Bioacoustics
The International Journal of Animal Sound and its Recording, 2007, Vol. 16, pp. 261–280
0952-4622/07 $10

THE STRUCTURE OF THE DISCRETE CALL REPERTOIRE OF KILLER WHALES *ORCINUS ORCA* FROM SOUTHEAST KAMCHATKA

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ABSTRACT

The problem of categorization arises in any classification system because classes should be discrete while the characteristics of most natural objects and aspects of nature are more or less gradual. In systematics, this problem usually is solved by creating several levels of categories, such as class, order, family, genus and species. In the existing killer whale discrete call classification, only two levels occur – call type and call subtype. In this paper we describe structural categories at a broader level than call type in the discrete sounds of killer whales and compare these categories between and within vocal clans in a community of resident killer whales from Southeast Kamchatka, Russian Far East, and also with killer whales outside this community. We found four main classes of discrete calls in the repertoire of resident killer whales from Southeast Kamchatka. The calls of Southeast Kamchatka transient killer whales and Sakhalin killer whales do not fall into these classes. This suggests that the resident killer whale community from Southeast Kamchatka has some rules defining the structure of calls which are typical for this community. Consequently, all resident killer whales from Southeast Kamchatka can be said to share the same vocal tradition.

Keywords: Killer Whale, *Orcinus orca*, calls, classification, Kamchatka

INTRODUCTION

The term "vocal learning" has been used to describe the influence of learning on a variety of different aspects of vocal communication (Janik & Slater 1997, 2000). Learning can affect the generation of sounds, their usage and their comprehension. Vocal learning refers only to learning sounds, that is, to instances where the vocalizations themselves are modified in form as a result of exposure to vocalizations from other individuals (Janik & Slater 1997). Vocal learning is common among birds (Kroodsma & Miller 1996) but less studied and probably rare for mammals. Among mammals vocal learning was shown only for cetaceans (Caldwell & Caldwell 1972; Richards *et al.* 1984; Payne & Payne 1985; Janik & Slater 1997; Rendell & Whitehead 2001), true seals (Phocidae) (Ralls *et al.* 1985; Morrice *et al.* 1994), some bats (Esser & Schmidt 1989; Jones & Ransome 1993; Boughman 1998), and humans. Geographic variations in acoustic repertoires typical for many terrestrial mammals are usually a result of geographic isolation and pass from generation to generation genetically, rather than by vocal learning (Nikol'skii 1980; Conner 1982).

The specific vocal traditions of sympatric or neighbouring groups or sub-populations of mammals are called dialects (Conner 1982). Ford (1991) showed that killer whale groups in the Northeast Pacific have unique vocal repertoires of discrete call types and documented various levels of sharing of discrete call types between groups: certain groups shared a number of discrete call types and others had entirely different call repertoires.

The basic unit of the Northeast Pacific resident killer whale's social organization is the "matriline", which consists of a living female and several generations of her offspring (Bigg *et al.* 1990). "Pods" were previously defined as matrilines observed together on 50% or more of observation days (Bigg *et al.* 1990). However, later association analyses have revealed considerable fluidity in the bonds among matrilines across years (Ford & Ellis 2002). Thus, "pod" is defined mostly acoustically as a group of whales that share a unique repertoire of discrete calls and have social bonds (Ford 1991). Ford (1991) referred to each set of pods which shared a number of discrete call types as a "clan".

The existence of vocal dialects was also shown for killer whales in the Northeast Atlantic (Moore 1988; Strager 1995) and the Northwest Pacific (Filatova *et al.* 2003). Killer whale dialects appear to be vocally learned because a calf shares only the repertoire of its mother's pod, although most calves are fathered by non-pod males (Barrett-Lennard 2000). In captivity, killer whales are known to be able to copy calls of conspecifics from other groups and populations (Bain 1986; Ford 1991).

Most studies of killer whale acoustic behaviour have been made in the coastal waters of the Northeast Pacific where two main ecotypes of killer whales exist: resident (fish-eating) and transient (mammal-eating). These two ecotypes differ greatly in vocal activity, as well as in ecology, social organization and genetics (Ford *et al.* 1998; Baird & Whitehead 2000). Transient (mammal-eating) killer whales are less vocal than resident (Morton 1990; Deecke *et al.* 2005), because their prey probably can detect killer whale calls and respond with avoidance behaviour. Transients usually produce calls only after a marine mammal kill or during surface-active behaviour, while residents are much more vocal during most activity states (Deecke *et al*. 2005).

Killer whale sounds include whistles, echolocation clicks and pulsed calls. The traditional model for classifying dolphin vocalizations assumes that these categories are discrete; however, click trains and whistles may be at opposite ends of a continuum with pulsed sounds being intermediate (Murray *et al*. 2003). Most killer whale pulsed signals fall into discrete call types with higher or lesser variability inside them (Ford 1984). There are also some variable calls that could not be arranged into clearly defined structural categories, and aberrant calls include signals that were based clearly on a discrete call format, but were highly modified or distorted in structure (Ford 1989).

Call type categorisation is critical to killer whale acoustic research. The main units of the Northeast Pacific resident killer whale social system – "pod" and "clan" – are defined by a repertoire of discrete call types. Thus, the researcher's decision to categorize some calls as the same type or to make them different types can alter the whole picture of killer whale society. However, no one has yet provided a satisfactory definition of "call type" in killer whales, and the most common description of the categorisation process refers to "the distinctive audible characteristics of the calls" – a subjective approach. Although the subjective approach has been approved through several studies (Deecke *et al*. 1999; Janik 1999; Jones *et al*. 2001), there remains no consistent method of call type classification.

Calls change continuously over time (Deecke *et al*. 2000) and call type divergence is a gradual process (Bigg *et al*. 1990; Ford 1991). Consequently, calls of different matrilines can differ to a greater or lesser extent and it is not always obvious where to erect the border. Moreover, the existing approach disables dialect comparisons at a level higher than intra-clan, because there can be no comparison at all if call types are considered totally different.

The problem of categorization arises in any classification system because classification should be discrete while the characteristics of most natural objects and aspects of nature are more or less gradual. In systematics, usually this problem is solved by creating several levels of categories, such as class, order, family, genus and species. In the existing killer whale discrete call classification, only two levels occur – call type and call subtype (Ford 1984; Yurk 2002).

In this paper we put call types into separate and distinguishable structural categories – call classes – and compare them between and within vocal clans in a community of resident killer whales from Southeast Kamchatka, Russian Far East, and also with killer whales outside of this community.

METHODS

Data Collection

Recordings from Southeast Kamchatka killer whales were collected as part of the Far East Russia Orca Project (FEROP) in Avacha Gulf, Kamchatka, in 2001-2006. A recording of killer whales from the Sakhalin area was made in September 1999 in the Piltun Bay region of Sakhalin Island (tape provided by the Marine Biology Institute, Vladivostok) (Figure 1).

The underwater sound recordings were made from a 4 m inflatable boat. For the recording we moved the boat approximately 500m ahead of the animals and waited until they passed us. If the whales were feeding or milling, we stayed at a distance of 100-500m from them to avoid disturbing their natural behaviour. In cases when the whales tried to avoid the boat, we stopped our activities and kept a distance of at least 500 m from the group.The photographic identification method (Bigg *et al*. 1983) was used for identifying individual killer whales and groups. To make photographs, we approached the whales to a distance of 30-70m when they were traveling, or moved the boat 200-300m ahead of the animals and waited until they passed us. A Canon EOS 1D digital camera and 100-400 mm lens were used for taking the photographs.

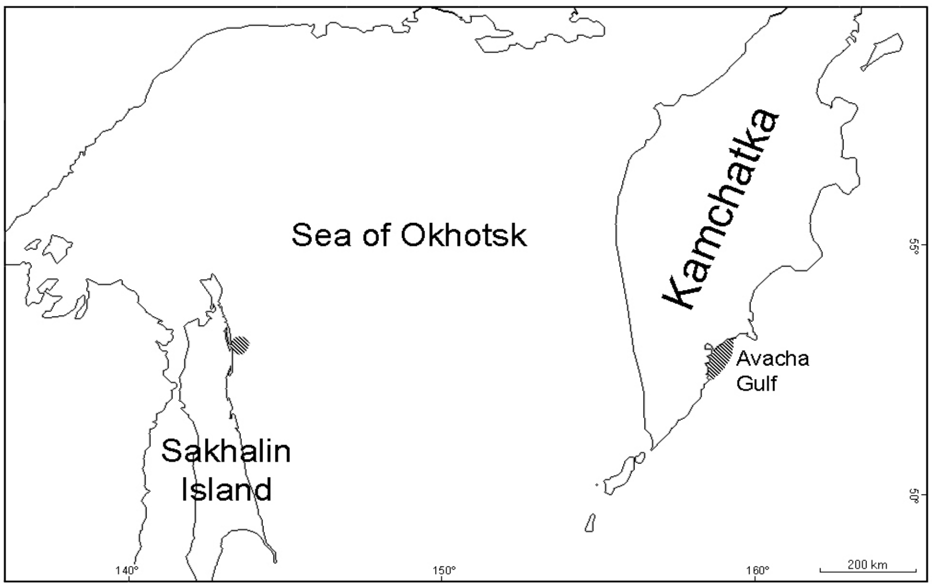

Figure 1. Map of the study area. Places where recordings were made are shown in the shaded areas.

Sound recordings were made on a Sony TCD-D100 DAT recorder. Recordings were obtained using a sampling frequency of 48 kHz (recordings of Sakhalin killer whales were made using a sampling frequency of 22.05 kHz). For omnidirectional recording we used an Offshore Acoustics hydrophone with a bandwidth of 10 Hz to 40 kHz and a sensitivity of −154 dB ± 4 dB re 1V/μPa at 100 Hz (6 Hz to 14 kHz ±1-3dB, 5 Hz to 40 kHz ±1-10dB). It was lowered to a depth of 5-10m. We used a stereo mobile hydrophone system for finding the direction of underwater sounds (Filatova *et al.* 2006a).

Study populations

48 stable groups of fish-eating killer whales were distinguished in the Avacha Gulf area (Ivkovich 2006). 29 "local groups" came to the gulf regularly while 15 "strange groups" visited the area only from time to time (Ivkovich 2006). The ecological specialization and social structure of all these whales appear similar to that of the Northeast Pacific resident killer whales (Tarasyan *et al.* 2005; Ivkovich 2006). Besides this, 7 groups of killer whales were found to have features similar to transient (mammal-eating) killer whales. They probably represent a separate population because they differed morphologically from fish-eating killer whales and did not intermix with them (Ivkovich 2006).

Kamchatka resident killer whales have group-specific vocal dialects (Filatova *et al.* 2003). In the Avacha Gulf area there are at least three acoustic clans of resident killer whales – "Avacha clan", "K19 clan" and "K20 clan" (Filatova *et al.* 2006b). Avacha clan, consisting of more than 200 whales in at least 12 pods, is the most common.

We have no information about the status of killer whales from the Sakhalin area.

Sound analysis

Discrete call classification was based on the existing catalogue (Filatova *et al.* 2004) with some additional call types found in groups rarely visiting the area. We initially divided all calls into two main categories. The first category includes sounds with an overlapping high-frequency component, or biphonic sounds, hereafter indicated with the prefix "Biph". The second category includes sounds without an overlapping high-frequency component, the monophonic sounds, indicated by the prefix "Moph". All call analyses were made with Avisoft SASLab Pro software (R. Specht). Spectrograms were created using a Hamming window, FFT-length 1024 points, frame 100%, and overlap 87.5%. These settings provided a bandwidth of 61 Hz, frequency resolution of 47 Hz and time resolution of 2.7 ms.

To measure sound parameters on the spectrogram we used the "automatic parameter measurements" option built into Avisoft SASLab Pro to extract the peak frequency values. After removing background noise and non-target parts of the sound with the eraser cursor, we automatically measured the peak frequency at 6 regularly spaced points. Then we calculated the fundamental frequency (frequency of the lowest band) by dividing the measured peak frequency by the number of measured band. For the biphonic sounds we measured both a low frequency component and an overlapping high-frequency component (Figure 2). Below we refer to the fundamental frequency values from a low frequency component as *lfc1-lfc6,* and to the frequency values from an overlapping high-frequency component as *hfc1-hfc6* (the number indicates at which of 6 regularly spaced points the measurement was done).

Many calls contained several abrupt frequency shifts which allowed the call to be divided into different syllables, or parts of the call, as defined by Yurk (2005). Different call subtypes can contain

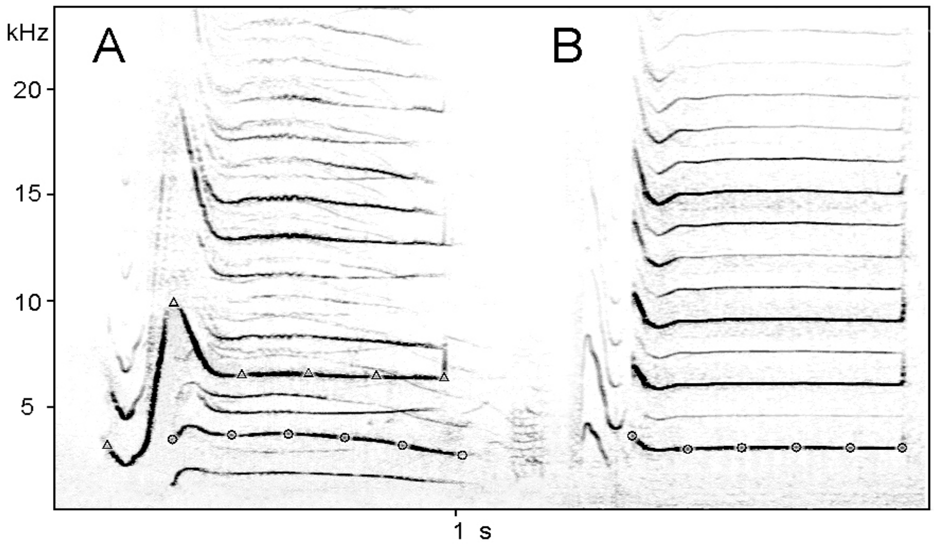

Figure 2. Measurements made on a sonogram. A. Biphonic sound: measurements from a low frequency component are marked with circles, and measurements from an overlapping high-frequency component are marked with triangles. Measurements from a low frequency component are made from the second band, because it carries more energy than the first band. To find the fundamental frequency (the frequency of the first band), these measurements were divided by two. B. Monophonic sound: measurements are marked with circles.

different numbers of syllables. In such complex calls, measurements were made for the main syllable which was present in all subtypes of a particular type and which was the longest in most of the subtypes.

Statistical analyses

We applied the nonparametric Mann-Whitney U-test to compare the corresponding measurements of calls between classes within categories (e.g. *lfc1* of Biph1 class calls with *lfc1* of Biph2 class calls and so on). We performed forward stepwise discriminant function analysis to find the variables that contributed mostly to the discrimination of classes. All statistical analyses were made in Statistica 6.0 (StatSoft, Inc).

RESULTS

We measured 344 sounds with an overlapping high-frequency component and 86 sounds without an overlapping high-frequency component from the Southeast Kamchatka resident killer whales; 50 sounds with an overlapping high-frequency component from the Sakhalin killer whales; and 20 sounds with an overlapping high-frequency component from Southeast Kamchatka transient killer whales.

Calls with overlapping high-frequency component

Two main classes of biphonic calls were defined in the repertoire of killer whales from Southeast Kamchatka (Figure 3). These classes differ by the frequency of both high-frequency and low-frequency components (Table 1). The Mann-Whitney *U*-test showed significant differences in all corresponding measured parameters between these classes (for all $p<0.001$).

Forward stepwise discriminant function analysis showed 100% correct assignment to these classes. The first discrimination function accounted for 100% of the observed variance. The first two variables that contributed most to the discrimination of classes were *lfc2* and *hfc4*. The scatterplot of these variables clearly shows the differences between these two classes (Figure 4). Class Biph1 is more various than class Biph2, but the classes are obviously separated from each other.

Biphonic calls of transient killer whales from Southeast Kamchatka and some of the biphonic calls of the Sakhalin killer whales (Figure 5) do not fall into these two classes. The scatterplot (Figure 6) clearly shows that the calls of transient killer whales from

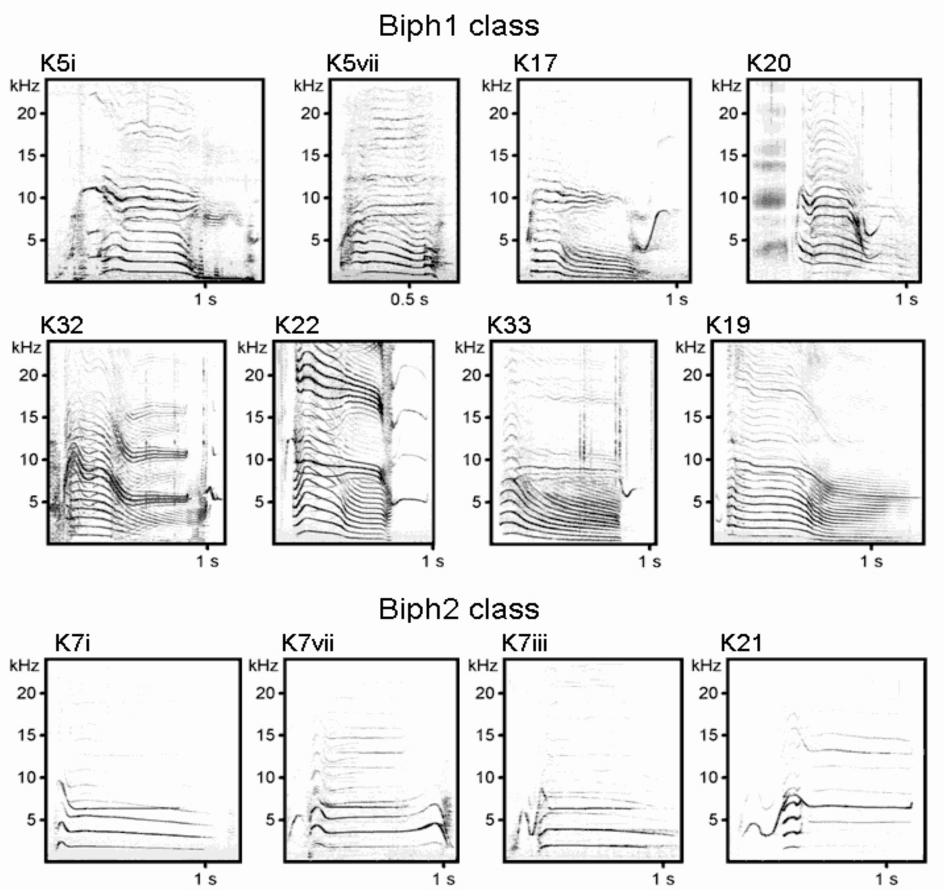

Figure 3. Examples of biphonic discrete calls from the repertoire of resident killer whales from Southeast Kamchatka.

Southeast Kamchatka and the Sakhalin killer whales could not be divided into classes typical for Southeast Kamchatka resident killer whales.

Calls without an overlapping high-frequency component

Calls without an overlapping high-frequency component could also be roughly divided into two main classes, but they are not so distinctive as in biphonic calls. The Mann-Whitney *U*-test showed significant differences in all corresponding measured parameters between these classes (for all $p<0.001$). The first class Moph1 contains squeak-like discrete sounds (Figure 7, Table 2). These sounds often have an upsweep contour resulting in a higher-frequency terminal part (Figure 7, K1i) which can be even longer than the squeak-like part (Figure

TABLE 1

Frequency (*mean*±SD, Hz) of high-frequency and low-frequency components of Biph1 and Biph2 class calls.

	Biph1	Biph2
lfc1	1183 ± 243	1960 ± 274
lfc2	1096 ± 191	1833 ± 138
lfc3	966 ± 244	1807 ± 151
lfc4	836 ± 281	1739 ± 153
lfc5	688 ± 304	1607 ± 197
lfc6	498 ± 259	1310 ± 282
hfc1	7241 ± 2376	5257 ± 2211
hfc2	9142 ± 1160	6441 ± 1428
hfc3	9171 ± 860	6380 ± 286
hfc4	9090 ± 866	6378 ± 284
hfc5	8755 ± 1152	6337 ± 282
hfc6	7935 ± 1874	6335 ± 298

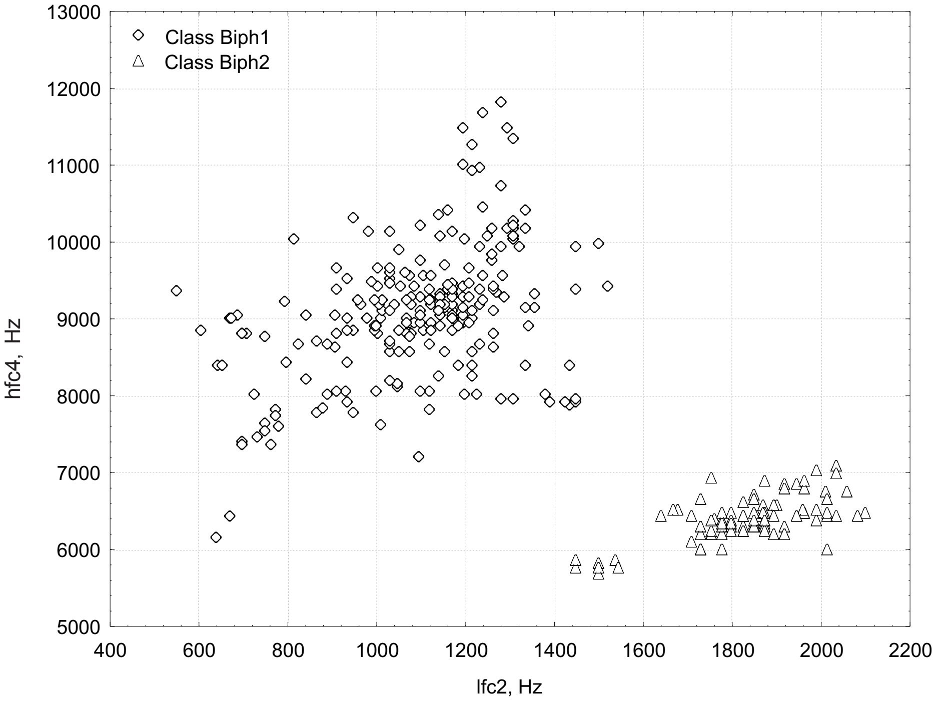

Figure 4. Classes Biph1 and Biph2 are clearly distinctive on the scatterplot of *lfc2* and *hfc4*.

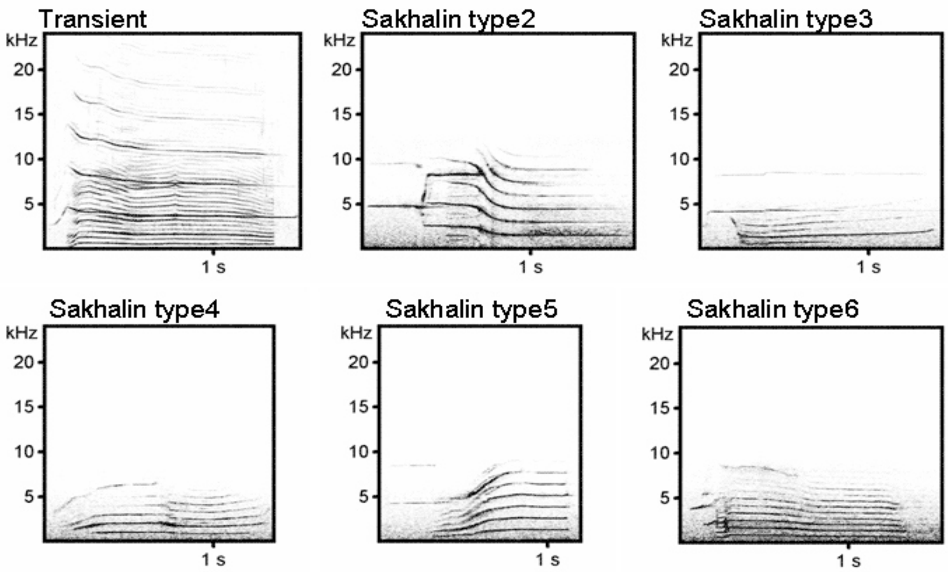

Figure 5. Examples of biphonic discrete calls of transient killer whales from Southeast Kamchatka and killer whales from the Sakhalin region.

7, K13). The second class Moph2 contains rather high-frequency calls (Table 2) which usually have weak frequency modulation (Figure 7, K3, K10). There is also one call type that does not belong to any of these classes. It is K11 which looks more like a whistle than a call (Figure 7, K11).

Repertoire structure and group dialects

None of the groups from the Southeast Kamchatka resident community has exclusively either Biph or Moph classes in their repertoire of stereotyped calls. The dialect of each group always contains Biph1 class calls and squeak-like Moph1 class calls. Besides this, all groups from Avacha clan produce Biph2 class calls, and some of them additionally produce Moph2 class calls. Other clans do not produce Biph2 class calls but produce Moph2 class calls.

The Biph1 class calls of Avacha clan include eight call types (Table 3). K5 (Figure 5) is the most common and typical call type for this clan. It is shared by most pods, but each pod has its own variety of this call type, producing at least eight subtypes in all.

The K14 call type has a frequency contour with rapid up-and-down pitch modulations. This type may be similar to “excitement calls” of the Northeast Pacific killer whales described by Ford (1989). It is clear that the K14 call type is closely related with the K5 type

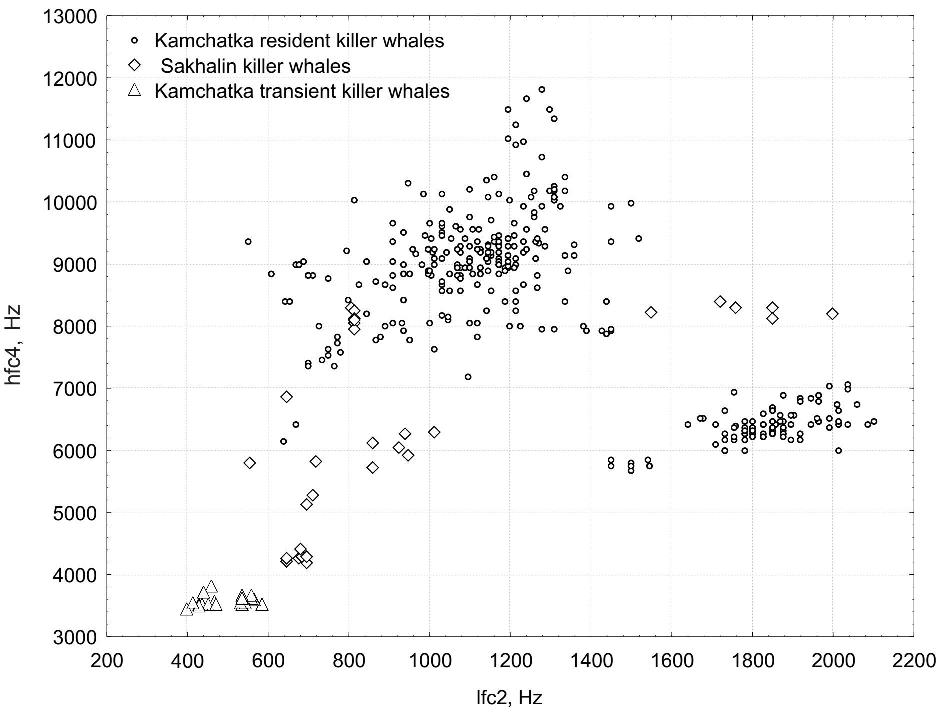

Figure 6. Calls of transient killer whales from Southeast Kamchatka and killer whales from the Sakhalin region could not be divided into classes typical for Southeast Kamchatka resident killer whales on the scatterplot of *lfc2* and *hfc4*.

and probably it is just an "excited form" of K5. The appearance of the K5 call differs depending on group dialect, and the appearance of the K14 call in each group is similar to the K5 call of this group (Figure 8). On the other hand, K14 occurs as a separate stereotyped call type, so it is debatable whether K14 is a discrete type or just a form of the K5 type.

Biph1 class calls of K19 clan include three call types (Table 3). To date we recognize only two pods in this clan – Gera pod and Zorro pod. K19 and K22 types are produced by Zorro pod, and K33 type is typical for Gera pod.

We found only one pod in K20 clan. The K20 call type is a typical Biph1 class call for this pod.

Biph2 class calls are shared only by the pods of Avacha clan (Table 3). K7 is a common, typical call type for this clan. Each pod produces at least one subtype like this. The K21 type is similar to the K7 type but it has a very short low-frequency component, while an overlapping high-frequency component is just the same as in K7 (Figure 5).

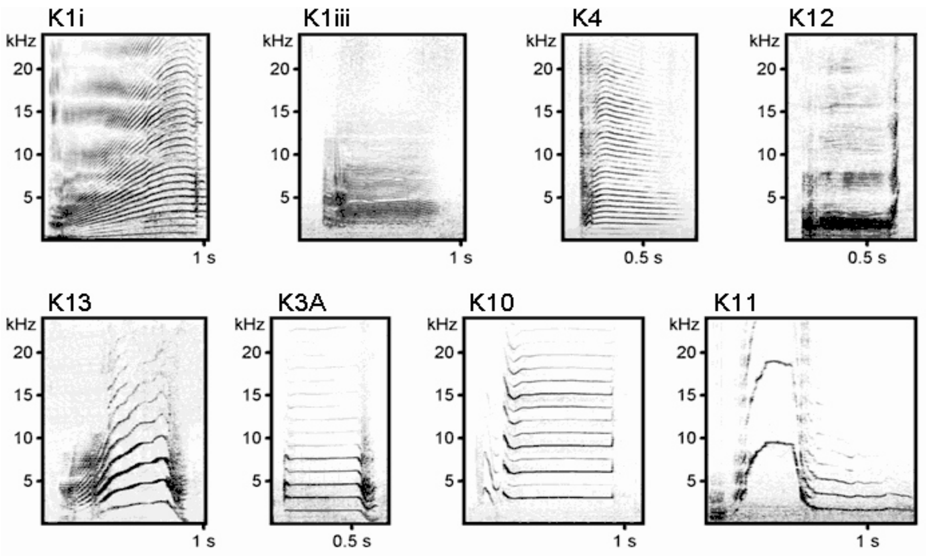

Figure 7. Examples of discrete calls without an overlapping high-frequency component from the repertoire of resident killer whales from Southeast Kamchatka (Moph1 class: K1i, K1iii, K4, K12, K13; Moph2 class: K3A, K10).

TABLE 2

Frequency (mean±SD, Hz) of low-frequency component of Moph1 and Moph2 class calls.

	Moph1	Moph2
lfc1	356 ± 194	2152 ± 1066
lfc2	560 ± 368	2110 ± 841
lfc3	694 ± 453	2104 ± 845
lfc4	750 ± 510	2090 ± 834
lfc5	841 ± 585	2083 ± 824
lfc6	819 ± 437	1955 ± 922

Moph1 class calls include 11 types of the squeak-like sounds (Table 3). K1 and K12 are the most common types shared by all pods of Avacha clan. Moph1 class calls of K19 clan include the K31 type shared by both pods and the K34 type produced only by Zorro pod. K30 is the only Moph1 class call recorded from K20 clan. The K28 and K38 calls were recorded from the groups with unknown status, which were encountered only once or twice.

Moph2 class calls include K3, K10 and K37 call types. The K3 type is produced by K19 and K20 clans, but each clan has its own version of this type. Initially we considered them to be subtypes of

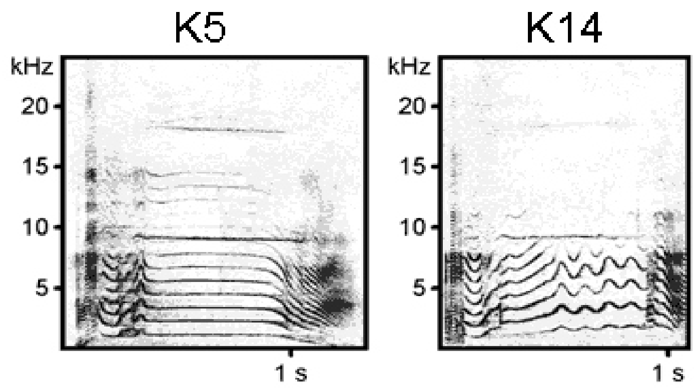

Figure 8. Call types K5 and K14 from the dialect of Moloko pod.

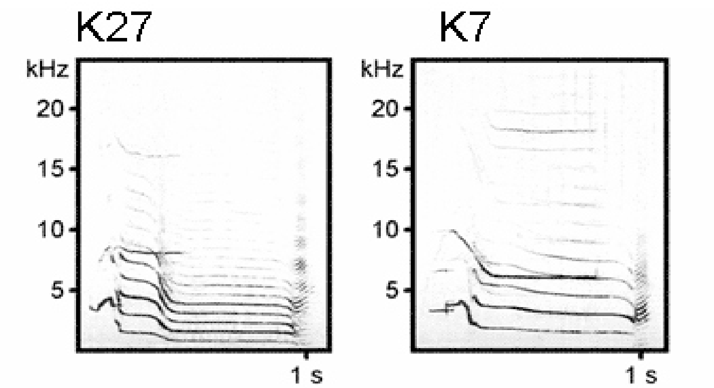

Figure 9. Call types K7 (Biph2 class call) and K27 (Biph1 class call) from the dialect of Hooky pod.

one type, but later we recognized them as two separate call types. The K10 call type is shared by the several Avacha clan pods (Table 3). K37 type was recorded from the group with unknown status, which was encountered only once.

The whistle-like K11 call type which does not belong to any of these classes is shared by the three Avacha clan pods (Table 3).

Calls from certain classes often display some similarity within group dialects. It appears that each group has its own "dialect form" of call, which can be applied to different call classes. This phenomenon gives additional evidence that call division into classes is natural, because it suggests that the whales themselves distinguish between these classes. For example, in the dialect of Hooky pod, call type K7 (Biph2 class call) is very similar to call type K27 (Biph1 class call). The only difference in the low-frequency component is that K7

TABLE 3

Call types from different classes produced by pods and clans of Southeast Kamchatka resident killer whales.

Clan		Avacha												K19		K20
Pod		Drkin	Moloko	KB	Chizh	AV2	Lucky	Kaplya	Ikar	0209	Nemo	Hooky	AV32	Gera	Zorro	K20
Biph1 class	K5	+	+	+	+	+	+	+	+	+	+					
	K6											+				
	K14		+		+				+	+		+	+			
	K17									+	+					
	K23	+	+													
	K24			+	+											
	K26												+			
	K27											+				
	K19														+	
	K20															+
	K22														+	
	K33													+		
Biph2 class	K7	+	+	+	+	+	+	+	+	+	+	+	+			
	K21			+			+									
Moph1 class	K1	+	+	+	+	+	+	+	+	+	+	+	+			
	K4	+	+	+	+			+								
	K8			+												
	K12	+	+	+	+	+	+	+	+	+	+	+	+			
	K13			+						+						
	K29		+	+	+	+			+			+				
	K30															+
	K31													+	+	
	K34														+	
Moph2 class	K3A															+
	K3B													+	+	
	K10					+		+	+	+	+					
	K11								+	+	+					

does not have lowered pitch in the middle part (Figure 9). But the frequency of the high-frequency component in K7 is typical for Biph2 class calls, and, in K27, for Biph1 class calls.

DISCUSSION

Communicative functions of different call classes

None of the killer whale groups which we have analyzed in the Russian Far East has exclusively either biphonic or monophonic classes in their repertoire of discrete calls. This points to the real significance of this structural classification. The dialect of each group always contains two different call classes: Biph1 class calls and squeak-like Moph1 class calls. This means that both of these two classes might have their own communicative function. In Northeast Pacific resident killer whales, Miller (2006) showed that source levels differ across types of vocal signals. Within the discrete calls, the low frequency ones without an overlapping high frequency component exhibited the lowest mean apparent source level, whereas high frequency calls containing an overlapping high frequency component showed the highest source levels. Miller (2006) suggests that the acoustic repertoire of Northeast Pacific killer whales can be partitioned into two primary groups: "long-range" high-frequency calls which contain a high-frequency component, and "short-range" low-frequency sounds without a high-frequency component. No attempt was made to estimate the source levels and active space for the Kamchatka killer whale acoustic signals, but while listening for calls from a distance of about 10 km we usually heard Biph1 and Biph2 class calls, although while listening at close range squeak-like Moph1 class calls were used more frequently. This indirectly indicates that Biph1 and Biph2 class calls with an overlapping high-frequency component are louder than squeak-like Moph1 class calls without an overlapping high-frequency component, which corresponds with source levels for Northeast Pacific killer whale calls of similar structure.

Filatova *et al.* (submitted) suggests different potential roles for the various types of vocal signals in communication. They found that calls with an overlapping high-frequency component varied with the number of pods in the area. The number of these calls was significantly fewer when one pod was present compared with the presence of several or many pods, which proves that they might be employed as markers of pod and matriline affiliation. Squeak-like calls without an overlapping high-frequency component did not vary with the number of pods, but varied with the type of activity (Filatova *et al.* submitted).

Calls from certain classes often show some similarity within group dialects. It appears that each group has its own "dialect form" of call, which can be applied to different call classes. Ford (1991) showed a similar phenomenon in the dialects of Northeast Pacific killer whales. As an example, pod A5's version of 5 of the 11 calls shared by the three A pods (A5, A4 and A1 or Stubbs pod) had strongly emphasized terminal components, in both duration and frequency shift. In pods A1 and A4, however, these calls all had weakly developed or nonexistent terminal parts.

There is also one call type that does not belong to any of described classes. It is K11 which looks more like a whistle than a call (Figure 7, K11). Stereotyped whistles have also been described for killer whales from the Northeast Pacific by Riesch *et al.* (2006).

Phonotactics as a killer whale vocal tradition

The fact that all of the discrete calls of Southeast Kamchatka resident killer whales can be divided into several distinctive structural classes suggests that they have some rules defining the structure of the calls. These rules are not common for killer whales as a whole. For example, calls of transient killer whales from Southeast Kamchatka and killer whales from Sakhalin region do not obey these rules. Thus these rules are presumably the cultural tradition of Southeast Kamchatka resident killer whales.

A similar example of pronunciation traditions is found in human languages. Native speakers of any human language have extensive, although unconscious, knowledge of the permissible sound sequences in their language (Pinker 1994); this is called phonotactics. For example, in Japanese, consonant clusters like /st/ are not allowed, although they are in English. Similarly, the sounds /kn/ and /gn/ are not permitted at the beginning of a word in Modern English but are allowed in German and Dutch.

If we assume that "vocal tradition" is a cultural tradition applied to vocal behaviour, then, to a great extent, all resident killer whales from Southeast Kamchatka share the same vocal tradition. Still, some of them share no call types, and, following Ford's (1991) definition of "clan", belong to different clans. Ford (1991) suggested that each clan has descended from a common ancestral group and has a unique vocal tradition. Yurk *et al.* (2002) provided genetical evidence that the vocal clans of Alaskan resident killer whales are maternal lineages. Still, although it may be the case for Northeast Pacific killer whales, in other regions of the world such as Kamchatka, the situation might differ. With reduced social contact, dialects of some previously related groups might diverge to such an extent that they would no longer be interpreted as members of one clan. Nevertheless, they could share some wider common rules defining the structure of calls, and their integrity would be maintained by phonotactics shared by all community members.

Mating among the Northeast Pacific resident killer whales takes place within communities, usually between rather than within clans (Barrett-Lennard 2000). Presumably females choose a mate with the most distinct dialect (Barrett-Lennard 2000). Thus, on the one hand, repertoires should tend to diverge, because males from groups with more distinct dialects will have more potentially dialect-changeable offspring but on the other hand, they should still maintain some acoustic markers of community membership. The acoustic markers of community membership – in the case of Southeast Kamchatka killer whales, with phonotactics – could help prevent the division of the community and, hence, a loss of potential mates.

The existence of community markers in discrete call repertoires was also shown by Yurk (2005). To investigate vocal similarity above the clan level, he split calls into syllables, and compared their occurrence and syntax between residents and transients of Southern Alaska, and among clans and communities within residents. However, it is difficult to compare Yurk's results with ours because he viewed syllables as independent call components and did not examine the joint variation of lower frequency and overlapping upper frequency components.

In future, both Yurk's and our approaches could be used in tandem to estimate the relationships between killer whales from distant, but accessible, geographical regions. Traditionally, researchers have simply established that different killer whale groups share no call types, and concluded that they represent different vocal traditions. Few attempts have been made to estimate vocal traditions on a wider scale, because there has been nothing to compare if all call types are totally different. Comparison of clan repertoires either at the level of phonotactics or on the level of syllables can help to reveal more distant relationships within and between killer whale communities. It would be useful to compare DNA samples from distantly related killer whales to help confirm or reject the results of the acoustic studies.

ACKNOWLEDGEMENTS

This research was supported by the Whale and Dolphin Conservation Society, the Humane Society of the United States, the Sacher Trusts, the Animal Welfare Institute, the Klüh Prize and the Rufford Maurice Laing Foundation. Thanks are also due to many individuals but we would especially like to mention our colleagues who have worked tirelessly to get to know more about killer whales in the Russian Far East: Hal Sato, Ilya Shevchenko, Tatyana Ivkovich, Evgenia Lazareva, Mikhail Nagaylik, Karina Tarasyan and Ekatherina Jikiya. We are grateful to Harald Yurk and two anonymous reviewers for the useful comments on the earlier versions of the manuscript.

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Received 6 March 2007, revised 29 June 2007 and accepted 10 July 2007