



MARINE MAMMAL SCIENCE, 27(2): E26–E42 (April 2011)  
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DOI: 10.1111/j.1748-7692.2010.00433.x

## Responses of Kamchatkan fish-eating killer whales to playbacks of conspecific calls

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### ABSTRACT

Killer whales produce repertoires of stereotyped call types that are primarily transmitted vertically through social learning, leading to dialects between sympatric pods. The potential function of these call repertoires remains untested. In this study, we compared the reaction of Kamchatkan fish-eating killer whales to the playbacks of calls from the same and different pods. After the playback of recordings from a different pod, in three cases whales changed the direction of their movement toward the boat, and in three cases no changes in direction were observed. After the playback of recordings from the same pod (either from the same or a different unit within the pod), in seven cases whales changed the direction of their movement toward the boat, and in only one case no change in direction was observed. Whales remained silent after all six playbacks of recordings from a different pod, even when they changed direction toward the boat. After the playback of recordings from the same pod, however, in all eight cases whales started calling in response. Our playback study shows that killer whales may react to playbacks of conspecific sounds and that reactions are dependent on the type of playback stimuli.

Key words: playback, killer whale, *Orcinus orca*, behavior, function of vocalizations, acoustic communication.

Testing hypotheses about responses to conspecific sounds using playback experiments could be a powerful approach for determining the function of vocalizations (Deecke 2006). Playback experiments have been used in research of acoustic

communication in various terrestrial species from fruit flies (Ritchie *et al.* 1998) to elephants (Poole 1999, McComb *et al.* 2000). However, in cetaceans, playback experiments are still used infrequently due to the high cost and logistic challenges of studies at sea and the difficulty of quantifying behavioral responses to underwater playbacks (Deecke 2006). Many playback experiments with cetaceans have addressed the question of how an animal responds to anthropogenic noise (*e.g.*, Miller *et al.* 2000, Croll *et al.* 2001, Koschinski *et al.* 2003). Relatively few experimental studies involving playbacks have been conducted to investigate the function of cetacean vocalizations; these include beluga whales (*Delphinapterus leucas*, Morgan 1973), bottlenose dolphins (*Tursiops truncatus*, Sayigh *et al.* 1999, Janik *et al.* 2006), sperm whales (*Physeter macrocephalus*, Rendell and Whitehead 2005), southern (*Eubalaena australis*) and North Atlantic (*Eubalaena glacialis*) right whales (Clark and Clark 1980, Parks 2003) and humpback whales (*Megaptera novaeangliae*, Tyack 1983, Mobley *et al.* 1988). In these studies, it was shown that cetaceans usually exhibit an interest in conspecific sounds, can discriminate between conspecific and other sounds (Clark and Clark 1980), between various conspecific sounds (Tyack 1983, Mobley *et al.* 1988, Parks 2003) and between sounds of familiar conspecifics (Sayigh *et al.* 1999, Janik *et al.* 2006). No results of playback experiments with free-ranging killer whales have been published to date, though this species appears to be a very promising subject for such studies due to its advanced vocal communication and stable social structure.

The basic unit of the northeast Pacific resident (fish-eating) killer whales' social organization is the "matriline," which consists of an adult female and up to four generations of her offspring (Bigg *et al.* 1990). The social structure of resident killer whales is characterized by natal philopatry, and both male and female offspring typically travel with their mothers for their entire lives (Bigg *et al.* 1990). Killer whale sounds include whistles, echolocation clicks, and pulsed calls. Most killer whale pulsed calls are highly stereotyped and fall into discrete categories (Ford 1991). 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).

A set of killer whale matriline that associate frequently and use a common repertoire of stereotyped calls or group-specific dialect is called a "pod" (Ford 1991, Ford 2002*a, b*). Matriline from the same pod are thought to be closely related (Bigg *et al.* 1990). Ford (1991) referred to each set of pods that shared a number of discrete call types as a "clan." Pods from different clans consequently do not have any stereotyped calls in common, but may still associate with each other.

The functional significance of killer whale discrete calls has been addressed by a number of studies. Studying call usage in different matriline, Ford (1989) showed that the relative use of different call types varied with type of activity, but no call was correlated exclusively with any particular behavior. Miller *et al.* (2004) studied vocal interactions between individual free-ranging killer whales and showed that the whales within matriline regularly exchange calls, often immediately matching the call type produced by another individual. Several studies (Weiß *et al.* 2007, Foote *et al.* 2008, Filatova *et al.* 2009*a*) showed that the usage of different call types depended more on the presence of other pods or matriline rather than on the type of activity. However, the particular function of each call type remains largely unknown.

Group-specific variation in vocal repertoires, typical for killer whales (Ford 1991, Strager 1995, Yurk *et al.* 2002, Filatova *et al.* 2007) and some other odontocetes, for example, sperm whales (Rendell and Whitehead 2003), complicates the analysis of behavioral responses to these sounds, because the variety of pod repertoires increases

the number of calls for which function has to be determined; on the other hand, it allows the study of the possible function of such variation. However, to date, the experimental research of group-specific vocal variation in whales has been limited to a single study by Rendell and Whitehead (2005). Rendell and Whitehead played back codas (stereotyped patterns of clicks, Watkins and Schevill 1977) to social groups of sperm whales to test if sperm whales would show a differential response to codas of their own clan over codas of other clans; they found few consistent responses.

The goal of the present study was to test the potential biological meaningfulness of played-back calls. For this, we compared the reaction of killer whales to the playbacks of calls from the same and different pods. Stereotyped calls are thought to function as intragroup contact signals to maintain pod cohesion and co-ordinate activities (Ford 1989); therefore, the intragroup calls from a pod, comprising its own dialect, should be different in significance to a whale, compared to the calls from a different pod. We expected to get more pronounced and consistent reaction to the playbacks of calls from the same pod, because the meaningfulness of calls from different pods can vary depending on the relationships between the played-back and the recipient pods and the current intention of the whales to communicate with unrelated conspecifics.

## METHODS

The materials and data used for this study were collected as part of the Far East Russia Orca Project (FEROP) in Avacha Gulf, Kamchatka, in 2006–2008.

### *Study Population*

Fish-eating killer whales in Avacha Gulf form stable social units that include maternal relatives with no dispersal observed (Ivkovich *et al.* 2010). These units are probably analogous to the matrilineal units of the northeast Pacific resident killer whales, but the shorter observation period for Avacha Gulf killer whales (since 1999) has not enabled the confirmation of this. If two units share all the discrete calls in their repertoires, they are considered to belong to the same acoustic pod. In Kamchatkan killer whales, social associations do not always correspond with the patterns of acoustic similarity (Ivkovich *et al.* 2010), so we use the term “pod” only to describe the acoustic similarity of the units.

In the Avacha Gulf area, at least three acoustic clans of fish-eating killer whales occur: Avacha clan, K19 clan, and K20 clan (Filatova *et al.* 2007, Ivkovich *et al.* 2010). Avacha clan, consisting of more than 250 whales in at least 11 pods, is the most common. K19 clan consists of more than 80 whales in at least three pods, and K20 consists of more than 80 whales in at least four pods.

During the experiments described in this study, 16 units from 11 pods and two acoustic clans were present (Table 1). Commandor and Cezar units from AV258 pod belong to K20 clan; all other units belong to Avacha clan (Table 1, pod identity shown in parentheses).

### *Playback Stimuli*

Recordings from seven different units were used as playback stimuli (Table 2). The recordings consisted of a 2-min-long recorded sequence from a specific unit (Fig. 1). The identity of the units from which the recordings were made was defined

*Table 1.* List of playback experiments showing the identity of played recordings and the unit(s) to which it was played (units from K20 clan are shown in italics), type of playbacks, behavioral changes (+ indicates changing direction toward the boat, increase in speed and distance between animals, - indicates decrease in speed, 0 indicates no changes), and the experiments that were used for the statistical analysis of direction and vocal changes in response to the playbacks.

No.	Date	Time	Units within 500 m of the boat (pod ID shown in parentheses)	Identity of played recording	Type of playback	Change after the experiment in			Used in analysis		
						Direction	Speed	Distance	Sounds	Direction	Sounds
1	10 August 2006	1800	AV2 (AV2)	Moloko (AV315)	Different	0	0	0	No	0	+
2	10 August 2006	1848	Moloko (AV315)	Moloko (AV315)	Same unit	0	-	0	Yes	+	+
3	22 July 2007	1641	Drkin (AV40), Figurny (AV337)	Drkin (AV40)	Same unit	0	0	0	Yes		+
4	22 July 2007	1656	Kaplya (AV132), Nemo (AV52)	Kaplya (AV132)	Same unit	0	0	0	Yes		+
5	05 August 2007	1832	Winnny (AV2)	AV2 (AV2)	Same pod	0	0	0	Yes	+	+
6	10 August 2007	1142	<i>Commandor</i> (AV258), <i>Cezar</i> (AV258)	AV140 (AV258)	Same pod	0	0	0	Yes	+	+

Continued

Table 1. (Continued)

No.	Date	Time	Units within 500 m of the boat (pod ID shown in parentheses)	Identity of played recording	Type of playback	Change after the experiment in			Used in analysis		
						Direction	Speed	Distance	Sounds	Direction	Sounds
7	10 August 2007	1550	<i>Commandor</i> (AV258), <i>Cezar</i> (AV258)	Drkin (AV40)	Different	+	0	0	No	+	+
8	20 August 2007	1742	Winnie (AV2)	AV140 (AV258)	Different	+	0	0	No	+	+
9	20 August 2007	1833	Winnie (AV2)	AV2 (AV2)	Same pod	+	0	0	Yes		
10	19 July 2008	1501	Kaplya (AV132), Nemo (AV52)	Kaplya (AV132)	Same unit	0	0	0	Yes		
11	20 July 2008	1325	AV421 (AV421)	Nemo (AV52)	Different	0	0	0	No	+	+
12	21 July 2008	1304	Kaplya (AV132)	Nemo (AV52)	Different	+	+	+	No	+	+
13	06 August 2008	1558	Businka (AV55), Misha (AV55)	Galkin (AV55)	Same pod	+	+	0	Yes	+	+
14	06 August 2008	2110	Arfa (AV165), Carmen (AV25), Goosly (AV25)	Galkin (AV55)	Different	0	0	0	No		+

Table 2. List of recordings used as playback stimuli showing behavioral context in which the recordings were made, call types contained in the recording, and the number of monophonic calls, biphonic calls, and total number of calls in the recording.

Unit	Date	Time	Behavior	Call types	Monophonic calls	Biphonic calls	Total number of calls
Moloko	15 July 2006	1138	Traveling	K1, K5, K7, K13, K14, K23	11	50	61
Drkin	02 August 2005	1605	Milling	K1, K5, K7, K14	2	30	32
Kaplya	27 July 2006	1247	Traveling	K1, K5, K7, K10	6	30	36
AV2	02 July 2005	1015	Traveling	K1, K5, K12	12	5	17
AV140	24 August 2005	1022	Milling	K3, K20, K30	48	6	54
Nemo	14 August 2005	1419	Traveling	K5, K10, K12, K17	3	13	16
Galkin	24 July 2006	1650	Traveling	K5, K7, K17	0	27	27

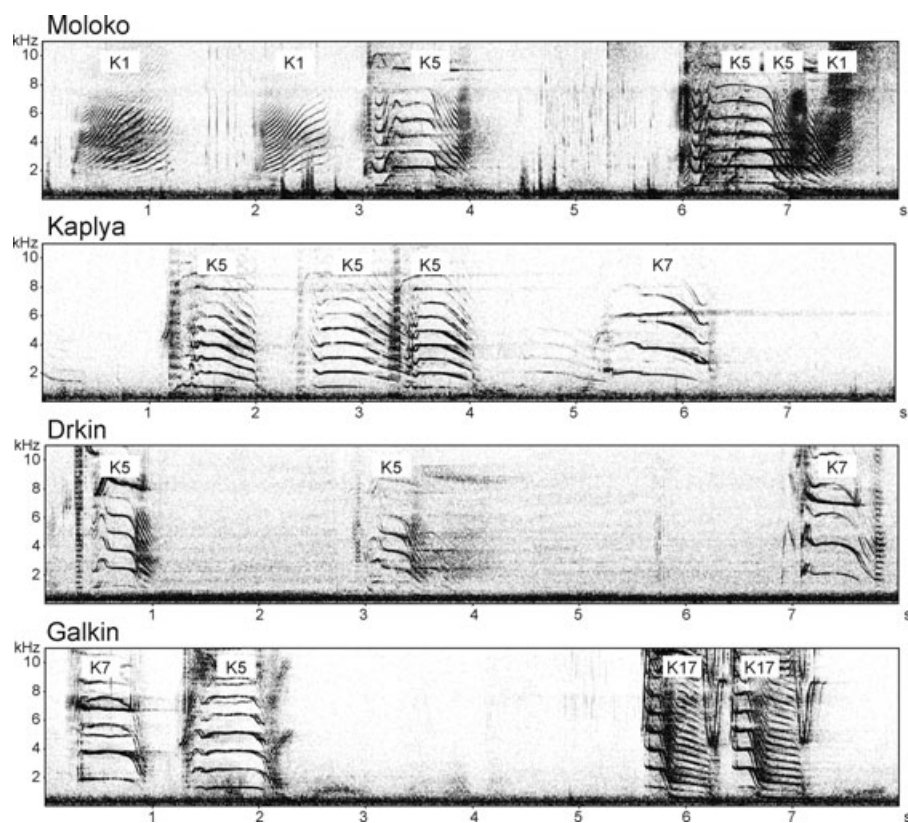


Figure 1. Examples of played stimuli: sections of playback sequences from four units. Sonograms were created using Hamming window, FFT length 1024, overlap 75%, frequency resolution 47 Hz, and time resolution 5.3 ms.

using the photo-identification method (Bigg *et al.* 1983). The recordings were made in similar behavioral contexts when the whales were traveling or milling (Table 2). None of these recordings were made during foraging, socializing, or resting. The source level of the playbacks varied from about 105 to 120 dB re 1  $\mu$ Pa at 1 m depending on the amplification ratio and the level of the played recording. The 15 dB variation in playback amplitude is equivalent to the variation in the source level of natural killer whale calls (Miller 2006). Sampling frequency of the played recordings was 22.05 kHz, which gave a frequency range up to 11.025 kHz. The recordings contained a variety of call types, including K1, K3, K5, K7, K10, K12, K13, K14, K17, K20, K23, and K30 types (Table 2).

#### *Design of Playback Experiments*

Playbacks were made from an inflatable boat with a spherical piezoceramic underwater speaker 50 mm in diameter. To reduce the effect of the behavioral context on the reaction of the animals, we conducted the experiments only in situations when whales were traveling in a tight group and were silent for at least half an hour before

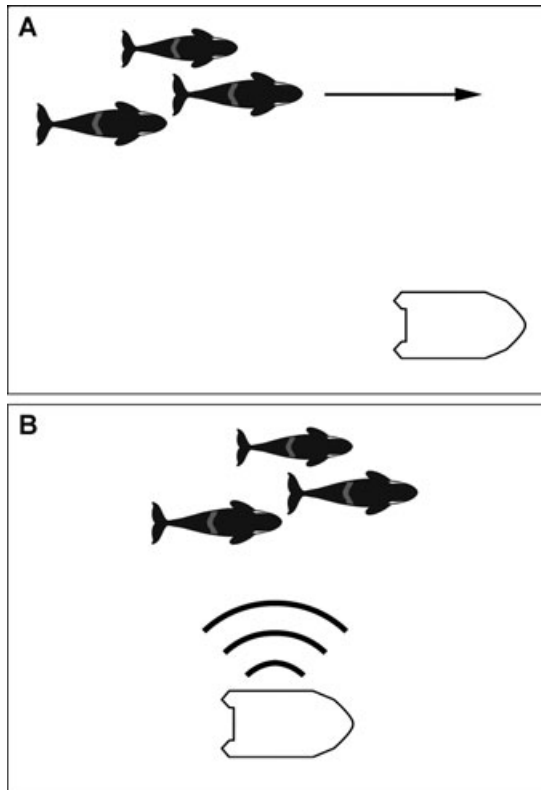


Figure 2. Design of playback experiments.

the experiment. To conduct the experiment, we moved the boat approximately 500 m ahead and 100–300 m beside the animals' course (Fig. 2A) and played the sounds as they were passing (Fig. 2B). During the playback, we recorded the underwater sounds with one omnidirectional "Offshore Acoustics" hydrophone with a sensitivity of  $-154 \text{ dB} \pm 4 \text{ dB re } 1 \text{ V}/\mu\text{Pa}$  at 100 Hz (6 Hz to 14 kHz  $\pm 1\text{--}13 \text{ dB}$ , 5 Hz to 40 kHz  $\pm 1\text{--}10 \text{ dB}$ ). In 2006–2007, we used two (one for playback, another for recording) Sony TCD-D100 DAT recorders with a sampling rate of 48 kHz (20–22 kHz  $\pm 1 \text{ dB}$ ). In 2008, we used a Zoom H4 flash-recorder that allowed us to play and record sounds simultaneously with a sampling rate of 48 kHz.

During the playback session and during the 10 minute interval after the playback, we noted if there were any changes in the follows parameters of killer whale behavior: direction of movement, speed of movement, distance between animals in the group, and acoustic activity. Changes in direction and speed of movement and distance between animals in the group were estimated by eye by two experienced observers (OF and IF) as following: direction changed toward the boat/away from the boat/did not change, speed increased/decreased/did not change, or distance between animals increased/did not change.

We carried out 14 playback experiments (Table 1). During the experiments, some groups were observed more than once, and up to three different units were



present during the playbacks (Table 1). We conducted two types of playbacks: (1) playback of recordings from the same pod (either from the same or a different unit) and (2) playbacks of recordings from a different pod. For further analysis, we pooled experiment numbers 4 and 10, and experiment numbers 5 and 9 to avoid pseudoreplication, because in these experiments the recipient units as well as playback stimuli were the same. In some experiments, units from more than one pod were present, and consequently the playback stimulus that was “from the same pod” for one unit, was inevitably “from a different pod” for another unit. In these cases, if change in direction and/or speed had occurred in response to a playback, we could not discriminate which unit (“same” or “different”) started the change, and therefore we excluded these experiments from the comparison of direction change in response to playbacks. However, for the vocal responses we were able to define which unit started to call in response due to the differences in the vocal dialects of units from different pods, and therefore we were able to use these data in the analysis.

### *Statistical Analysis*

We compared the difference in direction and speed of movement, distance between animals in a group and acoustic activity after the playbacks of recordings from the same and different pods with the two-tailed Fisher's exact test using Statistica 7.0 software. The significance level was set at 0.05 in all comparisons. To test if the inequality of the number of calls in playback stimuli had influenced the recipient's responses, we compared the number of monophonic calls (consisting of a single frequency contour), biphonic calls (containing an overlapped independently modulated high-frequency contour), and total number of calls in played recordings in experiments that evoked and that did not evoke vocal responses using the Mann–Whitney *U* test. We also calculated Spearman Rank Order Correlations of call number and number of evoked responses for each recording.

## RESULTS

We observed a variety of reactions from killer whale groups to the playback experiments: changes in direction ( $n = 10$ ), changes in speed (increasing speed  $n = 3$  and decreasing speed  $n = 1$ ), changes in the distance between animals ( $n = 1$ ), and changes in vocal activity (starting to call,  $n = 8$ ) (Table 1).

After the playback of recordings from a different pod ( $n = 6$ ), in three cases whales changed the direction of their movement toward the boat, and in three cases no changes in direction were observed. Increase in speed and distance between animals was observed only in one experiment; in the other five experiments, no change in speed and distance between animals was observed.

After the playback of recordings from the same pod (either from the same or a different unit,  $n = 8$ ), in seven cases whales changed the direction of their movement toward the boat, and in only one case no change in direction was observed. Speed increase was observed in two cases, speed decrease in one case, and no change in speed was observed in five cases. No changes in distance between animals were observed in any of the playback experiments after playing the recordings from the same pod.

For the statistical analysis of direction changes in response to playbacks, we used four playback experiments from the same pod and five playback experiments from a different pod. (Experiment numbers 4/10 and 5/9 were pooled to avoid

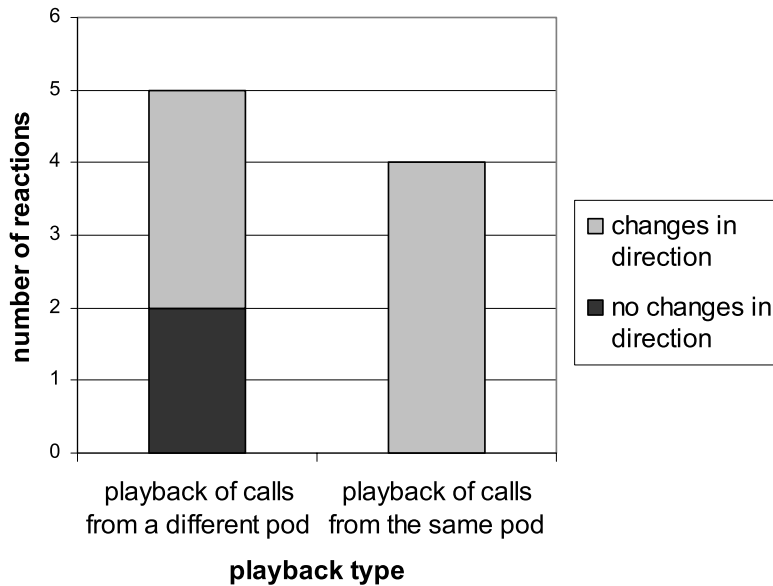
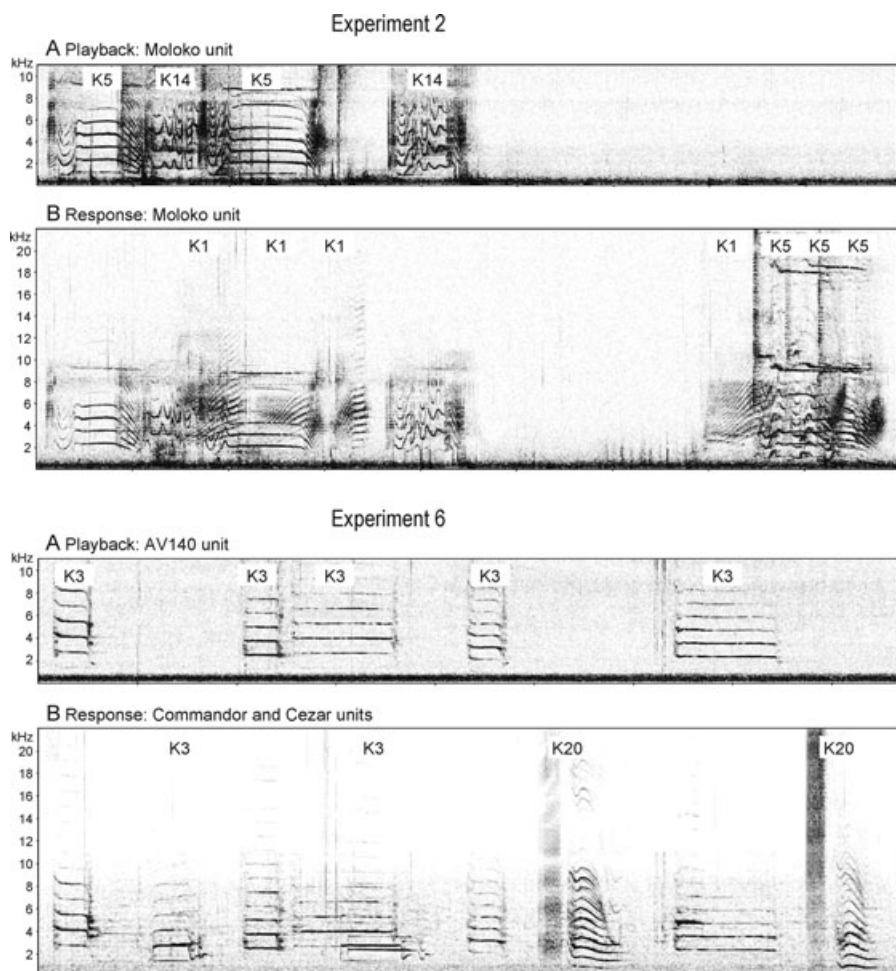


Figure 3. Changes in the direction of movement of killer whale groups after the playbacks of calls from the same and different pods.

pseudoreplication, and experiment numbers 3, 4/10, and 14 were excluded from this analysis because units from more than one pod were present during these experiments.) Despite the considerable difference in changes of direction after the playback of recordings from the same and different pods (Fig. 3), the difference was statistically nonsignificant (Fisher's exact test, two-tailed,  $P = 0.444$ ) due to the small sample size. We did not analyze changes in speed and distance between animals statistically because too few changes were observed.

The most pronounced difference, in reaction to the playbacks, was the acoustic activity of whales after the experiments. Whales remained silent after all six playbacks of recordings from a different pod, even when they showed an obvious interest in the sounds. For example, in experiment 7 after the playback of sounds from a different clan, the recipient units changed the direction of their movement  $90^\circ$  and moved toward the boat, passing it and continuing to move in the same direction for several hundred meters without making any sound. After all eight playbacks of recordings from the same pod, whales started calling in response (Fig. 4). Moreover, the whales responded vocally both to the playbacks of calls from their own unit (experiments 2, 3, 4, 10) and to those from different units of the same pod (experiments 5, 6, 9, 13). Because experiments 4 and 10 and experiments 5 and 9 were pooled to avoid pseudoreplication, a total of six playback experiments with the same pod was analyzed statistically. The difference in acoustic activity after the playbacks of recordings from the same ( $n = 6$ ) and different ( $n = 6$ ) pods was statistically significant (Fisher's exact test, two-tailed,  $P = 0.002$ ). In case two units from different pods were present during the experiment, a unit from the same pod to that of the playback stimuli was always the first to start calling in response to a playback. In some cases (experiments 3 and 4), the second unit also started to vocalize 1 or 2 min after the first unit.



*Figure 4.* Example of killer whale responses to the playback experiments 2 and 6. (A) Fragments of played recordings; (B) recordings made during the experiment: the same fragments of played call sequence with overlapping calls from the responding units. Sonograms were created using Hamming window, FFT length 1024, overlap 75%, frequency resolution 47 Hz, and time resolution 5.3 ms.

However, this may have been a reaction to the calls of the first unit or some other undetected stimulus, and therefore was not considered in the analysis.

To reject the possibility that the difference in the vocal responses to the playbacks was caused by the inequality of the number of calls and the proportion of different call types in the played recordings (Table 1), we compared the number of monophonic calls, biphonic calls, and total number of calls in played recordings in two types of experiments: those that evoked and those that did not evoke vocal responses. We found no significant differences in any of these comparisons (Mann–Whitney  $U$  test, monophonic calls:  $U = 18$ ,  $P = 0.44$ , biphonic calls:  $U = 23$ ,  $P = 0.90$ , total

Table 3. Call types in the vocal responses of killer whale groups to the playbacks of recordings from the same pod.

No.	Units within 500 m of the boat	Identity of played recording	Call types in response
2	Moloko	Moloko	K1, K5, K23
3	Drkin, Figurny	Drkin	K4, K5, K7
4	Kaplya, Nemo	Kaplya	K5, K7
5	Winy	AV2	K5, K12
6	Commandor, Cezar	AV140	K3, K20
9	Winy	AV2	K5, K7
10	Kaplya, Nemo	Kaplya	K4, K5, K7
13	Businka, Misha	Galkin	K5, K17

number of calls:  $U = 20$ ,  $P = 0.60$ ). Correlations of call number and number of evoked responses for each recording were also nonsignificant (Spearman Rank Order Correlations, monophonic calls:  $R = 0.18$ ,  $P = 0.70$ , biphonic calls:  $R = 0.34$ ,  $P = 0.46$ , total number of calls:  $R = -0.08$ ,  $P = 0.86$ ).

Various call types were used in the vocal responses of killer whale groups in the playbacks of recordings from the same pod (Table 3), including both biphonic (K5, K7, K17, K20, K23) and monophonic (K1, K4, K12) call types. Biphonic calls were used in all responses, while monophonic calls were used in five responses. In some cases, whales responded by matching the same call types that were played back, but in other cases they responded with other call types as well (Fig. 4).

#### DISCUSSION

Our experiments showed that killer whales react differentially to the playbacks of calls from their own and different pods. These results are consistent with the prediction that calls from the same pod, comprising a group's own dialect, should be different in significance to a whale compared to the calls from a different pod. Moreover, we provide the first experimental evidence that killer whales can discriminate between the calls of their own and different dialects. The structural differences in discrete calls from different dialects are generally so pronounced that it would seem obvious that the whales can recognize them, yet the presence of variation alone is insufficient evidence for discrimination (Deecke 2006). For example, McCulloch *et al.* (1999) detected pronounced individual variation in the call structure of gray seal pups on the Isle of May, Scotland, but playbacks showed that the females failed to discriminate between the calls of filial and nonfilial pups. The ability to recognize conspecifics through long-distance calls is beneficial for mammals with highly fluid social systems and a lack of territoriality, where individuals and social units frequently spread out or separate. For example, playback experiments with African elephants indicated that adult females are familiar with the contact calls of approximately 100 other individuals in the population, and can discriminate between calls on the basis of how often they associate with the caller (McComb *et al.* 2000). The only study to date devoted to the recognition of killer whale calls is the work of Deecke *et al.* (2002), who showed that harbor seals can distinguish between local marine mammal-eating and fish-eating killer whale calls.

The played recordings were limited to frequencies below 11 kHz. However, the harmonics of the high-frequency components of killer whale biphonic calls range to over 100 kHz, but these would be expected to degrade rapidly with distance due to higher sound absorption at higher frequencies. Given the relatively low source level of our underwater speaker, the whales might interpret the playbacks as rather distant conspecific calls that had degraded in volume and frequency range because of the distance. The average difference between the source level of the natural sounds (Miller 2006) and our playbacks was about 40.1 dB, which refers to the transmission loss at about 470 m if we use the equation  $TL = 15\log R$  (intermediate between spherical and cylindrical spreading). This corresponds with our observation that sometimes after the playback, the whales turned toward us, passed our boat and continued traveling for some time in the same direction, as if they expected the sound source to be somewhere beyond our boat. Similar results were obtained in experiments with songbirds, when playbacks of degraded songs provoked flights of subjects to positions beyond the loudspeaker, providing evidence of overestimation of distance for degraded songs (Naguib 1996). It is also possible that the whales interpreted the played-back calls as being received off axis, so that the caller was facing away from them. Miller (2002) showed that the relative energy in high-frequency bands was significantly lower in calls recorded off axis.

The frequency range and source level of the played sounds as well as the distance to the whales should be key considerations when conducting further playback experiments with killer whales. For example, playing calls with a reduced frequency range but high source level might allow the whales to recognize the falsification by the contradiction of the frequency and amplitude properties of the received sounds. On the other hand, the reduced frequency range does not necessarily lead to distortion or lack of response. Janik *et al.* (2006) showed that bottlenose dolphins extract identity information from signature whistles even after all voice features have been removed from the signal, so it seems the dolphins respond to the frequency modulated contours of the whistles. It could also be an explanation as to why the killer whales in our study responded to the playback calls even though the full frequency range of the calls was not broadcast.

Playback experiments often include playing back control recordings such as background noise or artificial sounds. We did not use playbacks as controls in our study, but we believe that it does not negate our results because in our experiments, the whales responded similarly in their vocal response to one type of playback stimuli, and did not respond to another type. If the reaction was caused by the whales' intention to respond to any playback stimulus irrespective of its biological meaning, they would start vocalizing in response to other stimuli types as well. Therefore, the difference in the reaction of the whales was apparently caused by the difference in the meaningfulness of the stimulus.

Our main goal in this study was to test if killer whales react differentially to the playbacks of calls from the same and different pods, but our results may also yield insights into the functions of discrete calls. In our experiments, killer whales always responded vocally to the playbacks of calls from their own pod. This fits with Ford's (1989) supposition that discrete calls function as intragroup contact signals to maintain pod cohesion and coordinate activities. Moreover, the whales responded vocally both to the playbacks of calls from their own unit and to those from other units of the same pod. There are two possible explanations for this. First, killer whales may not have been able to discriminate between calls from their own unit and another unit from the same pod. The structure of shared calls often shows subtle

variation between different matriline within the same pods (Miller and Bain 2000) as well as between different animals from the same matriline (Nousek *et al.* 2006), but these variations may not be recognizable in our experiments due to the lower source levels of played sounds and therefore the lower quality of the sounds received by the whales. Alternatively, it is possible that killer whales respond vocally to the calls from the same dialect irrespective of the unit affiliation of the caller. The latter hypothesis is especially interesting to test with the units that possess the same dialect but do not spend much time together, for example, the AV2 and Winny units. In our study, the Winny unit responded vocally to the playback of recordings from the AV2 unit in both experiments (5 and 9), although these units have a low level of association (Ivkovich *et al.* 2010).

The reaction of killer whales to playbacks of calls from a different pod was more diverse: whales never responded vocally, but often changed their direction toward the boat. This variability probably reflects the variety of relationships between pods and the intention of communication with a particular pod. Some observations suggest that killer whales do not always communicate with animals from different pods. For example, we once observed killer whales from one unit congregating in a tight group and silently passing three other units from a different pod, which were actively vocalizing and traveling nearby. The absence of reaction to the playback of calls from different pods could simply be explained by no need or desire to communicate with unrelated conspecifics. There are two generally accepted reasons why killer whale matriline travel together. First, closely related matriline could travel and forage together to enhance the fitness of their kin (Yurk *et al.* 2002). Second, unrelated matriline from different clans could form temporary aggregations for mating reasons (Matkin *et al.* 1997, Barrett-Lennard 2000). In Kamchatkan killer whales, associations between units sometimes do not correspond with either of these predictions (Ivkovich *et al.* 2010) and the overall picture appears to be more complex, for example, some aggregations appear to serve neither for foraging nor for mating, but rather to establish and maintain social bonds (Filatova *et al.* 2009b). This could help explain why units from different pods sometimes appear to ignore each other's calls.

Both biphonic and monophonic call types were used in the vocal responses of killer whale groups on the playbacks of recordings from the same pod. In Kamchatkan killer whales, monophonic calls prevail in intrapod communication, and the rate of biphonic calls increases when more than one pod is present (Filatova *et al.* 2009a). However, though during most of the experiments members of only one pod were present, biphonic calls were used in the vocal responses in all cases, and monophonic calls were used in only five cases. This discrepancy may be caused by the tendency of killer whales to match the previous call type in their vocal responses (Miller *et al.* 2004). Indeed, killer whales often (but not always) matched the played sounds in their vocal responses (Fig. 4). It is also possible that the whales used predominantly biphonic calls in their responses because they have interpreted the playbacks as off-axis distant calls, and biphonic calls are thought to function as long-distance contact calls (Foote *et al.* 2008, Filatova *et al.* 2009a) due to the mixed-directionality and higher source level measured by Miller (2002, 2006). A promising direction for further experiments would be to play only monophonic sounds to the whales and see if they will respond with monophonic or biphonic sounds.

Studies of killer whale acoustic communication are now mature enough to formulate hypotheses that could be tested using playback procedures. Our playback study is the first record to show that we can provoke different killer whale units to react to biologically meaningful stimuli. This finding opens the way to a variety of

playback experiments that could help to explain more details of the complex social relationships of killer whales as well as help to reveal the function of killer whale vocalizations.

#### ACKNOWLEDGMENTS

This research was supported by the Whale and Dolphin Conservation Society, Humane Society International, Animal Welfare Institute, Sacher Trusts, the Klüh Prize Foundation, and the Russian Fund for Fundamental Research, grant number 08–04–00198-a. We are grateful to Tatyana Ivkovich for supplying information on the identity of killer whale groups. We are grateful to Andrew Foote and two anonymous reviewers for very useful comments and suggestions. All research methods comply with the current laws of the Russian Federation. No permission is needed to conduct playback experiments with free-ranging killer whales in the waters of Russian Federation. A precautionary approach was adopted, however, with only very limited exposure to the playback sounds by any one unit or pod. Volume levels, as described in the Methods, were comparatively low.

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Received: 9 January 2010

Accepted: 7 July 2010