulation call similarity, we calculated the similarity between each pair of calls from each major category (monophonic/biphonic) within each population.

For the comparison of intra- and interpopulation similarity of calls, we calculated the interpopulation similarity for each pair of populations as a set of similarity values between each call from the first population and each call from the second population. The median interpopulation similarity obtained by this method would depend not only on the true similarity between populations, but also on the intrapopulation call similarity of each population. To get a less biased interpopulation similarity measure, we divided the median interpopulation similarity by the median of the pooled intrapopulation similarity values for each pair of populations.

To measure call similarity within types and subtypes, we divided each of the six intrapopulation sets of similarity values into the following three subsets: (1) similarity values between pairs of calls from the different types; (2) similarity values between pairs of calls from the same type; and (3) similarity values between pairs of calls from the same subtype. To test for differences in the type/subtype threshold between monophonic and biphonic calls, the combined sets from all three populations were used. To test the differences in the type/subtype threshold across populations, subsets 2 and 3 were compared for the each pair of populations.

Statistical analysis was performed using R software (R Development Core Team 2010). Distribution of similarity values in most cases differed significantly from normal, so we used the nonparametric two-tailed Mann–Whitney U test for all statistical comparisons. Bonferroni correction was applied in cases of multiple pairwise comparisons. A Mantel matrix permutation test (Schnell et al. 1985) was used to estimate the correlation of call similarity and geographical distance between populations. Distances were approximate based on the core summer distribution, as the full extent of population ranges is unknown. In all statistical comparisons the significance level was accepted to be 0.05.

RESULTS

Intrapopulation Similarity of Monophonic and Biphonic Calls

We compared levels of similarity among monophonic calls with the levels of similarity among biphonic calls. Within each of the

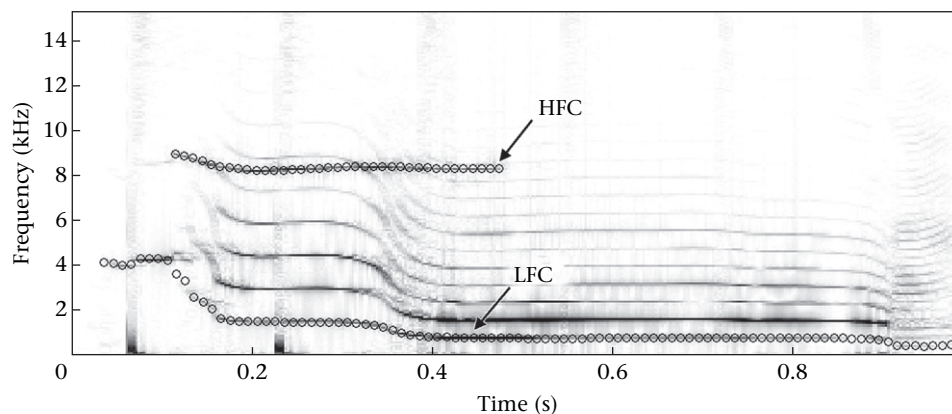


Figure 3. Example of frequency contours extracted from the low-frequency component (LFC) and the high-frequency component (HFC) of a K27 call from the eastern Kamchatka resident population.

four populations, call similarity was significantly lower among monophonic calls than it was among biphonic calls (monophonic versus biphonic: Mann–Whitney U test: KR: $U = 109$, $N_1 = 46$, $N_2 = 56$, $P < 0.0001$; AR: $U = 89$, $N_1 = 48$, $N_2 = 40$, $P < 0.0001$; NR: $U = 98$, $N_1 = 34$, $N_2 = 62$, $P < 0.0001$) except SR in which the difference was close to significant ($U = 338$, $N_1 = 34$, $N_2 = 28$, $P = 0.051$). Differences between populations within these two categories were less pronounced (Fig. 4), but also significant in all cases except AR versus KR and NR versus SR monophonic, and AR versus NR biphonic (Table 1).

SR had the highest median similarity (that is, the lowest call diversity) for monophonic calls followed by NR, AR and KR. KR had the highest median similarity for biphonic calls followed by AR, NR and SR. Including the high-frequency component in the analysis of biphonic calls increased the call similarity within all populations (Table 2). In this case, KR again had the highest median similarity, followed by NR, AR and SR.

Intra- and Interpopulation Call Similarity

We compared intra- and interpopulation similarity of monophonic and biphonic calls in each pair of populations (Table 3). Differences between intra- and interpopulation similarity of monophonic calls were nonsignificant for all comparisons but intrapopulation similarity of biphonic calls was significantly higher than interpopulation similarity for all comparisons (Table 3).

The fact that the interpopulation similarity of monophonic calls did not differ significantly from the intrapopulation similarity means that monophonic calls are equally diverse within and between populations. For this reason we did not compare the interpopulation similarity of monophonic calls in separate pairwise comparisons.

Interpopulation similarity of biphonic calls was highest between AR and KR, followed by KR–SR, NR–KR, NR–SR, SR–AR and NR–AR (Table 3). After we divided this value by the intrapopulation similarity to obtain a normalized similarity measure, SR and NR were the most similar, followed by NR–KR, SR–AR, AR–NR, AR–KR and SR–KR (Fig. 5a).

Interpopulation similarity of biphonic calls compared by analysing both the low-frequency and the high-frequency components was highest between KR and NR, followed by KR–AR, SR–AR, NR–AR,

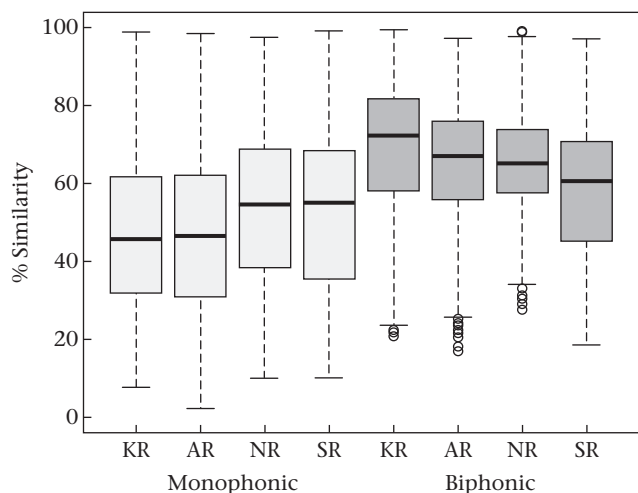


Figure 4. Intrapopulation time-warped frequency contour similarity between monophonic and biphonic calls of four resident killer whale populations. Horizontal lines represent medians, boxes interquartiles, whiskers the 90% confidence interval and circles outliers.

Table 1

Results of Mann–Whitney U test comparison of intrapopulation call similarity of monophonic and biphonic calls across different resident populations

	Populations	U	N_1	N_2	P
Monophonic	AR–KR	1068	48	46	0.789
	AR–NR	403	48	34	<0.001
	NR–KR	322	34	46	<0.001
	SR–NR	447	34	34	0.109
	SR–KR	416	34	46	<0.001
	SR–AR	429	34	48	<0.001
Biphonic	AR–KR	606	40	56	<0.001
	AR–NR	1205	40	62	0.814
	NR–KR	915	62	56	<0.001
	SR–NR	345	28	62	<0.001
	SR–KR	217	28	56	<0.001
	SR–AR	292	28	40	<0.001

SR–NR and SR–KR (Table 3). After we divided this value by the intrapopulation similarity, SR and AR were the most similar, followed by NR–KR, AR–NR, SR–NR, AR–KR and SR–KR (Fig. 5b). The correlation between approximate geographical distance and call similarity measured by the low-frequency component and by both the low-frequency and the high-frequency components was nonsignificant in both cases.

Call Similarity within Types and Subtypes

We measured the similarity between monophonic and biphonic calls from different types, calls from the same type, and calls from the same subtype for each population (Table 4). Similarities between calls from different types followed the pattern revealed by the comparison of call similarities within populations: similarities between monophonic calls were significantly lower than between biphonic calls ($U = 826$, $N_1 = 86$, $N_2 = 71$, $P < 0.0001$; Fig. 6). The difference in similarity between monophonic and biphonic calls within types and subtypes was nonsignificant, as were the differences in similarity of calls within types and subtypes across different populations.

DISCUSSION

The comparison of monophonic and biphonic calls from the four North Pacific resident killer whale populations revealed a pronounced difference in the amount of structural variation between monophonic and biphonic calls for each population. For all four populations, the diversity of monophonic calls was higher than that of biphonic calls. Differences between populations in the

Table 2

Median time-warped frequency contour similarity (%) between monophonic and biphonic call types of different resident killer whale populations in the North Pacific, calculated by the low-frequency component (LF) and by both low- and high-frequency components (LF + HF)

	Population	Median similarity
Monophonic	KR	45.75
	AR	46.58
	NR	54.47
	SR	55.01
Biphonic LF	KR	72.16
	AR	66.38
	NR	65.08
	SR	60.55
Biphonic LF+HF	KR	77.73
	AR	72.36
	NR	72.87
	SR	71.19

Table 3
Results of Mann–Whitney *U* test comparison of intra- and interpopulation similarity, median time-warped frequency contour similarity (%) and normalized median similarity between repertoires of different resident killer whale populations in the North Pacific

Populations	Mann–Whitney test				Similarity			
	<i>U</i>	<i>N</i> _{intra}	<i>N</i> _{inter}	<i>P</i>	Inter population	Intra population	Normalized inter population	
Monophonic	AR-KR	2188	94	48	0.771	45.62	46.23	NA
	AR-NR	1634	82	48	0.108	47.21	49.15	NA
	NR-KR	1727	80	46	0.569	49.12	48.41	NA
	SR-NR	909	68	34	0.080	52.31	54.66	NA
	SR-KR	1663	80	46	0.371	48.77	47.84	NA
Biphonic LF	SR-AR	1717	82	48	0.227	46.72	48.80	NA
	AR-KR	2037	96	56	<0.05	64.95	70.29	0.924
	AR-NR	1614	102	62	<0.001	60.71	65.43	0.928
	NR-KR	2825	118	62	<0.05	63.93	67.37	0.949
	SR-NR	1719	90	62	<0.001	62.14	64.48	0.964
Biphonic LF+HF	SR-KR	1480	84	56	<0.001	64.03	69.71	0.919
	SR-AR	837	68	40	<0.001	60.76	64.70	0.939
	AR-KR	1447	96	56	<0.001	70.83	76.25	0.929
	AR-NR	1590	102	62	<0.001	69.05	72.86	0.948
	NR-KR	2567	118	62	<0.01	71.58	74.78	0.957
	SR-NR	1455	90	62	<0.001	68.42	72.65	0.942
	SR-KR	647	84	56	<0.001	68.01	76.33	0.891
	SR-AR	874	68	40	<0.01	69.22	72.22	0.958

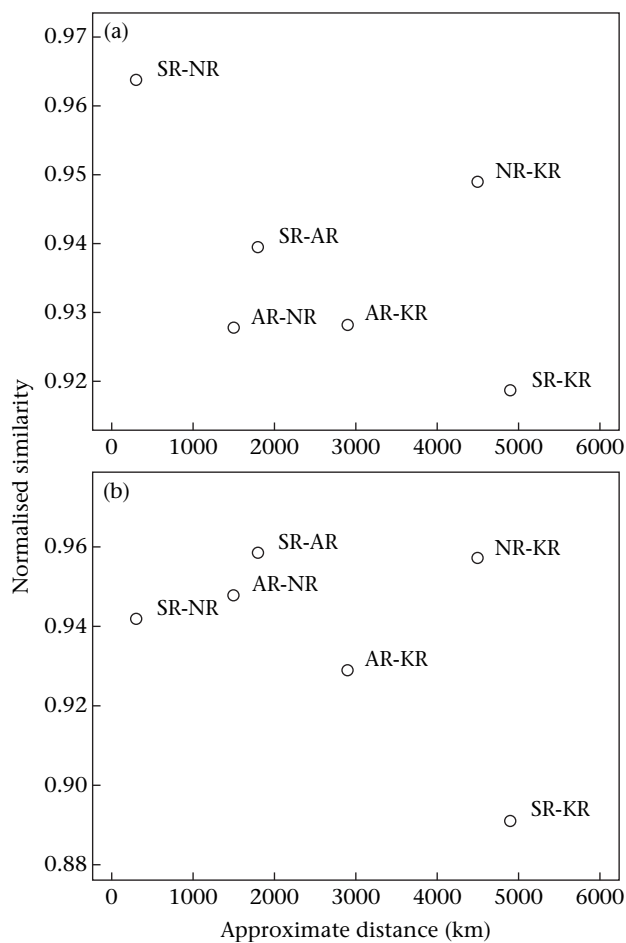


Figure 5. Normalized similarity (interpopulation divided by intrapopulation time-warped frequency contour similarity) of biphonic stereotyped call repertoires plotted by the approximate geographical distance between four resident killer whale populations. (a) Similarity measured by the low-frequency component; (b) similarity measured by both the low- and the high-frequency components.

diversity of call types from the corresponding category (monophonic or biphonic) were less pronounced. This result suggests that monophonic and biphonic calls have different principles of evolution that are shared among the different resident populations. This supports the suggestion that monophonic and biphonic calls are discrete categories.

Our results are consistent with previous studies, which found differences in source levels (Miller 2006), directionality (Miller 2002) and usage (Filatova et al. 2009) between monophonic and biphonic calls. Miller (2006) measured source levels of different killer whale sounds and showed that monophonic calls exhibited mean source levels lower than biphonic calls. This variation in intensity suggests that killer whale pulsed calls fall into two functional groups: 'long-range' biphonic calls with a mean estimated active space of 10–16 km in sea state zero and 'short-range' monophonic calls with an active space of 5–9 km (Miller 2006). Miller (2002) showed that the relative energy in the high-frequency components of biphonic calls was significantly greater when animals were oriented towards rather than away from the hydrophone array. It is likely that this difference could help listening whales to determine the direction of movement of a caller. Filatova et al. (2009) showed that the proportion of biphonic calls in the vocalizations of the eastern Kamchatka residents increased

Table 4
Median and mean (in parentheses) time-warped frequency contour similarity (%) between all calls within the vocal repertoire belonging to the different call types, between calls belonging to the same call type and calls of the same subtype for different resident killer whale populations in the North Pacific

	Population	Different types	Same types	Same subtypes
Monophonic	KR	44.99 (45.87)	89.19 (84.03)	91.40 (89.95)
	AR	45.53 (44.82)	90.44 (85.17)	91.83 (86.26)
	NR	51.40 (50.12)	85.34 (82.47)	90.79 (90.04)
	SR	53.51 (52.88)	91.56 (86.77)	92.84 (91.74)
Biphonic LF	KR	71.15 (68.34)	92.62 (91.26)	93.87 (92.04)
	AR	65.88 (63.61)	88.69 (84.4)	93.76 (92.17)
	NR	64.46 (64.97)	90.73 (89.1)	93.45 (91.45)
	SR	59.30 (57.16)	87.66 (76.44)	93.97 (91.26)
Biphonic LF+HF	KR	77.42 (75.05)	92.88 (91.43)	93.53 (92.51)
	AR	72.21 (70.97)	89.63 (89.66)	94.74 (93.97)
	NR	72.44 (71.74)	92.51 (90.69)	95.08 (92.58)
	SR	70.35 (69.25)	82.94 (83.79)	95.40 (93.35)

For biphonic calls, similarity of the low-frequency component and both components combined are given separately.

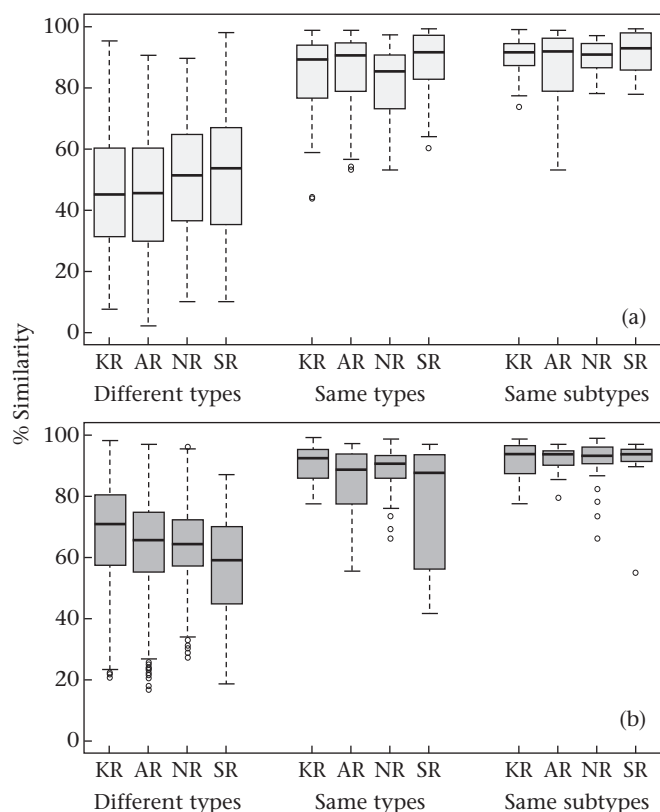


Figure 6. Time-warped frequency contour similarity between (a) monophonic and (b) biphonic calls from different call types, from the same types and from the same subtypes. Horizontal lines represent medians, boxes interquartiles, whiskers the 90% confidence interval and circles outliers.

when more than one pod was present in the area. The combination of these findings suggests that biphonic calls function mostly as group identifiers and help whales to define group affiliation and monitor the position of group members over long ranges. The function of monophonic calls is less clear, but like killer whale whistles (Thomsen et al. 2002), they may serve as short-range communication signals.

The similarity of diversity levels in monophonic and biphonic calls in four populations raises the question of whether the repertoire structure in resident killer whales is inherited genetically or culturally. It is now generally accepted that killer whales acquire the detailed structure of stereotyped calls in their repertoire through vocal learning (Bowles et al. 1988; Ford 1991; Deecke et al. 2000; Foote et al. 2006); however, other aspects of the vocal repertoire could be innate. Many songbirds learn their songs from fathers or neighbouring males, but despite some variation their song remains species-specific and retains a certain structure. Moreover, gradual differences in the function, usage and raw structural difference of the songs versus calls appear to be innate in songbirds (Marler 2004). The same is probably true for human languages: although languages are learned and therefore extremely diverse, there is some inherited structure common to all human languages (Pinker 1994; but see Evans & Levinson 2009).

The comparison of stereotyped call repertoires among populations produced rather unexpected results. The classical theory of call change through random drift predicts that the highest call similarity should occur in populations that are geographically close and therefore may share the recent common ancestors. However, our analysis revealed no direct correlation between call repertoire similarity and geographical distance (Fig. 5). There are several

possible explanations for this. First, it is possible that call evolution is too rapid to be phylogenetically meaningful on a population scale: call repertoires may be already so diverse that they retain no signs of common ancestry beyond the acoustic clan, and all similarities could be the result of random convergence. It has been suggested in resident killer whales that females choose mates with the most dissimilar dialects (Barrett-Lennard 2000). This would drive sexual selection towards faster call evolution to provide greater resolution in the recognition of kin (e.g. allowing discrimination between first- and second-degree cousins). The opposite selection force may be caused by the need of killer whale groups to possess markers of population identity. Biphonic calls of all three clans of the eastern Kamchatka resident population have certain frequency features in common (Filatova et al. 2007). In southern Alaska resident killer whales, distinct lower frequency syllables are shared by clans within this population (Yurk 2005). In Northern residents, most stereotyped whistle types are structurally identical in two of the three acoustic clans (Riesch et al. 2006). Southern and Northern resident populations from British Columbia and Washington State share a substantial part of their geographical range but retain strong behavioural reproductive isolation, although it is not obvious if the isolation is based on acoustic or other cues.

The interaction of these opposite evolutionary forces (diversifying and standardizing) may lead to the 'maximum diversity within the permitted range', where the 'range' is represented by vocal population markers. This scenario is consistent with our finding that the diversity of biphonic and monophonic calls between populations was very similar to that within populations, suggesting that every population had already reached some optimal level of diversity for each call category. Moreover, the intra- and interpopulation diversity of monophonic calls did not differ significantly, suggesting that for monophonic calls the pressure to standardize is lower.

The diversity of monophonic and biphonic calls appeared to be negatively correlated. This pattern was also related to the population size: monophonic calls were more diverse and biphonic calls less diverse in larger populations. Although the SR population of about 86 animals (Ellifrit et al. 2011) is the smallest of the four populations, it has the highest diversity of biphonic calls and the lowest diversity of monophonic calls, followed by the NR with 261 animals (Ellis et al. 2011), KR (650 individuals; T. V. Ivkovich, unpublished data) and AR (more than 1000 individuals; Allen & Angliss 2010). In human languages, speaker population size was shown to be a significant predictor of phonemic diversity, with a smaller population size predicting smaller overall phoneme inventories (Atkinson 2011). Our results demonstrate that the diversity of monophonic calls follows the same pattern as phonemic diversity in human languages, which suggests that their evolution is driven by the same stochastic processes that also affect human phonemes (Labov 2001). By contrast, diversity in biphonic calls shows the opposite pattern. This may be caused by the fact that in larger populations the inbreeding risk is lower, and the need for unique vocal population markers is higher, which shifts the balance of diversifying and standardizing forces in favour of the latter. Therefore, we suggest that the evolution of both monophonic and biphonic calls is caused by an interaction between stochastic processes and directional selection, but the relative effect of directional selection is greater for biphonic calls.

An alternative hypothesis suggests that call similarity between populations does reflect their ancestry, but the ancestry is not directly correlated with geographical distance. Killer whales are highly mobile and phylogeographical structure could very easily be disturbed by long-distance movements. For example, genetic studies showed that the resident killer whales of the North Pacific are more related to the North Atlantic killer whales than to

sympatric transient populations (Morin et al. 2010). This suggests a complex and multistage history of population formation and colonization of the North Pacific Ocean. Moreover, the southern Alaska resident population possesses two haplotypes of the control region of mitochondrial DNA; one matches the single haplotype of the Northern resident population, the other the single haplotype of the Southern resident population (Barrett-Lennard 2000) and the eastern Kamchatkan resident population (Hoelzel et al. 2007). It is possible that the AR population retains genetic diversity of an ancestral population, while the NR, SR and KR populations have reduced diversity owing to a founder effect. Founder effects have been shown to reduce the diversity of syllables in birdsong (e.g. Baker & Jenkins 1987) and phonemic diversity in human languages (e.g. Atkinson 2011). This is in agreement with the reduced diversity in KR biphonic and NR and SR monophonic calls, but it is in contradiction to the high diversity in SR biphonic calls. However, the information currently available does not allow testing of this hypothesis, and further study of genetic and acoustic similarity is required to reveal the population history of North Pacific killer whales. A comparison of repertoire similarity with mitochondrial haplotype similarity across populations could provide an important insight into population history and dialect evolution.

Similarities of biphonic stereotyped call repertoires measured by the low-frequency component and by both the low- and the high-frequency components were generally not consistent, although they agreed in some aspects (Fig. 5a, b). It appears that the evolution of low-frequency and high-frequency components of biphonic calls is not always parallel, suggesting that it is influenced by different factors. The inclusion of the high-frequency component in the analysis of the intrapopulation similarity always increased the similarity values (Table 1), indicating that the high-frequency component is less diverse within populations than the low-frequency component. It is possible that the high-frequency component may be a more stable and reliable marker of population relatedness than the more diverse and variable low-frequency component. Alternatively, the stability of the high-frequency component may be related to the radiation pattern of biphonic calls. The high-frequency component is more directional than the low-frequency component (Miller 2002), so it is clearly audible only when the signaller is oriented towards the receiver. Therefore, the more omnidirectional low-frequency component would appear to be more useful for the long-range recognition of pod members. This may result in the higher contour variability in the low-frequency component to make the call more discernible. Consequently, the type-specific variation in the contour shape of the high-frequency component may be redundant because the call type is already identifiable by the low-frequency component. In that case, the function of the high-frequency component may be restricted to marking the orientation of a signaller while the low-frequency component encodes pod membership.

The diversity of calls within type and subtype categories had a high degree of correspondence between populations, despite the fact that the initial categorizations were made by different researchers (Ford 1991; Yurk et al. 2002; Filatova et al. 2004). Unlike the graded vocalizations of some other odontocetes (e.g. Weilgart & Whitehead 1990), killer whale pulsed calls are highly stereotyped showing little variation within call types, but there are consistent differences between them. Differences in type/subtype diversity between populations were nonsignificant. Moreover, the difference in diversity within types and subtypes of calls was nonsignificant between monophonic and biphonic calls. This suggests that the observers had rather similar ideas of what they meant by call type and subtype. No one has yet provided a satisfactory definition of 'call type' in killer whales, and the most common description of the categorization process refers to 'the distinctive audible characteristics of the calls'. Call structure changes subtly but

continuously over time (Deecke et al. 2000), and call type divergence is thought to be a gradual process (Bigg et al. 1990; Ford 1991). Consequently, calls of different matrilineages can differ to a greater or lesser extent, and it is not always obvious where to place the border. Deecke & Janik (2006) performed an automatic neural network categorization of calls recorded from North Pacific transient killer whales and identified eight monophonic and five biphonic call types. Our study provides an equally objective approach to call categorization by comparing contours and using a threshold similarity level to delineate call types.

In conclusion, our results suggest that divergence of vocal repertoires may not result solely from the accumulation of random errors and innovations by vertical cultural transmission. Repertoire diversity appears to be related to the population size: monophonic calls are more diverse and biphonic calls less diverse in larger populations. Call similarity across populations does not correspond with geographical distance. All this suggests that dialect evolution is a complex process subject to an interaction between directional and nondirectional agents of structural change. These may include opposing selective forces to diversify and standardize vocal repertoires, horizontal transmission of calls, as well as random drift.

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