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ORIGINAL INVESTIGATION

The social organization of resident-type killer whales (*Orcinus orca*) in Avacha Gulf, Northwest Pacific, as revealed through association patterns and acoustic similarity

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Abstract

Northeast Pacific resident-type killer whales (*Orcinus orca*) are known to form stable associations based on kinship between maternal relatives (matrilines) with a system of vocal dialects thought to reflect kinship relationships. We analyzed association patterns and acoustic similarity to study the social organization of killer whales in Avacha Gulf (Kamchatka, Russia), in the Northwest Pacific. The resident-type killer whales of Avacha Gulf formed temporally stable units that included maternal relatives with no dispersal observed. Acoustically, the killer whale community of Avacha Gulf was characterized by a system of dialects comparable to the communities of Northeast Pacific resident-type killer whales. Different units rarely associated with each other and these associations were nonrandom. Associations at different spatial levels did not always coincide with each other and with the patterns of acoustic similarity. Associations between units could change quickly irrespective of kinship relationships. The vocal dialect of a unit, which is more stable than the association patterns between units, might better reflect the overall kinship relationships. The stability and frequency of associations between units depended on the number of mature males in a unit, which could contribute to differences in the speed of change in vocal dialects and association patterns.

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Introduction

Most knowledge of killer whale biology comes from the Northeast Pacific (British Columbia, Washington and Alaska), where, on the basis of long-term studies,

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scientists have found that at least two different ecotypes of killer whales inhabit the same area: (1) resident, fish-eating, and (2) transient, mammal-eating, killer whales. These two ecotypes differ in social organization, behaviour, foraging and travel patterns, and morphology (Baird and Stacey 1988; Ford et al. 1998, 2000; Ford and Ellis 1999). The killer whales of these two sympatric but reproductively isolated ecotypes never associate (Barrett-Lennard 2000).

Bigg et al. (1990) described societies of resident killer whales based mostly on traveling patterns and associations (co-occurrence in frames of photographs and direct observations of animals in close proximity) and discovered that killer whales form long-term stable matrilineal groups (matrilines) with a lack of dispersal by both sexes. Four tiered, or hierarchical, levels are distinguished in the social organization of the resident killer whales of the Northeast Pacific (Ford 2002): matrilines, pods, clans and communities (Table 1).

Long-term investigations of killer whale acoustic behavior (Ford 1991; Yurk et al. 2002; Foote et al. 2008) have established that each pod has its own unique repertoire of discrete calls, which remains stable for tens of years. Some of the calls are shared by several pods and some are unique. Pods that share calls belong to the same acoustic clan. Ford (1991) suggested that different clans could represent independent maternal lineages that have independent call traditions.

The population structure of resident killer whales in the Northwest Pacific is unknown and has only been briefly described for eastern Kamchatka (Burdin et al. 2007). The whales regularly observed in Avacha Gulf are considered to be the resident ecological type according to their behaviour and appearance (Burdin

et al. 2004, 2007; Tarasyan et al. 2005; Ivkovich 2006). There are known to be at least three acoustic clans that regularly use Avacha Gulf (Filatova et al. 2007). Killer whales from the transient ecological type are also found in the area but visit the gulf rarely (Burdin et al. 2004, 2007).

Studying the killer whale populations in the Northwest Pacific is important because a quota for capturing between 6 and 10 killer whales for the Russian Far East (including in the Avacha Gulf area) has been granted every year since 2002. Without information on population structure, it is impossible to predict the impact of such captures on killer whale population viability in the region (Williams and Lusseau 2006).

Comparing different populations of resident killer whales may contribute to a better understanding of the fundamental traits of social organization and social behaviour of the species *Orcinus orca*. Cetaceans display high plasticity in behaviour which allows them to adapt to different environmental conditions and to use resources effectively. A given species may display different feeding strategies, strategies of area usage and association patterns as shown in bottlenose dolphins (Connor et al. 2000). Gowans et al. (2008) suggested that differences in habitats such as geomorphological features, habitat size and predictability of resources may lead to the development of different social strategies in delphinids. The differences in the ecology of killer whales could occur between the Northeast and Northwest Pacific due to the geomorphological characteristics of the habitat. The Russian Far East generally has a straighter shoreline with an absence of deep bays and small islands (Fig. 1), unlike the fjordic western North American coast from Puget Sound to Alaska with its

Table 1. Terms that are used in literature and in this paper to describe association patterns between killer whales (*Orcinus orca*).

Term	Type of association	Definition
<i>Definitions in literature</i> (Ford 2002)		
Matriline	Social	Maternally related individuals that form long-term highly stable associations and are seldom seen apart from each other for more than a few hours. Matrilines may include up to four generations and are characterised by lack of natal dispersal.
Pod	Social	Related matrilines that share a common maternal ancestor in the recent past.
Clan	Acoustical	Pods that share a number of discrete call types.
Community	Social	Pods that inhabit the same area and regularly associate with one another.
<i>Definitions for this paper</i>		
Grouping	Spatial-temporal	Whales within three body lengths of each other moving together and displaying a similar type of activity.
Aggregation	Spatial-temporal	Groupings moving together within visual range of the research boat.
Unit	Social	Individuals that form long-term stable associations and spend most of the time together. Members of a unit typically come to an area together and form into a grouping with each other more often than with other killer whales.
Acoustic pod	Acoustical	Units that share a unique repertoire of discrete calls.



Fig. 1. Study area with different management zones denoted by numbers.

thousands of islands and islets. These differences may have an effect on killer whale distribution, size of home range, habitat use and as a result, on social organization (Burdin et al. 2007).

The killer whale's multi-tiered social structure (matrilines to communities) might represent various types of bonds between individuals. The dynamic of the bonds in such a population is influenced by different ecological and social factors depending on the social tier of these bonds (Wittemyer et al. 2005). Ford and Ellis (2002) showed that association patterns between matriline could vary from year to year and remain unstable inside pods. The influence of various demographic features (such as the proportion of males in a matriline) on the association patterns between matriline has been suggested as a potential factor in some studies (Matkin et al. 1999b; Ford and Ellis 2002). In this study we used statistical methods to reveal the influence of different features of matriline composition on the association patterns.

To obtain a deeper understanding of social behaviour and the demographic processes within a killer whale population, we used a combination of approaches, namely the analysis of acoustic similarity (call-type sharing) and association patterns. The objectives of our research were to investigate: (1) the stability and composition of the resident killer whale units of Avacha Gulf, (2) the stability of inter-unit associations at different spatial scales, (3) the relationships between units based on acoustic similarity and (4) the influence of a unit's size and composition on associations between units.

Material and methods

Study area and duration

Studies were conducted in the central part of Avacha Gulf off the Eastern Kamchatka Peninsula, Russia, in the Northwest Pacific. The data were collected during

the northern summers from 1999–2006, for a total of 150 days spent with killer whales.

Data collection

We used two 4 m Zodiac inflatable boats to approach the whales for observations, obtain photographs and make underwater sound recordings. Killer whales were found visually from boats and from the top of Starichkov Island, overlooking Avacha Gulf, and by listening for their calls on a hydrophone.

To describe the association patterns of whales in the field, we distinguished groupings and aggregations (Table 1). A grouping was defined as all killer whales within three body lengths of each other, moving together and displaying a similar type of activity. Solitary killer whales were treated as separate groupings. An aggregation was defined as all killer whale groupings moving together within visual range of the research boat.

A Canon EOS 1D camera with a 100–400 mm lens was used for the photographs. After killer whales were encountered, the boat approached different groupings, following at a distance of 20–30 m, for about 10–20 min to photograph each whale. Photographs of the left side of individual whales were taken to show the details of dorsal fin and saddle patch, using the technique developed by Bigg et al. (1990). Animals that were not photographed were noted.

To make sound recordings, we moved the boat approximately 500 m ahead of the animals and waited until they passed us. If the whales were feeding or milling, we stayed at a distance of 50–500 m from them to avoid disturbing their natural behaviour. In all cases, the hydrophone was lowered into the water when the boat engine was turned off. Before 2005, we used the same boat for taking photographs and making sound recordings, so the recordings were made between photo sessions. Since 2005, we have used two boats (one for photography, the other for sound recording), allowing the recordings to be made at the same time as the whales

were vocalising. Sound recordings were made on a Sony TCD-D100 DAT recorder using a sampling frequency of 44.1 or 48 kHz. For omnidirectional recording we used an 'Offshore Acoustics' hydrophone with a bandwidth of 10 Hz to 40 kHz and a sensitivity of $-154 \text{ dB} \pm 4 \text{ dB re } 1 \text{ V}/\mu\text{Pa}$ at 100 Hz. It was lowered to a depth of 5–10 m. For finding the direction of underwater sounds we used a mobile hydrophone stereo system (Filatova et al. 2006). In some cases, the recordings were made with the stereo system hydrophones, instead of our regular hydrophone. The response of these hydrophones is flat up to 40 kHz with sensitivity of -153.8 to $-158.3 \text{ dB re } 1 \text{ V}/\mu\text{Pa}$.

Data analysis

The number of whales identified in the three field seasons of 2004–2006 totaled 440 whales.

Associations between individuals

Direct observations and statistical analyses of associations were used to determine the membership of killer whale units. A unit was defined as individuals that form long-term stable associations, come to an area together and form into a grouping with each other more often than with other killer whales, as defined in Table 1.

At first we determined the membership of units by observing which individuals formed groupings most frequently with each other. Then we measured the degree of association between individuals using SOCPROG 2.2 (Whitehead 2004) and a simple ratio association index (SRI) (Ginsberg and Young 1992; Whitehead 2004) with data collected during the 2004–2006 field seasons. The whales found in one grouping during the day were considered to be associated for the day (the sampling period). Whales seen in more than three groupings and on more than two days were included in the analysis. In all, 977 groupings and 267 individuals (61% of all identified whales) were included in the analysis. To illustrate the association patterns of the whales, a dendrogram was constructed using average-linkage cluster analysis. The results of direct observations were compared to the results of association analysis to reveal the units. The permutation test was used for testing if the association patterns observed between individuals differed from what might be expected at random (Whitehead 2004). SRI values were also calculated and dendrograms were constructed separately for 2005 and 2006 and used to examine changes in the membership of units.

Unit composition and genealogy

Bigg et al. (1990) established genealogical relationships based on the observation that the bond between an offspring and its mother lasts for many years and is stronger than with any other potential mother. The genealogical assignments were divided into three levels of certainty: (1) positive (for offspring born during the study), (2) highly probable (for offspring that were juveniles when first encountered), and (3) probable (for offspring that were mature when first encountered). The genealogical assignments based on behavioural observations were later confirmed by molecular methods (Barrett-Lennard 2000).

We used the photographs collected from 1999–2006, together with direct observations, to determine the sex and approximate age of the whales and to establish possible maternal relations in the units (Bigg et al. 1990; Matkin et al. 1999b; Baird and Whitehead 2000). We used six categories to describe the sex and stage of maturity: (1) males – males that have already reached sexual maturity, (2) females – mature females unaccompanied by calves or small juveniles, (3) females with calves or small juveniles, (4) calves and small juveniles – whales younger than 3–4 years, (5) juveniles (both sexes) – whales older than 3–4 years but still not mature, and (6) other animals – whales for which age and stage of maturity were impossible to determine.

Associations between units

We used SRI and SOCPROG 2.2 to reveal the association patterns between different units.

Units associated at the grouping level

Two different units were considered to be associated at the grouping level for a day (the sampling period) if any animals from these two units were seen in the same grouping during that day. A sociogram was used to illustrate the association patterns between units at the grouping level. The permutation test was used for testing if the association patterns observed between units differed from what might be expected at random (Whitehead 2004).

We built sociograms separately for 2005 and 2006 based on grouping-level associations to check if there were any changes in association patterns between units. To compare between years, we used units which were encountered in more than two aggregations during each season.

Units associated at the aggregation level

We also checked if different units of killer whales were seen in the same aggregations nonrandomly. For this, 148 aggregations encountered in 1999–2006 were used.

Two different units found in the same aggregation were considered to be associated for the day. Aggregations which consisted of whales from a single unit were also included in the analysis. To illustrate the association between units, a sociogram was constructed.

The influence of a unit's composition on associations between units

A linear, forward, stepwise model of multiple regression analysis was used to study relationships between the unit's size, number of males, proportion of males, number of calves and small juveniles, proportion of calves and small juveniles in a unit and (a) the frequency of the unit's occurrence in groupings with other units, and (b) the unit's maximum SRI value in grouping-level associations.

Acoustic analysis

The acoustic analysis was 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, with a frequency resolution of 47 Hz, and a time resolution of 2.7 ms. All recordings were inspected using Avisoft SASLab Pro, and discrete calls were saved separately for each recording both as wav files and sonogram images, which were linked for viewing and playback in ACDSee software.

For defining unit repertoires we selected the recordings when the calling unit ID was obvious, e.g. when the unit was alone or far away from other units. The repertoire of discrete calls, or vocal dialect, was defined for most of the identified units. Discrete call classification was based on the existing catalogue (Filatova et al. 2004) with some additional call types found in units rarely visiting the area.

To illustrate the hierarchy of the acoustic similarity between pods, a dendrogram was constructed from index values using weighted pair-group average cluster analysis. A quantitative measure of the similarity of call repertoires for each pair of units was obtained by calculating an index from the degree of discrete call sharing (Ford 1991). This index is based on Dice's coefficient of association, which normalizes the data to account for differences in repertoire size:

Index of acoustic similarity = $2(N_c + N_s) / (R_1 + R_2)$, where N_c is the total number of call types shared, N_s is the total number of subtypes shared, and R_1 and R_2 are the repertoire sizes (call types plus subtypes) of the two units.

We distinguished two major levels of acoustic similarity – acoustic pods and acoustic clans. If a pair of units shared all discrete calls in their repertoires, they were considered to belong to the same acoustic pod. The index of acoustic similarity between these units

was 1. If a pair of units shared not all but some discrete calls in their repertoires, the index of acoustic similarity was between 0 and 1, and they were considered to belong to different acoustic pods, but to the same acoustic clan. If they shared no calls, the index of similarity would be 0, and they would then belong to different acoustic clans.

Comparing the results of the acoustic and association data analysis

To find out if the associations of killer whales were related to the acoustic similarity of dialects, we compared the SRI values between units with different levels of acoustic similarity using the Mann–Whitney U-test. First, we compared the SRI values between units from the same acoustic pods versus the SRI values between units from different pods. Second, we compared the SRI values between units from the same versus different acoustic clans. For this we used SRI values calculated for the units associated at the grouping level.

Results

Associations between individuals

We distinguished 36 units and one solitary male based on direct observation and statistical analysis of the associations (Table 2), totaling 276 killer whales. The lowest maximum SRI value inside units ($0.1 \leq \text{SRI-max} \leq 0.36$) was found for seven individuals. They were six physically mature males and one juvenile. The lowest maximum SRI value (0.06) in the studied population was found for the male Brodyaga. He was not included as part of any unit. On most occasions (23 observations out of 30), Brodyaga was encountered as a solitary whale.

The number of killer whales per unit varied from 1 to 16 (mean \pm SD = 7.49 ± 3.49). Most of the units consisted of 5–6 whales. The typical composition of a unit was two males, one female accompanied by a calf, one juvenile and one other animal.

The standard deviation of association indices was significantly higher in the real data set than in the permuted data sets ($p < 0.0001$). So, the null hypothesis that the individuals associated randomly was rejected (Whitehead 2004).

Temporal stability of killer whale units

The comparison of association patterns between the 2005 and 2006 field seasons showed that the membership of units was stable over at least two years. The changes

Table 2. Names and numbers of killer whale units, the relations between units based on acoustic similarity, grouping-level and aggregation-level associations between units and number of males in units.

Unit name	Unit number	Acoustic clan	Acoustic pod	Formations based on grouping-level associations	Formations based on aggregation-level associations	Number of males in the unit
Businka	55	Avacha	AV55	Gr01	Ag01	1
Galkin	110	Avacha	AV55	Gr01	Ag01	2
Misha	37	Avacha	AV55	0	Ag01	1
Pirate	49	Avacha	AV55	0	0	3
Prizrak	65	Avacha	AV55	0	Ag01	0
Nemo	52	Avacha	AV52	0	Ag01	0
AV2	2	Avacha	AV2	0	0	6
Winy	286	Avacha	AV2	0	0	4
AV32	32	Avacha	AV32	0	0	2
Drkin	40	Avacha	AV40	Gr02	0	2
Drkin's friends	43	Avacha	AV40	Gr02	0	0
Hooky	98	Avacha	AV98	0	0	4
Ikar	62	Avacha	AV62	0	0	3
Kaplya	132	Avacha	AV132	0	0	3
Arfa	165	Avacha	AV165	Gr03	0	2
Carmen	22	Avacha	AV25	Gr03	Ag02	0
KB	25	Avacha	AV25	Gr03	Ag02	1
Goosly	19	Avacha	AV25	0	Ag02	2
Chaika	80	Avacha	AV25	Gr04	0	1
Hooky the Young	16	Avacha	AV25	Gr04	0	1
Botsman	127	Avacha	AV165	Gr05	0	3
Chizh	137	Avacha	AV165	Gr05	0	2
AV84	84	Avacha	AV90	Gr06	Ag03	2
Lucky	90	Avacha	AV90	Gr06	Ag03	2
Tigrenok	96	Avacha	AV90	Gr06	Ag03	2
Figurnii	335	Avacha	AV315	0	0	2
Moloko	315	Avacha	AV315	0	0	1
Brodyaga	28	Avacha	Unknown	0	0	1
Ladoshka	70	Avacha	Unknown	0	0	2
AV300	300	Unknown	Unknown	0	0	3
Voronika	119	Unknown	Unknown	0	0	3
AV140	140	K20	AV258	0	0	1
Commandor	258	K20	AV258	0	0	3
Cezar	171	K20	AV258	0	0	3
Gera	340	K19	AV340	0	0	2
Zevs	326	K19	AV340	Gr07	0	5
Zorro	207	K19	AV207	Gr07	0	1

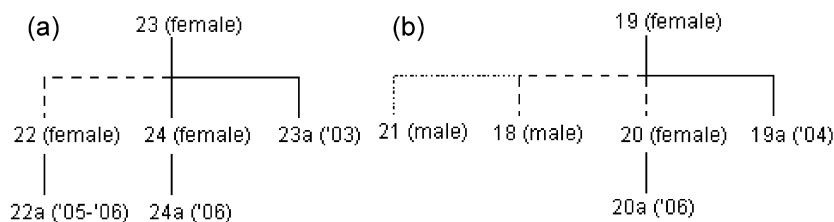


Fig. 2. Genealogical trees of two killer whale units: (a) Carmen's (22) and (b) Goosly's (19) units. In the brackets after each numbered killer whale is the sex and year of birth and death, if known. Dotted lines show mother-offspring probable relationships for offspring that were mature when first encountered. Dashed lines show probable relationships for offspring that were juveniles when first encountered. Positive relationships are denoted by a solid line for offspring born during the study.

in membership were due to the births or deaths of calves.

For most of the units the data on genealogy were absent or only partly available. 17 of the units were known to be stable since 1999. The genealogy of two of them was fully established based on known mother and offspring relationships (Fig. 2). The remaining units had not been encountered before 2002 or were only seen in part. Seven young males and seven females were known to have remained with their natal unit until they reached sexual maturity which occurred during the study period.

Associations between killer whale units

Units associated at the grouping level

Only 212 (22%) of 978 groupings were formed by whales from different units. We used these 212 groupings for the analysis which included 32 units and the male Brodyaga. Groupings consisting of killer whales from only a single unit were excluded from the analysis.

The results indicated that (a) on most occasions killer whales from different units did not form groupings with each other and (b) when killer whales from different units formed groupings with each other they tended to associate nonrandomly.

Killer whales from eight units were never seen or were found only once in groupings with killer whales from

other units. That might be explained by the low encounter rate with these units. But unit AV2 was also never seen in mixed groupings, even though it was encountered in nine aggregations and seven of these aggregations were formed by different units. Some 24 units were encountered in more than four mixed groupings. According to the sociogram, 13 units could be grouped into seven formations with the $SRI \geq 0.43$ (Fig. 3, Table 2).

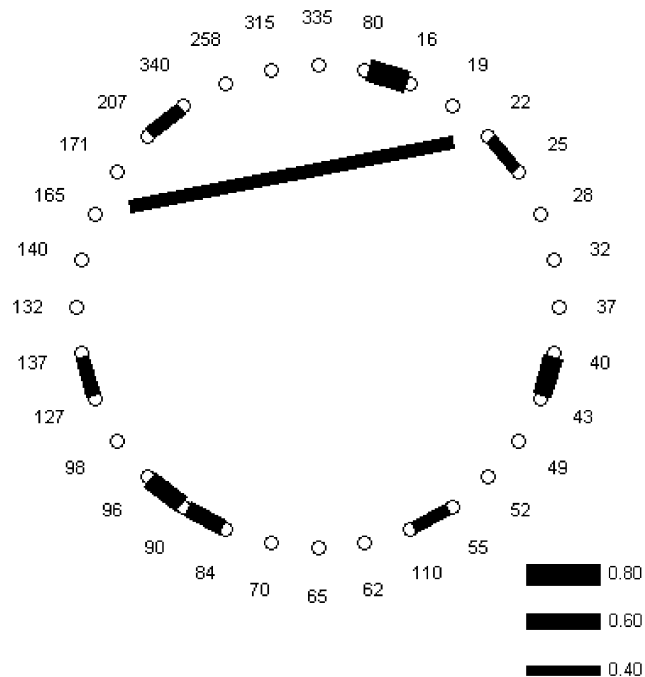


Fig. 3. Sociogram of units seen in groupings comprised of killer whales from two or more different units. The key shows simple-ratio index values at grouping-level associations between killer whale units.

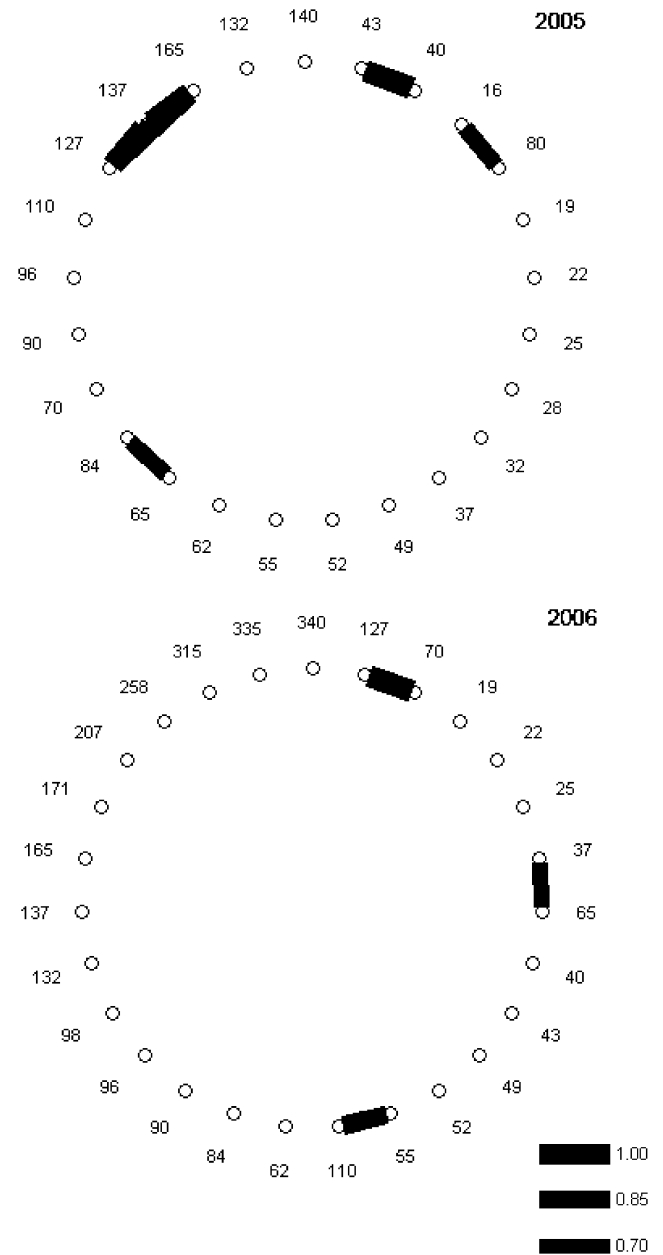


Fig. 4. Sociograms of units seen in groupings comprised of killer whales from two or more different units in 2005 and 2006. The key shows simple-ratio index values at grouping-level associations between killer whale units.

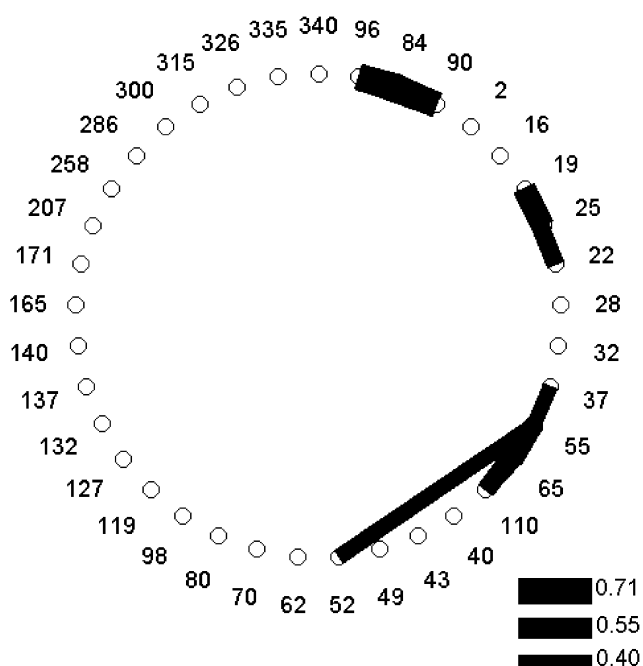


Fig. 5. Sociogram of killer whale units seen in the same and different aggregations. The key shows simple-ratio index values at aggregation level associations between units.

The standard deviation of association indices was significantly higher in the real data set than in the permuted data sets ($p < 0.001$). So, the null hypothesis that the units associated randomly was rejected (Whitehead 2004).

The comparison of dendrograms constructed separately for 2005 and 2006 based on individual associations showed that association patterns between some units changed. In 2005, Prizrak's unit (n or number of aggregations = 11) was associated ($0.2 < \text{SRI} < 0.3$) with AV84's unit ($n = 9$) and was not associated with Misha's unit ($n = 8$). In 2006, Prizrak's unit ($n = 8$) and AV84's unit ($n = 3$) were not associated, but an association ($0.3 < \text{SRI} < 0.4$) developed between Prizrak's unit and Misha's unit ($n = 10$).

In 2005, Galkin's unit ($n = 6$) was not associated with any of other units at an index value of $\text{SRI} > 0.1$, including Businka's unit ($n = 14$). But in 2006, Galkin's unit ($n = 11$) was associated ($0.4 < \text{SRI} < 0.5$) with Businka's unit ($n = 11$).

Sociograms built separately for 2005 and 2006 based on grouping-level associations between units (Fig. 4) showed that AV84's unit and Prizrak's unit in 2005 tended to form groupings with each other more often than with other units. And in 2006, Prizrak's unit tended to form groupings with Misha's unit more often than with other units. These associations were revealed using only groupings that included animals from more than one unit. Groupings that consisted of whales from a single unit were excluded.

Units associated at the aggregation level

In an aggregation killer whales usually formed separate groupings. The analysis of association patterns between units based on co-occurrence in the same aggregations revealed that some units tended to come to the area together.

According to the sociogram, 11 units could be grouped into three formations with the $\text{SRI} \geq 0.4$ (Fig. 5, Table 2).

The influence of a unit's composition on associations between units

Results of the stepwise regression analysis revealed a negative relationship between the number of mature males in a unit and (a) the frequency of the unit's occurrence in groupings with other units ($R^2 = 0.29$,

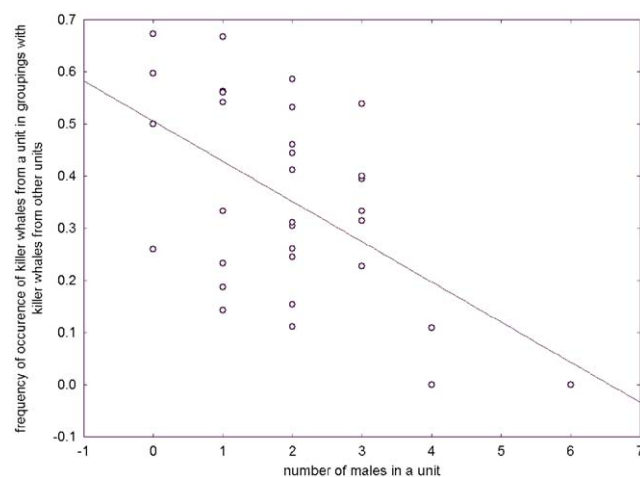


Fig. 6. The relationship between number of males in a unit and the encounter rate of killer whales from the unit in groupings with killer whales from other units.

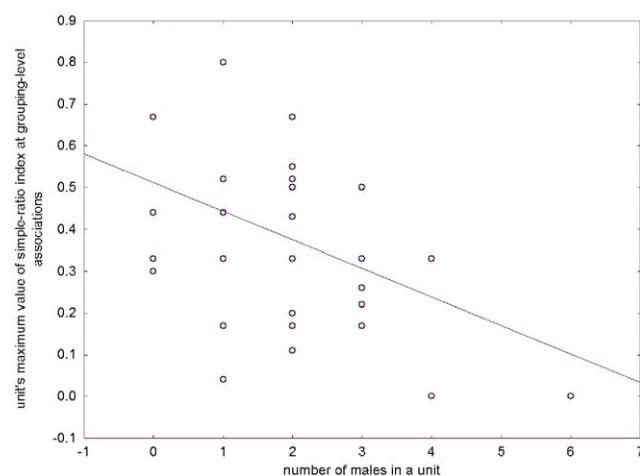


Fig. 7. The relationship between number of males in a killer whale unit and the maximum value of the simple-ratio association index in the grouping-level associations.

$F = 12.34$, $p < 0.01$) and (b) the value of the unit's maximum SRI in grouping level associations ($R^2 = 0.17$, $F = 6.04$, $p < 0.05$). No relationships were revealed between a unit's size, proportion of males, number of calves and small juveniles, proportion of calves and small juveniles and (a) the frequency of the unit's occurrence in groupings with other units and (b) the value of the unit's maximum SRI in grouping level associations.

The units with a large number of mature males rarely formed groupings with other units (Fig. 6) and had low maximum SRI values at grouping-level associations (Fig. 7).

The similarity of vocal dialects

We were unable to define the full repertoires of discrete calls for some units due to lack of recordings. In all, 32 units were included in the analysis of dialect similarity. Among them we identified 14 acoustic pods in three acoustic clans: Avacha clan, K20 clan and K19 clan. Avacha clan was more common and numerous; it included 29 units. We found 11 acoustic pods in Avacha clan. The number of units per acoustic pod varied from one to five (mean \pm SD = 2.2 ± 1.37).

The 11 acoustic pods from Avacha clan had distinct repertoires of 6–11 discrete call types. A single-linkage dendrogram based on the Dice's association coefficient between dialects shows the acoustic pod associations based on acoustic similarity (Fig. 8).

K20 clan was represented by one acoustic pod which included three units. K19 clan included two acoustic pods. One of these pods included two units and another consisted of only one unit.

There were also some units with dialects that differed from all those described above. The acoustic pods and clans for these units have not been defined to date due to insufficient data.

Comparing the results of the acoustic and the social analysis

The values of SRI (grouping-level associations) between pairs of units from the same acoustic pods ($N = 32$) were significantly higher than the values between pairs of units from different acoustic pods ($N = 374$) ($p < 0.001$, $U = 2106.5$). The values of SRI between pairs of units from the same acoustic clans ($N = 280$) were significantly higher than the values of

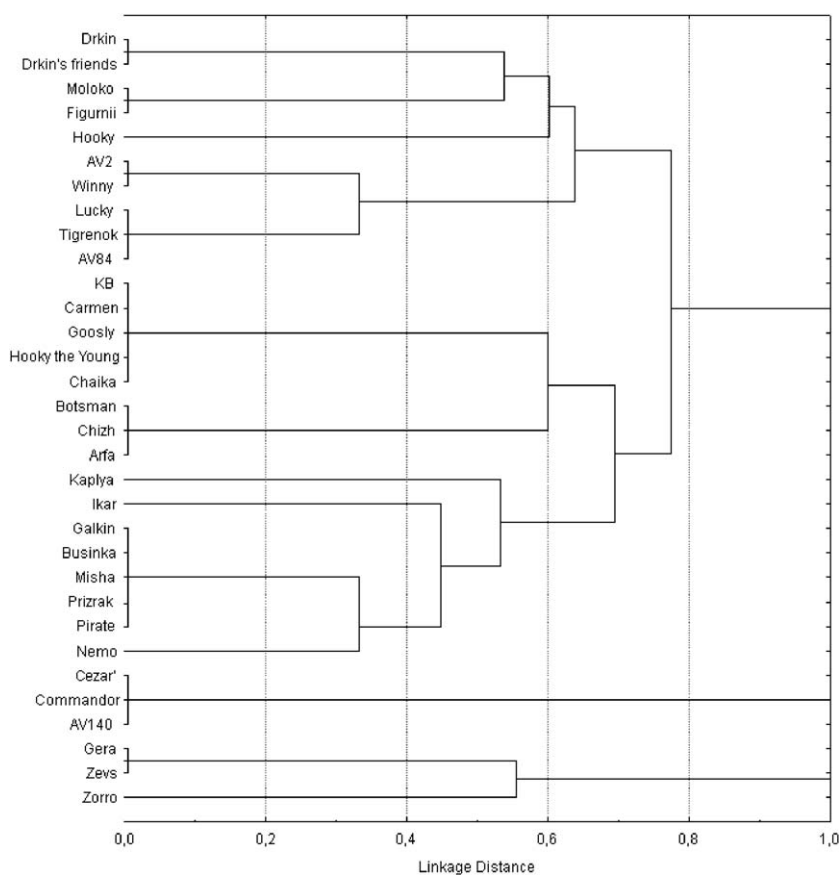


Fig. 8. Dendrogram showing the degree of acoustic similarity between killer whale units.

SRI between pairs of units from different clans ($N = 126$) ($p < 0.001$, $U = 14310.5$).

Most aggregation-level strong associations ($0.4 \leq \text{SRI} < 1.0$) were between units within the same acoustic pods (AV90 pod, AV55 pod and AV25 pod). The only strong association ($\text{SRI} > 0.4$) on the aggregation level outside of an acoustic pod was between Nemo's unit (part of the AV52 pod) and Misha's unit (part of the AV55 pod) (Table 2).

Discussion

The analysis of association patterns between individuals showed that the killer whales of Avacha Gulf form nonrandom associations and stable social units. As with the units of Northeast Pacific killer whales called matriline (Bigg et al. 1990; Matkin et al. 1999b; Baird and Whitehead 2000), the units of Avacha Gulf killer whales consisted of animals of different age–sex classes, and included maternal relatives. There is little data on the kinship between whales within most units in Avacha Gulf. Still, most of the units included at least one mature female accompanied by one calf or two offspring of different ages. All the units were observed to have stable membership at least over two years (2005–2006). Some units were known to be stable for more than seven years. Long-term associations between individual whales were also described for the resident and transient killer whales of the Northeast Pacific (Bigg et al. 1990; Matkin et al. 1999b; Baird and Whitehead 2000). Killer whale units from Avacha Gulf were found to have various features consistent with the social organization of the resident killer whales of the Northeast Pacific (Bigg et al. 1990; Matkin et al. 1999b; Baird and Whitehead 2000):

1. The mean size of a unit is close to the mean size of Northeast Pacific matriline (4–8 animals).
2. A unit can include three generations of whales as do matriline.
3. At least some males and females exhibit absence of dispersal from a unit after reaching sexual maturity.

Thus, it is supposed that the units of resident-type Avacha Gulf killer whales are equivalent to matriline.

Aside from the 36 units consisting of 3–16 animals, there was one male Brodyaga who was not included in any unit and spent most of the time as a solitary male. He also had no stable associations on an aggregation level, though he was never seen alone in the area and could be found in aggregations with different units from Avacha clan. Among resident killer whales in the Northeast Pacific, there were no comparable examples of long-time observations of lone killer whales remaining outside of stable associations with other individual

whales (Bigg et al. 1990; Matkin et al. 1999a, b; Ford et al. 2000). Brodyaga's behaviour could be explained by the loss of all his close relatives or by his possible dispersal from his natal group. However, his consistent presence in various aggregations and in some groupings indicated that he maintained associations within his community.

Thus, the picture of a killer whale community that is emerging is of a kind of fission-fusion society with a multi-tiered social structure. Killer whales form groups that represent temporally stable individual associations as well as more fluid and temporally variable associations. Maternal kinship plays an important role in determining the stability of bonds between resident killer whales.

The differences in the association patterns could be reflected not only in terms of time (temporal associations) but also in terms of space (spatial associations) as shown for sperm whales (*Physeter macrocephalus*) (Whitehead and Weilgart 2000). Killer whales that form a grouping might associate not only by means of vocal communication but also through visual and tactile contact. Yet within an aggregation, a high degree of coordination also appears to be occurring between killer whales, although aggregations are often formed by animals from different units and different acoustic pods, and groupings within the aggregation can be farther than 3–5 km away from each other. Vocal communication in killer whales makes it possible to establish associations between groupings of whales at distances of more than 10 km (Miller 2002). Thus, killer whale aggregations seemed to be more than a casual form of killer whale association and may be based on extrinsic ecological factors, such as prey distribution. Filatova et al. (2008) found that the level of social behaviour increased in large multi-pod killer whale aggregations. The groupings recorded during these aggregations generally travelled in the same direction, often approaching each other and usually making the same activity changes.

The different levels of association patterns – grouping level and aggregation level – could reflect different types of relationships in killer whale communities and be underlain by different social and ecological factors. The aggregation-level association analysis of killer whale units showed that particular units were often seen in aggregations together although they rarely formed groupings with each other. This corresponds with the observations made in a community of resident killer whales from Alaska. Although the intrapod groups from the AB pod were often a part of the same aggregation, they tended not to mix with each other as a single pod (Matkin et al. 1999b). All three units from the AV90 acoustic pod also had stable associations at the aggregation level. At the same time, during 2005, killer whales from AV84's unit within the AV90 acoustic pod

formed such strong grouping-level associations with the whales of Prizrak's unit from the AV55 acoustic pod that they could be considered members of the same unit.

Our results showed that units have stronger associations within, as opposed to outside, acoustic pods. In a few cases high levels of associations were found between units from different acoustic pods. Such associations could be explained by common ancestries as reflected in the similarity of vocal dialects (Fig. 8, Table 2). The dialect similarity could contribute to the forming of associations between different acoustic pods.

At the same time, in several cases, killer whale units from the same acoustic pod had low levels of association. For example, AV2's unit and Winny's unit were members of the same acoustic pod and yet they were never seen to form groupings and had no associations at the aggregation level. Also, Pirate's unit shared a vocal dialect with other units from the AV55 acoustic pod, but usually traveled separately. Such apparent disparity in social and acoustic associations can be explained by the differing speed of change in social structure and vocal dialects. The changes in associations and the fission of related units might lead to dialect change, but the speed of such changes might be highly variable and depend on sex and age composition, and the size of the unit. Ford and Ellis (2002) remarked that different demographic factors such as maturation of offspring, proportion of males in the matriline, and death of a matriarch may have a strong influence on the pod splitting. The influence of demographic factors on social structure can be seen in various mammalian fission-fusion societies. The social structure of the African elephant (*Loxodonta africana*), for example, is affected by various factors including the age of a matriarch which influences the size of the group led by the matriarch (Wittemyer et al. 2005). In chimpanzees (*Pan troglodytes verus*), with decreasing population size and fewer males, chimpanzees form larger and more cohesive groups affecting the community social structure (Lehmann and Boesch 2004). A killer whale matriline with a high percentage of males tends to travel more independently (Bigg et al. 1990; Matkin et al. 1999b).

Our results indicated that the number of males influences stable associations as well as occasional associations between units. The units of AV2, Winny and Pirate all included more males than average for a unit (Table 2). The behaviour of mature males which tended to spend more time as solitary animals apparently influenced the behaviour of the whole unit (Bigg et al. 1990; Matkin et al. 1999b). The competition for resources could be one of the explanations for these processes. The foraging behaviour of resident killer whales is often correlated with fission into smaller subgroups and rarely occurs in large multi-pod killer whale aggregations (Hoelzel 1993; Filatova et al. 2008). Adult males tend to forage independently and share

prey with other killer whales less often than do adult females and subadults (Hoelzel 1993; Ford and Ellis 2006). Thus, foraging in a group with a large number of males may be less beneficial than foraging in a smaller group. The number of mature males might be causing the low frequency of associations of AV2's unit with other units in the community, including Winny's unit although it is the same acoustic pod. The composition of AV2's unit and Winny's unit could have led to a faster split between them, even though the dialect has not changed yet.

In the Northeast Pacific, killer whale pods were initially revealed based on traveling patterns and later defined as typically 1 to 3 related matrilineal lines that travel together most of the time (>50%) (Bigg et al. 1990; Ford 2002) (Table 1). Later, Ford and Ellis (2002) disputed the use of the term 'pod'. They showed that in some years, strong associations could be found between the related matrilineal lines of the same pod while in other years matrilineal lines might associate with matrilineal lines from different pods. In these cases, there would be no strong associations within the given pod. Therefore, using 'pod' to identify matrilineal lines that travel together might not always reflect the genealogical relationships between matrilineal lines. A specific vocal dialect was found for each pod in the Northeast Pacific (Ford 1991). The results of our acoustic analysis indicated that Avacha Gulf killer whales have vocal dialects at the level of a single unit or several units. As the vocal dialect of a pod remains stable for a long time (Ford 1991; Yurk 2005; Foote et al. 2008) compared to associations between matrilineal lines or killer whale units, we recommend using the specific term 'acoustic pod' to identify one or more units or matrilineal lines which share the same vocal dialect. Thus, 'acoustic pod' does not reflect associations between killer whale matrilineal lines or units based on traveling patterns that could change rather quickly. Instead, 'acoustic pod' might better reflect the kinship relationships between matrilineal lines or units based on vocal traditions (Barrett-Lennard 2000; Deecke et al. 2000).

Most units showed a higher level of association inside acoustic pods compared to outside them. The units belonging to one acoustic pod preferred to form groupings with each other more often than with units from other acoustic pods. Some of them formed strong associations at the aggregation level. Our results also showed that the association patterns between units could change rather quickly and do not always reflect the level of acoustic similarity. But the vocal dialect of a unit is more stable than the association patterns between units and might better reflect the overall kinship relationships.

All known acoustic clans – Avacha, K19 and K20 clans – were regularly seen in the same aggregations and sometimes encountered in the same groupings. We suppose that the three clans are members of the same community of Avacha Gulf resident killer whales. Besides

these three clans, some units were encountered in the area only rarely during the eight-year study period and their dialects differed from the known clans. The Avacha Gulf area could be a 'core area' in the Russian Far East for killer whales of one community as well as a place where other communities visit or pass through. There are also known core areas in the Northeast Pacific, as well as overlapping home ranges, used by killer whales from different communities (Ford et al. 2000).

In 2003, captors targeted and removed two female killer whales from Avacha acoustic clan, one of which suffocated and died in the net while the other was flown to an aquarium on the Black Sea where she died 13 days later (Burdin et al. 2007). Subsequently, killer whale capture permits were moved to other management zones of the Russian Far East, outside of eastern Kamchatka (Fig. 1).

However, with killer whales potentially travelling considerable distances and using large habitat areas in the Russian Far East, the current annual capture quotas (6–10 individuals per year) divided between four management zones (Fig. 1), continue to be permitted in ignorance of the abundance, distribution, and social structure of these animals. Avacha acoustic clan might still continue to be captured and cropped on its travels, as happened repeatedly with the northern and southern (Vancouver Island) communities in the Northeast Pacific (1965–1977) before there was an understanding of the social structure (Bigg and Wolman 1975).

The capture and removal of the two female killer whales from Avacha acoustic clan leave these units with fewer breeding females. This could affect the breeding potential of the units and association patterns between units. Whales of different age–sex classes might play different roles in the maintenance of the social integrity of the community critical to their survival (Williams and Lusseau 2006). Williams and Lusseau showed that juveniles and immature females appear to play an important role in maintaining cohesion between matriline. Analyzing 30 years of data around Vancouver Island, they found that the social network of resident killer whales was more likely to fragment under targeted captures of whales of preferable age–sex classes, compared to random removals. The targeted whales for aquarium captures are often young individuals, mostly young females (Williams and Lusseau 2006).

The population structure, habitat use and distribution of the killer whale communities encountered in Avacha Gulf will become clearer as studies are extended to cover other parts of their range – and the range of other killer whale communities – in the vast Northwest Pacific.

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