Social complexity and cultural transmission of dialects in killer whales

Olga A. Filatova [a,*], **Tatiana V. Ivkovich** [b], **Mikhail A. Guzeev** [b], **Alexandr M. Burdin** [c] **and Erich Hoyt** [d]

[a] Faculty of Biology, Moscow State University, Vorobiovy gory 1/12, Moscow 119992, Russia
[b] Department of Vertebrate Zoology, Faculty of Biology, Universitetskaya emb. 7/9, St. Petersburg State University, St. Petersburg 199034, Russia
[c] Kamchatka Branch of Pacific Institute of Geography FEB RAS, Pr. Rybakov 19-a, Petropavlovsk-Kamchatsky 683024, Russia
[d] Whale and Dolphin Conservation, Park House, Allington Park, Bridport, Dorset DT6 5DD, UK
[*] Corresponding author's e-mail address: alazorro@gmail.com

Abstract

Many social animals have cultural traditions that may shape their societies while the social structure can in turn influence how the culture is acquired. Killer whales possess culturally transmitted dialects. The divergence of dialects was thought to occur simultaneously and consistently with the gradual fission of matrilines. In this paper we compare the social associations across matrilineal units, Bayesian phylogeny of dialects and similarity of particular syllables to test whether dialects affect social structure and whether associations or common origin define similarity of call types. We found that neither phylogeny of dialects nor similarity of syllables was correlated to associations between matrilineal units, but similarity of syllables was correlated to phylogeny of dialects for four of the six syllables analysed. The complexity and fluidity of social ties between matrilineal units and the variation in cultural transmission patterns produce a complex relationship between the social network and the socially learned vocalizations.

1. Introduction

Does culture shape society or does society shape culture? In humans it goes both ways. Many social animals also have cultural traditions (Laland

& Galef, 2009) that shape the structure of their societies while the social structure can influence how the cultural information or behaviour is acquired. Some of the most impressive examples of culture are found in whales and dolphins which include various socially transmitted behaviour patterns ranging from sophisticated foraging tactics to group-specific vocalizations (Rendell & Whitehead, 2001).

Social structure can influence cultural traditions in many ways, but mostly through cultural transmission that relies on the social bonds between animals. Cultural transmission can be vertical, horizontal or oblique (Cavalli-Sforza & Feldman, 1981), and its direction and precision is closely linked to the structure of the social network (e.g., Allen et al., 2013). On the other hand, the social network itself can be shaped by traditions if animals choose social partners based on culturally inherited behaviour.

For example, bottlenose dolphins have developed various hunting techniques in different regions (Connor et al., 2000) that are mostly transmitted from mother to offspring and in some cases between adult associates (Sargeant et al., 2005). Since dolphins tend to associate with individuals that utilize the same foraging strategies, the preference for a particular foraging strategy can influence the social relationships that form between individuals (López & Shirai, 2008; Ansmann et al., 2012; Mann et al., 2012).

In sperm whales (*Physeter macrocephalus*), social units with similar acoustic repertoires are organised into clans that do not associate with each other. Different clans can vary in movement patterns, foraging and social behaviour (Cantor & Whitehead, 2015). Cantor et al. (2015) demonstrated that clans are likely the result of cultural transmission through biased social learning of codas; thus, cultural transmission has helped shape sperm whale society.

The killer whale (*Orcinus orca*) is a model species for studying cultural evolution in cetaceans because the species is easily recognizable individually (Bigg et al., 1983) and possesses culturally transmitted repertoires of stereotyped call types, called vocal dialects (Ford, 1991). Killer whales, such as the resident-type in the North Pacific, live in stable matrilineal groups usually consisting of an old female and several generations of her offspring; new groups form through a gradual fission of a matriline after a matriarch's death (Ford, 2002). Ford (1991) suggested that the divergence of dialects occurs simultaneously and consistently with the gradual fission of matrilines. Deecke et al. (2010) found that acoustic similarity was correlated both

to social bonds and genetic relatedness and hypothesized that similarity of repertoires may strengthen social bonds. Crance et al. (2014) showed that captive young males learned the calls of an unrelated male with whom they had social bonds, supporting the idea that social bonds (but not necessarily relatedness) are closely connected to dialect transmission.

However, similarity patterns of killer whale calls do not always correlate with social associations between particular matrilines (Deecke, 1998); moreover, similarity patterns of different call types do not correlate with each other (Filatova et al., 2013). Filatova et al. (2013) suggested several mechanisms for how the differences in similarity patterns of call types from the same dialect might develop: horizontal transmission between matrilines, saturation of structural variation that increases the rate of call convergence, and/or the varying speed of change in different call types. To estimate the role of these processes in dialect evolution, a comparison of acoustic similarity with other factors, such as group relatedness and social bonds between groups, is necessary.

Deecke et al. (2010) compared relatedness with social associations and dialect similarity using whole contours of three call types. They found that relatedness did not correlate with associations, but similarity of some call types did correlate with relatedness and associations. The authors suggest that call structure plays a role in kin recognition and shapes the social bonds. However, the results may equally suggest that kinship is responsible for some similarities in calls while social associations are responsible for the other, i.e., some changes in call structure accumulate over time, while others are copied between associating groups. To reveal these connections, a detailed comparison of group relatedness, social network and call similarity is required.

In killer whales it is hard to determine maternal relatedness between matrilineal groups because mitochondrial DNA in this species is very conservative; for example, all Kamchatkan resident killer whales studied to date have the same control region haplotype (Parsons et al., 2013). Deecke et al. (2010) used microsatellites to determine the relatedness between matrilines, but in contrast to maternally transmitted mitochondrial DNA, microsatellites are inherited from both parents, so that the relatedness determined by this method is confused with paternal kinship that has no influence on the transmission of dialects.

In this study, instead of using genetic relatedness, we construct a phylogenetic tree of the full call repertoires (dialects) of Kamchatkan resident killer whales. Killer whale dialects consist of 7–17 call types (Ford, 1991), which can change in time with different speed (Deecke et al., 2000) and in different directions (Filatova et al., 2013). This system is analogous to a set of independently evolving phenetic traits and therefore appears to be a good basis for phylogenetic reconstructions. As socially learned calls change much faster than genetically transmitted traits, phylogenetic reconstructions of dialects work on the time scale of matriline divergence that we are interested in. Despite the inconsistency in similarity patterns of different syllables (Filatova et al., 2013), the phylogeny of full dialects should be generally consistent with relatedness patterns between matrilineal units: even if the call change is not linear and borrowing is possible, phylogenetic reconstructions would be robust to a limited amount of borrowing (Greenhill et al., 2009). Indeed, Deecke et al. (2010) showed that similarity patterns of some call types correlated with genetic relatedness. In this study we compare the data on call similarity with the phylogeny of dialects and social associations across killer whale matrilineal units to reveal whether culturally learned dialects affect social structure and which factors — common origin or current social associations — define the similarity of particular call types.

2. Methods

2.1. Study population

The resident killer whales of Eastern Kamchatka, Russia, are known to range along the east coast of Kamchatka peninsula from Avacha Gulf to Karaginsky Gulf and east to the Commander Islands (Filatova et al., 2012). Whales from this population live in stable social units that include maternal relatives with no dispersal observed (Ivkovich et al., 2010). Our data set does not go far enough back to reconstruct the full genealogies of these units, and we suspect that in some cases one unit can include more than one matriline, so we use the term 'matrilineal units' to denote these groupings.

Matrilineal units that share the same vocal dialect are attributed to the same pod, and pods with similar dialects form clans. To date, we recognize at least 62 matrilineal units, belonging to 20 pods in three acoustic clans which form a single community: the Avacha clan, the K19 clan and the K20 clan (Filatova et al., 2007; Ivkovich et al., 2010). The Avacha clan, consisting

of more than 13 pods and 30 matrilineal units, is the most commonly sighted. For this study we used only matrilineal units from the Avacha clan for which sufficient data were available.

In this paper we use three-letter abbreviations for the names of matrilineal units to make the text and the figures more concise (for the full unit names, see for example Ivkovich et al., 2010). The name of a matrilineal unit usually comes from the name of its most well-marked individual. The list of pods and matrilineal units of the Avacha clan can be found on our website (http://www.russianorca.com/orcas.php?mode=our&lang=en&pod=0).

2.2. Data collection

The data for this study were collected as part of the Far East Russia Orca Project in the Avacha Gulf, Kamchatka, during the summer months of the years 2000–2012. The underwater sound recordings were made from a 4 m inflatable boat while the engine was turned off, at sampling frequencies of 48 and 96 kHz. For the recording we used an Offshore Acoustics hydrophone (Offshore Acoustics, North Vancouver, BC, Canada) and CetaPhone hydrophone (Moscow State University, Moscow, Russia) with a Sony TCD-D100 DAT recorder (Sony, Tokyo, Japan) from 2000–2006 and a Zoom H4 flash recorder (Zoom, Tokyo, Japan) from 2007–2012.

Photographic identification was used to identify individual killer whales and matrilineal units. To take photographs, we approached the whales to a distance of 20–50 m, or moved the boat 200–300 m ahead of the animals and off to the side and waited until they passed. 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. (1983).

2.3. Bayesian phylogeny of dialects

Calls were classified according to the existing catalogue (Filatova et al., 2004). Stereotyped calls of killer whales often show some variations within types (Ford, 1991). When these variations are discrete, the type is divided into several subtypes; when the variations are gradual, no subtypes are traditionally distinguished (Ford, 1991). However, these variations can be important for the calculation of the phylogeny of dialects. Therefore, for the call types that displayed a graded continuum of structural variations we identified several subtypes that covered the full range of variation for each type within each matrilineal unit (Table 1).

Table 1.
Full repertoires of stereotyped call types used for the Bayesian phylogenetic analysis of dialects.

	K1	K2	K4	K5	K6	K7	K8	K10	K11	K12	K17	K21	K23	K24	K25	K27	K50
Arf	1	0	1	1	0	1	0	0	0	1	0	?	0	0	2	0	0
AV2	3, 4, 5	0	0	2	0	2	0	2	0	1, 2, 5	0	1	0	1	0	0	0
Bot	1	0	1	1	0	1	0	0	0	1, 2	0	?	0	0	?	0	0
Bro	1	0	0	3	0	?	0	?	0	?	1	0	0	0	0	0	0
Bus	2	0	0	3	0	3	0	1	?	2, 3	1	0	0	0	0	0	0
Car	1	?	1	5	0	2	1	0	0	1, 2, 4	0	2	0	0	?	0	0
Chi	1, 3	0	1	1	0	1	0	0	0	1, 2	0	1	0	0	2	0	0
Drk	3	1	1	6	0	2	0	0	0	1, 2	0	0	1	0	0	0	0
Fig	1, 3, 4	0	?	6	0	2	0	0	0	?	0	0	1	0	0	0	0
Gal	2	0	0	3	0	3	0	1	?	1, 2, 3	1	0	0	0	0	0	0
Goo	1	1	1	5	0	2	1	0	0	2, 4	0	2	0	0	1	0	0
Hoo	3, 4	0	0	0	1	2	0	1	0	1	0	1	0	0	0	1	1
Ika	1, 2	0	0	1, 4	0	3	0	1	1	1, 3	0	0	0	0	0	0	0
Kap	1, 2, 3, 6	0	1	4	0	3	0	1	0	2	0	0	0	0	0	0	0
Luc	3, 4	0	0	2	0	2	0	0	0	1	0	1	0	1	0	0	0
Mol	1, 3, 4	0	1	6	0	2	0	0	0	?	0	1	1	0	0	0	0
Nem	1	0	0	7	0	3	0	1	?	2	1	0	0	0	0	0	0
Pir	1, 3	0	0	3, 4	0	3	0	1	1	1, 2, 3	1	0	0	0	0	0	0
Pri	2, 3	0	0	7	0	3	0	1	1	2, 3	1	0	0	0	0	0	0
Tig	4	0	0	2	0	2	0	0	0	?	0	?	0	1	0	0	0
Win	3, 4, 5	0	0	2	0	2	0	2	0	1, 2, 5	0	1	0	1	0	0	0

Numbers 1–6 indicate the particular subtype of the given call type, zeros indicate the absence of the call type in the given matrilineal unit.

In order to define the phylogenetic relationships between the repertoires of matrilineal units (dialects), we performed Bayesian phylogenetic analysis using the software MrBayes (Nylander et al., 2004). A set of calls produced by each matrilineal unit was formatted as a matrix of phenetic traits; call types represented different traits, while subtypes represented variations of the same trait. A gamma model was run for 300 000 generations with sampling every 100 generations. Matrilineal units were divided into 'dialect groups' according to the results.

2.4. Analysis of social structure

For the analysis of social structure we used the data on the encounters of individually identified eastern Kamchatkan killer whales from 2002 and 2004–2011. The membership of individual whales in the matrilineal units

has been defined previously (Ivkovich et al., 2010). In this study we measured the strength of the social associations between matrilineal units, so that a matrilineal unit (and not individual whales) was used as the unit of analysis.

For the statistical analysis of associations we used the software SOCPROG 2.4 (Whitehead, 2009). As killer whales are well identified from photographs, we employed a simple ratio index (SRI) to measure associations between killer whale matrilineal units (Ginsberg & Young, 1992). We used the test for preferred/avoided associations (permuting associations within samples) to examine long-term associations for significance (Whitehead, 2008).

An aggregation was defined as all killer whales moving together within visual range of the research boat (Ivkovich et al., 2010). On a typical day we recorded 1–2 aggregations (max = 4). We therefore adopted a three-day sampling period so that the test for preferred/avoided associations had power for aggregation-level associations (Whitehead, 2009): matrilineal units were considered to be associated if they were found together in an aggregation within a three-day period.

We used a Mantel test (Schnell et al., 1985) in SOCPROG to check if the associations of matrilineal units within dialect groups differed from the associations between dialect groups. We used the Mantel test function in the R package 'vegan' (Oksanen et al., 2016) to test the significance of correlation between associations across matrilineal units and their dialects on the Bayesian phylogenetic tree.

We visualized the social network based on the social association indexes using the software NetDraw 2.141 (Borgatti, 2002).

2.5. Similarity of syllables

Killer whale calls consist of syllables, i.e., multiple sequential components, separated by abrupt frequency shifts (Ford, 1991; Shapiro et al., 2011). In addition, some calls (so-called 'two-voiced' or 'biphonic' calls) contain an overlapping high-frequency component that is independently modulated.

We analysed the similarity of syllables across different matrilineal units in the three most common call types: K1, K5 and K7 (Figure 1). The set of calls used for this study was the same as in Filatova et al. (2013), where details of the call selection process are given. We used ten calls of each type per matrilineal unit, except for the K5 call type. The K5 call type was represented
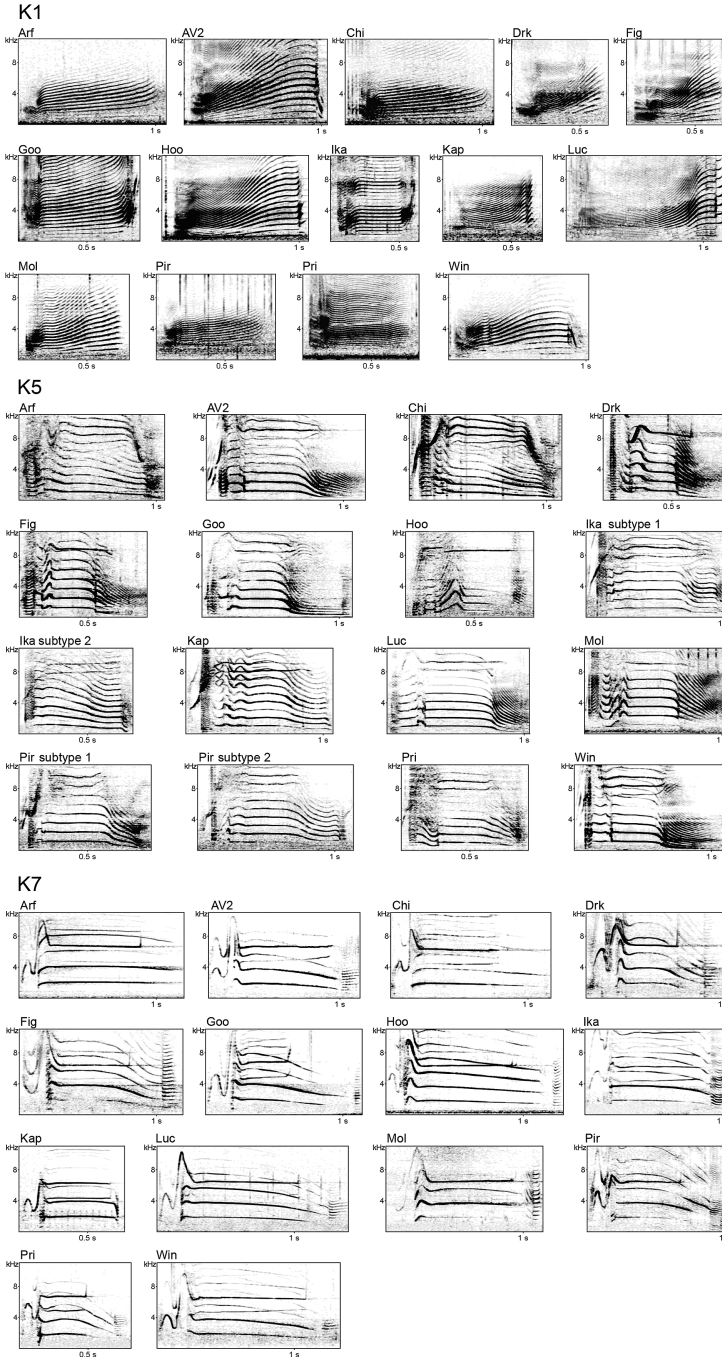
Figure 1. Sample sonograms of K1, K5 and K7 calls of 14 matrilineal units used for the analysis of syllables.

by two distinct subtypes in the Ika and Pir units, so we used ten calls from each of those subtypes (twenty K5 calls per unit in total).

We used only the syllables for which we were able to extract contours from all ten sounds for each matrilineal unit. As some syllables are usually more pronounced than others, and some can be totally absent in some matrilineal units, not all syllables of each call type were suitable for obtaining the required sample size. Two of the three analysed call types (K5 and K7) were biphonic, but only for the K7 type we were able to measure the high-frequency component in a sufficient number of calls. As a result, we used one syllable of the K1 call type, three syllables from the lower-frequency component of the K5 call type, and two syllables of the K7 call type: one from the lower-frequency and one from the higher-frequency component (Figure 2).

Call contours were extracted using a custom-made MATLAB script for manually tracking frequency contours of each syllable. After the operator selected enough points to track all modulations of the frequency contour, the algorithm smoothed and interpolated them to produce a vector of frequency measurements with a sampling interval of 0.01 s.

The similarity of contours was measured using dynamic time-warping, which allows limited compression and expansion of a signal's time axis to maximize the frequency overlap with a reference signal (e.g., Itakura, 1975). For this study, we adopted a modified version of the warping algorithm developed by Deecke & Janik (2006). For any two compared contours, the similarity matrix was calculated by dividing the smaller frequency value by the larger value at each point and multiplying by 100. Then the algorithm calculated a warping path through the cells of the similarity matrix with maximum similarity values. For two identical contours, this path lies on the diagonal of the similarity matrix; if input contours differ, the warping path can deviate from the diagonal, which enables the matching of contours that are similar in shape but different in length (see Figure 1 in Deecke & Janik, 2006). The percent similarity of the contours was calculated as a sum of the similarity values along the warping path divided by the length of the warping path.

To determine the similarity of each syllable between each pair of matrilineal units, we calculated the mean of the similarity values between each pair of contours for that syllable from the two units. From the similarity matrix of units a complete linkage dendrogram (Everitt et al., 2001) was constructed.

To reveal the specific parameters responsible for the differences between the syllables of different units, we used linear discriminant analysis. We
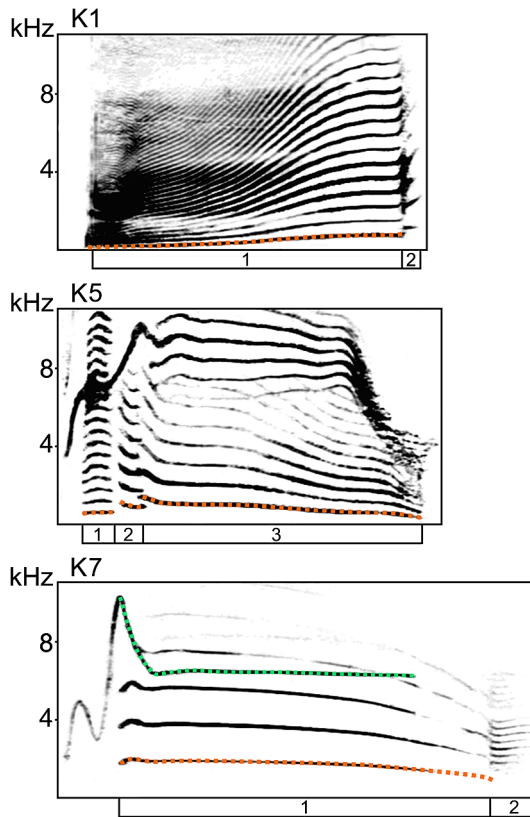
Figure 2. Syllables of K1, K5 and K7 calls, from which the contours were extracted. Syllables of the low-frequency components are shown in red, and the syllable of the high-frequency component is shown in green. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

automatically measured 14 parameters from each syllable contour using a custom-made MATLAB script (see Table 2 and Figure 3).

These parameters were then used to perform linear discriminant analysis in R (R Core Team, 2014) using the package 'MASS' (Venables & Ripley, 2002). The coefficients of linear discriminants were used to determine which parameters contributed more to the discrimination between matrilineal units.

We used the Mantel test in R package 'vegan' (Oksanen et al., 2016) to compare associations, dialect distances on the Bayesian phylogenetic tree and syllable similarity matrices calculated though dynamic time warping

Table 2.
Fourteen parameters from each syllable contour used to perform linear discriminant analysis.

1. f_{start}	Frequency at the start of the contour
2. f_{middle}	Frequency in the middle of the contour
3. f_{end}	Frequency at the end of the contour
4. f_{max}	Maximum frequency
5. f_{min}	Minimum frequency
6. t_{max}	Time interval between the start of the contour and the point with the maximum frequency
7. t_{min}	Time interval between the start of the contour and the point with the minimum frequency
8. length	Length of the contour
9. mod1	Modulation (i.e., frequency rise or fall) of the first quarter of the contour
10. mod2	Modulation (i.e., frequency rise or fall) of the second quarter of the contour
11. mod3	Modulation (i.e., frequency rise or fall) of the third quarter of the contour
12. mod4	Modulation (i.e., frequency rise or fall) of the fourth quarter of the contour
13. med1	Median frequency value of the first half of the contour
14. med2	Median frequency value of the second half of the contour
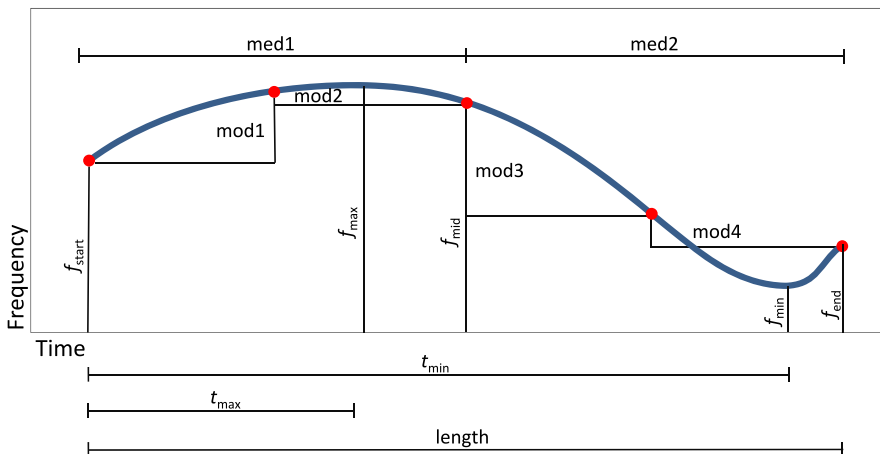
Figure 3. Time and frequency parameters measured from each syllable. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

and linear discriminant analysis to infer the interplay between the social structure, the phylogeny of dialects and the similarity of specific syllables.

3. Results
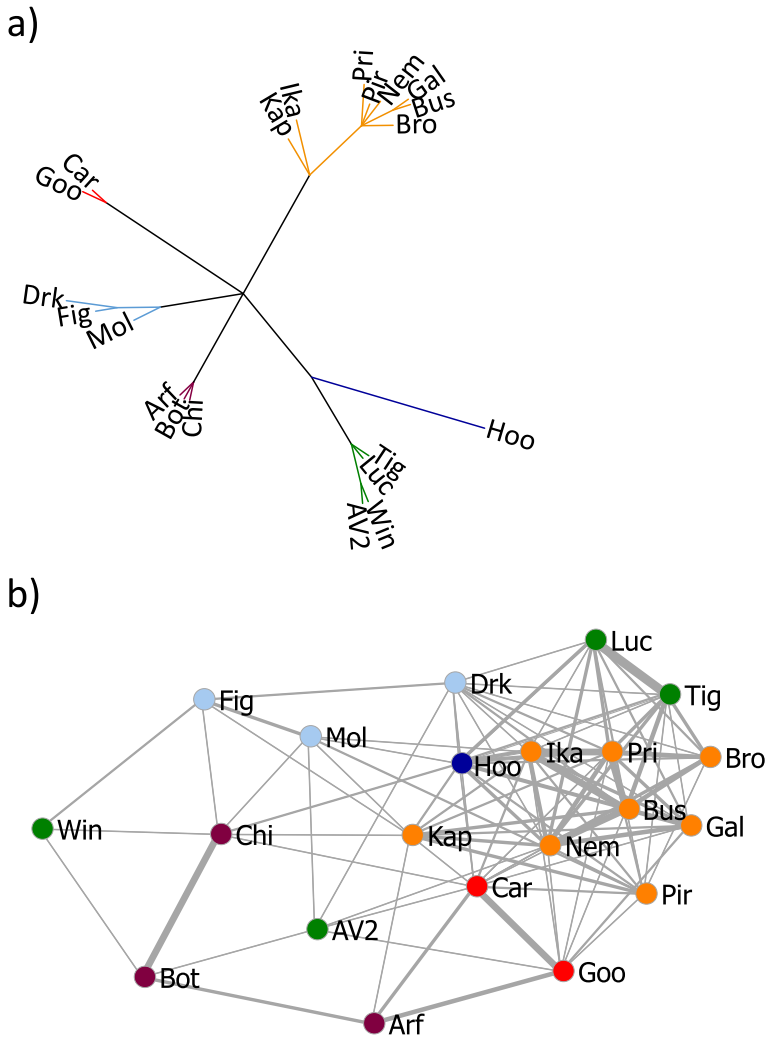
3.1. Bayesian phylogeny of dialects

For this analysis we used 21 killer whale matrilineal units for which we were able to obtain sufficient recordings to determine the full repertoires of stereotyped call types (dialects). We divided these units into dialect groups by the distances on the Bayesian phylogenetic tree (Figure 4a). We accepted 0.2 as a natural cutoff value based on the shape of the histogram of the Bayesian distances (Figure 5). As a result, we distinguished six dialect groups:

1. Chi, Bot, Arf;

2. Mol, Fig, Drk;

3. Goo, Car;

4. Pri, Pir, Nem, Gal, Bus, Bro, Ika, Kap;

5. Win, AV2, Tig, Luc;

6. Hoo.

3.2. Social structure

We analysed the degree of social associations between the 21 matrilineal units that were included in the analysis of the Bayesian phylogeny of the full repertoires (Figure 4b). These units were encountered on at least 10 separate days (mean 30.4 days) and in at least three different years (mean 7 years) during the study period. The test for preferred/avoided associations was significant for long-term preferred associations (SD of real data > SD of permuted data, $p < 0.005$; CV of real data > CV of permuted data, $p < 0.005$).

Strength of associations between units was not significantly correlated to the distances between their dialects determined through Bayesian inference. However, units from the same dialect group had significantly stronger associations than units from different dialect groups (Mantel test, $p < 0.005$; median simple ratio index (SRI) within dialect groups $= 0.25$ (range 0–0.66), median SRI between dialect groups $= 0.10$ (range 0–0.36)).

Figure 4. (a) Phylogeny of full repertoires of 21 killer whale matrilineal units calculated through Bayesian inference. The colour of the edges indicates the dialect group. (b) Unit-level social network for 21 killer whale matrilineal units. The colour of the nodes corresponds to the dialect group. Only the connections with a simple ratio index above the median level between dialect groups (0.1) are shown. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.
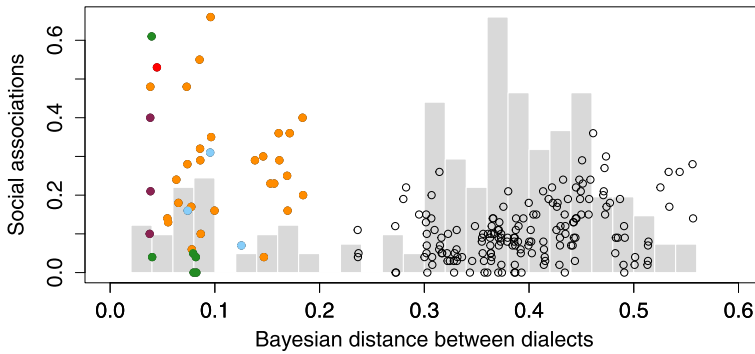
Figure 5. Social associations between matrilineal units plotted against Bayesian distances between dialects. Open circles indicate the relationships of units/dialects between dialect groups, and closed circles indicate the relationships within dialect groups; the colour corresponds to the dialect group in Figure 4. Histogram of Bayesian distances between dialects is shown in the background in grey. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

3.3. Similarity of syllables

We determined the acoustic similarity of six specific syllables of the three most common call types (K1, K5 and K7) from 14 matrilineal units using dynamic time warping (DTW, Figure 6) and linear discriminant analysis (LDA, Figure 7). The distances between the units obtained through the linear discriminant analysis of syllable parameters were consistent with the distances measured by dynamic time warping: distance matrices were significantly correlated for all syllables (Mantel test, LDA vs. DTW, $p < 0.01$ for all six syllables).

The parameters that contributed most to the LDA division of matrilineal units for the K1 syllable were the modulation of the third quarter of the contour and the middle frequency. For the first and second syllables of K5, the most important parameters were length and the position of the minimum frequency point, while for the third syllable of K5 both position and frequency of the minimum frequency point were important. For K7, the low-frequency syllable differs the most across matrilineal units in the modulation of the second quarter of the contour and the maximum frequency, while the high-frequency syllable was the most different in length and in the median frequency of the second half of the contour.

Neither the distances between matrilineal units obtained through the linear discriminant analysis of syllable parameters nor the distances measured by dynamic time warping of contours were significantly correlated to the social associations (Mantel test, $p > 0.05$). The distances obtained through the LDA were correlated to the Bayesian phylogenetic distances for four syllables: for the K1 syllable, for the third syllable of K5 and for both syllables of K7 (Mantel test, $p < 0.01$). The distances obtained through the DTW were correlated to the Bayesian phylogenetic distances for the third syllable of K5 and the high-frequency syllable of K7 (Mantel test, $p < 0.01$).

4. Discussion

The traditional model of dialect evolution in killer whales suggests that dialects diverge gradually along with the divergence of matrilines, and therefore similarity of dialects and specific calls should correlate to the social associations between matrilines (Ford, 1991). Indeed, Deecke et al. (2010) found that similarity of two call types in Canadian Northern Resident population was correlated to associations. On the contrary, in our study neither phylogeny of dialects nor similarity of specific syllables were correlated to associations. Associations within dialect groups were stronger on average because matrilineal units with the strongest bonds always belonged to the same dialect groups. However, many units from the same dialect groups also had weak or zero associations, contributing to the lack of overall significant correlation.

What factors define social preferences in killer whales? Deecke et al. (2010) suggested that the similarity of dialects drives killer whale groups to stay together. However, our results show that at least in some cases it does not work that way: some matrilineal units with shared dialects had no or weak social bonds. Williams & Lusseau (2006) found that juvenile killer whales, especially females, appeared to play a central role in maintaining the social network. Therefore, the ratio of young females may affect the cohesion of particular matrilineal units. Ivkovich et al. (2010) showed that units with a high number of adult males were less social — they rarely formed groupings with other units and had lower association strengths. Two units in our analysis that were very similar acoustically but had weak associations — AV2 and Win units — were also among the units with the highest number of adult males (Ivkovich et al., 2010). This at least partly explains the lack of social bonds between them.

Animals usually come together to mate, to defend themselves from predators or to cooperate in food search and prey capture. Resident killer whales may form large aggregations of many matrilineal units for social and mating purposes (Filatova et al., 2009), but these aggregations are fluid, lasting only up to several hours. However, small aggregations of two to three killer whale matrilineal units can travel together for many days. The function of these smaller aggregations is unknown: they may play some role in mating behaviour or have other functions. Killer whales are said to have no natural predators; however, transient (mammal-eating) killer whales could conceivably pose a threat to young residents, driving residents with newborns to seek the company of other matrilineal units to strengthen collective defence. Prey search and capture may be another reason, as resident killer whales sometimes cooperate in herding schooling fish (Tarasyan et al., 2005).

In theory, closely related matrilineal units should benefit from travelling together, because it reduces competition and enables kin-selection-based altruism (e.g., food sharing, Ford & Ellis, 2006). However, we found that some matrilineal units with completely different repertoires spent a substantial amount of time together.

The phylogeny of dialects calculated through Bayesian inference was correlated to the similarity patterns of four syllables: the K1 syllable, the third syllable of K5 and both syllables of K7. Only the similarity of the first and the second syllables of K5 was not correlated to the dialect phylogeny neither by LDA nor by DTW distances. These two syllables are the shortest among the six syllables analysed (Figure 2), which limits their structural variation. The lack of correlation to the dialect phylogeny can therefore result from structural saturation: short syllables quickly reach the maximum divergence and then can only converge, which erases the phylogenetic signal.

The patterns of syllable similarity obtained through the LDA were significantly correlated to the distances measured by DTW for all six syllables. These methods are based on different principles — LDA calculates the distances using a set of time and frequency measurements, while DTW compares the shape of complete frequency contours. The fact that the distance matrices obtained through both methods were correlated confirms that these methods are appropriate for measuring syllable similarity.

None of the syllables analysed demonstrated the complete concordance of their similarity patterns and the phylogeny of dialects calculated through

Bayesian inference. In many cases, matrilineal units from the same dialect group clustered together on the DTW similarity trees and LDA plots, yet some inconsistencies were present in each syllable. Different syllables showed different patterns of inconsistencies, confirming that they were caused not by mistakes in the phylogeny estimation, but by deviations in syllable evolution. There were no specific time or frequency parameters that were responsible for the differences between matrilineal units in all syllables. Generally it appears that syllables change in a rather stochastic manner, though most of them have a somewhat pronounced correlation to the phylogeny.

The greatest discrepancy between repertoire phylogeny and syllable similarity on the one hand, and social associations on the other, was in AV2 and Win matrilineal units. They were close acoustically, in terms of both repertoires and syllables, but shared no social bonds. Luc unit from the same dialect group was often close to them on the syllable similarity trees (Figure 6) and LDA plots (Figure 7), though also having no social bonds with them. In this case the acoustic similarity appears to be the consequence of a common origin, while social bonds have been weakened in the process of unit divergence. This probably reflects the fluidity of social bonds compared to the much more conservative acoustic repertoires: social bonds between killer whale units can change even over a span of several years (Foster et al., 2012), while repertoires remain more or less stable over tens of years (Ford, 1991; Foote et al., 2008).

Some clusters clearly demonstrated the simultaneous process of social and acoustic divergence. Arf and Chi matrilineal units were clustered together on all similarity trees except the trees for the second syllable of the K5 type and the high-frequency syllable of the K7 type (Figure 6c, f). Arf and Chi units have weak social bonds but they both have strong bonds with Bot unit from the same dialect group (Bot unit was not included into the syllable analysis due to the lack of good-quality calls). Therefore we can speculate that these units share a recent common origin, but have already started to diverge socially and acoustically. Their acoustic divergence has started from the second syllable of the K5 type and the high-frequency syllable of the K7 type, but it does not mean that these syllables are more flexible than others: they retain substantial similarity within other dialect groups. For example, the dendrogram for the second syllable of the K5 type clusters together Drk and Fig units and Ika and Pir units from the same dialect groups, and the
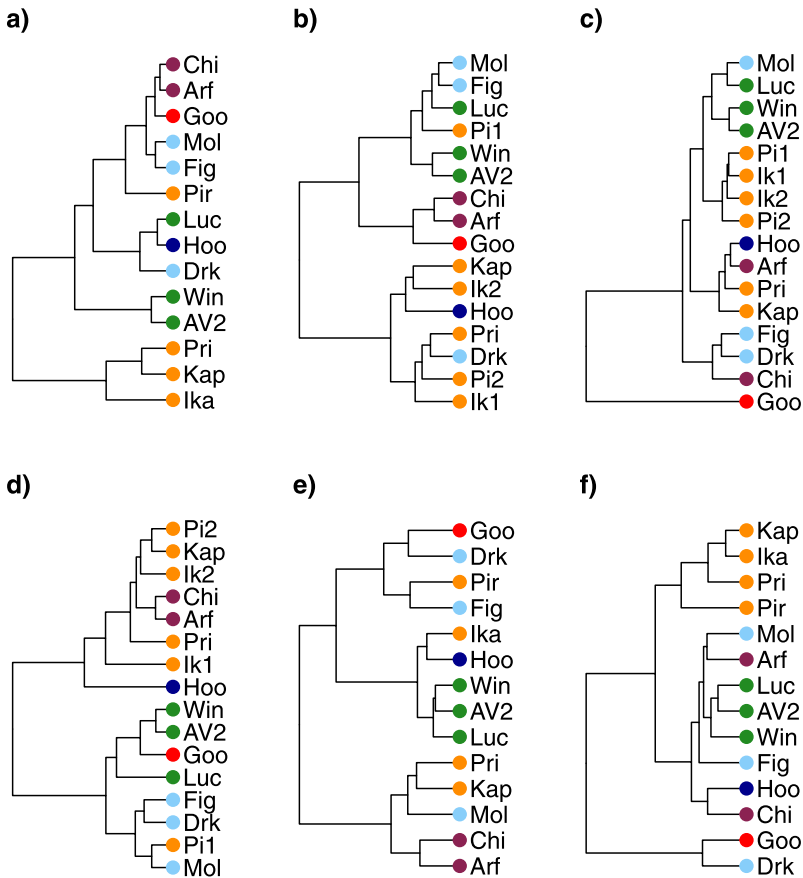
Figure 6. Acoustic similarity of six syllables of K1, K5 and K7 call types from 14 matrilineal units determined using dynamic time warping: (a) main syllable of K1 call type; (b) first syllable of K5 call type; (c) second syllable of K5 call type; (d) third (main) syllable of K5 call type; (e) main syllable of K7 call type; (f) high-frequency syllable of K7 call type. The colour of the circles corresponds to the dialect group in Figure 4. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals. brillonline.com/content/journals/1568539x.

dendrogram for the high-frequency syllable of the K7 type clearly separates the fourth dialect group (Kap, Ika, Pri, Pir) from all others.

Despite none of the syllable similarity patterns being significantly correlated to associations, some patterns in acoustic similarity corresponded to social structure. For example, Arf and Goo units form the most prominent social bond outside their dialect groups and cluster together on the similarity
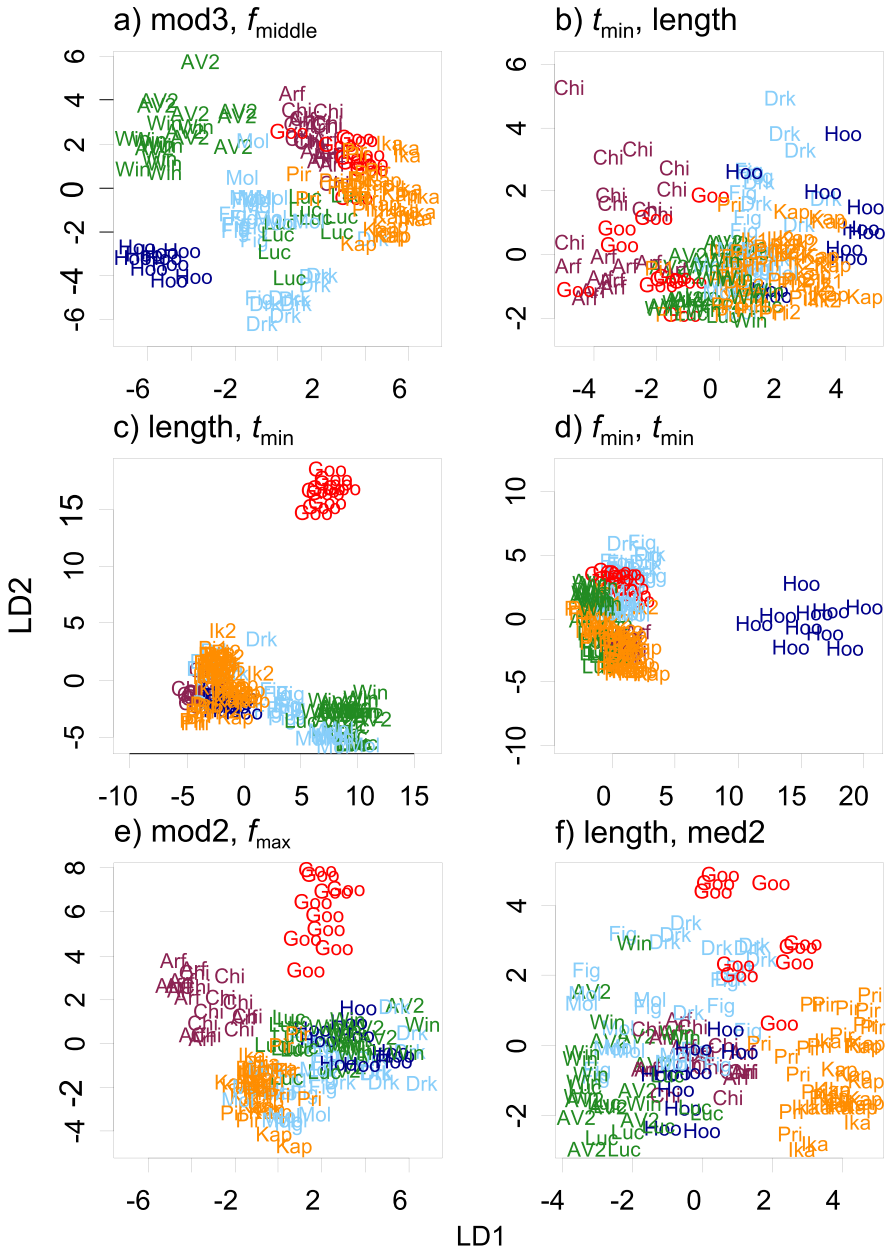
Figure 7. Plots of the six measured syllables of 14 matrilineal units in the space of the first two linear discriminants. Two parameters that contributed most to the discrimination of matrilineal units are indicated above each plot. The colour of the unit abbreviations corresponds to the dialect group in Figure 4. This figure is published in colour in the online edition of this journal, which can be accessed via http://booksandjournals.brillonline.com/content/journals/1568539x.

trees of the main syllable of the K1 type and the first syllable of the K5 type (Figure 6a, b), as well as on the corresponding LDA plots (Figure 7a, b). We cannot claim that these similarities were caused by horizontal transmission and not just by random convergence, but the fact that this pattern arose in two syllables from different call types supports the former hypothesis.

The Goo unit also showed an interesting example of non-gradual divergence of syllables. The fundamental frequency of the second syllable of the K5 call type in this unit was double the frequency used by other units. This is most likely caused by the abrupt octave shift such that the first harmonic becomes the new fundamental frequency. This has been described in killer whales previously — N7iii subtype in Northern Resident killer whales has a frequency of its main syllable half that of the other subtypes of N7 type (Ford, 1991). This example demonstrates that in some cases killer whale calls can abruptly change even in recently diverged units.

In general, it appears that the relationships between phylogeny, social associations and the similarity of specific syllables are complex and can depend on various factors. Sometimes matrilineal units rapidly diverge socially, while the dialects and almost all the syllables remain similar. In other cases, acoustic divergence may occur at the same pace or even faster than social divergence. Syllables change at varying speeds in different matrilineal units, such that the same syllable can be similar in some units and dissimilar in others, while for another syllable the similarity pattern can differ. In some cases social and/or syllable convergence can occur, leading to some similarities in social structure and syllable patterns but not in the full repertoires. No syllables in the three call types analysed appear to be significantly more conservative or flexible than others.

The complex interplay between social associations and culturally transmitted vocalizations suggests that the structure of a killer whale community is more complex than previously understood. Centola et al. (2007) argued that if social ties can change with cultural influence, this suggests a complex relationship between heterogeneity and cultural diversity, in which increased heterogeneity can reduce cultural group formation while simultaneously increasing social connectedness. In killer whales, social dynamics are also influenced by other non-social and non-cultural factors, such as sex ratio in groups (Ivkovich et al., 2010) and prey abundance (Foster et al., 2012). Our results provide some evidence in favour of horizontal transmission, and also support the idea that call types and even syllables within a call can change at

different speeds, and sometimes this change can be abrupt rather than gradual. The complexity and fluidity of social ties between matrilineal units on the one hand, and the variation in cultural transmission patterns on the other hand, produce a complex non-linear relationship between the social network and the socially learned vocalizations. Syllable similarity can run counter to social associations and/or repertoire phylogeny, and social associations and repertoire phylogeny can, in turn, contradict each other. The interplay between associations and cultural transmission in cetaceans has been little studied theoretically or empirically, but may be an important determinant of social and cultural evolution in these large-brained animals.

Acknowledgements

References

Allen, J., Weinrich, M., Hoppitt, W. & Rendell, L. (2013). Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. — Science 340: 485-488.

Ansmann, I.C., Parra, G.J., Chilvers, B.L. & Lanyon, J.M. (2012). Dolphins restructure social system after reduction of commercial fisheries. — Anim. Behav. 84: 575-581.

Bigg, M.A., MacAskie, I. & Ellis, G. (1983). Photo-identification of individual killer whales. — Whalewatcher 17: 3-5.

Borgatti, S.P. (2002). NetDraw: graph visualization software. — Analytic Technologies, Cambridge, MA.

Cantor, M., Shoemaker, L.G., Cabral, R.B., Flores, C.O., Varga, M. & Whitehead, H. (2015). Multilevel animal societies can emerge from cultural transmission. — Nature Commun. 6: 8091.

Cantor, M. & Whitehead, H. (2015). How does social behavior differ among sperm whale clans? — Mar. Mamm. Sci. 31: 1275-1290.

Cavalli-Sforza, L.L. & Feldman, M.W. (1981). Cultural transmission and evolution: a quantitative approach. — Princeton University Press, Princeton, NJ.

Centola, D., Gonzalez-Avella, J.C., Eguiluz, V.M. & San Miguel, M. (2007). Homophily, cultural drift, and the co-evolution of cultural groups. — J. Conflict Resolut. 51: 905-929.

Connor, R.C., Wells, R.S., Mann, J. & Read, A.J. (2000). The bottlenose dolphin: social relationships in a fission–fusion society. — In: Cetacean societies (Mann, J., Connor, R.C., Tyack, P.L. & Whitehead, H., eds). University of Chicago Press, Chicago, IL, p. 91-126.

Crance, J.L., Bowles, A.E. & Garver, A. (2014). Evidence for vocal learning in juvenile male killer whales, *Orcinus orca*, from an adventitious cross-socializing experiment. — J. Exp. Biol. 217: 1229-1237.

Deecke, V.B. (1998). Stability and change of killer whale (*Orcinus orca*) dialects. — Doctoral dissertation, University of British Columbia, Vancouver, BC.

Deecke, V.B., Ford, J.K. & Spong, P. (2000). Dialect change in resident killer whales: implications for vocal learning and cultural transmission. — Anim. Behav. 60: 629-638.

Deecke, V.B., Barrett-Lennard, L.G., Spong, P. & Ford, J.K.B. (2010). The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus* orca). — Naturwissenschaften 97: 513-518.

Deecke, V.B. & Janik, V.M. (2006). Automated categorization of bioacoustic signals: avoiding perceptual pitfalls. — J. Acoust. Soc. Am. 119: 645-653.

Everitt, B.S., Landau, S. & Leese, M. (2001). Cluster analysis. — Arnold, London.

Filatova, O.A., Burdin, A.M., Hoyt, E. & Sato, H. (2004). A catalogue of discrete calls of resident killer whales (*Orcinus orca*) from the Avacha Gulf of Kamchatka peninsula. — Zoologicheskyi J. 83: 1169-1180.

Filatova, O.A., Fedutin, I.D., Burdin, A.M. & Hoyt, E. (2007). The structure of the discrete call repertoire of killer whales *Orcinus orca* from Southeast Kamchatka. — Bioacoustics 16: 261-280.

Filatova, O.A., Fedutin, I.D., Ivkovich, T.V., Nagaylik, M.M., Burdin, A.M. & Hoyt, E. (2009). The function of multi-pod aggregations of fish-eating killer whales (*Orcinus orca*) in Kamchatka, Far East Russia. — J. Ethol. 27: 333-341.

Filatova, O.A., Fedutin, I.D., Shabalina, A.O., Burdin, A.M. & Hoyt, E. (2012). Vocal dialects and population structure of killer whales from Eastern Kamchatka and the Commander Islands. — In: Proceedings of the workshop on killer whales, VIIth international conference marine mammals of the Holarctic, p. 8-11.

Filatova, O.A., Burdin, A.M. & Hoyt, E. (2013). Is killer whale dialect evolution random? — Behav. Proc. 99: 34-41.

Foote, A.D., Osborne, R.W. & Hoelzel, R.A. (2008). Temporal and contextual patterns of killer whale (*Orcinus orca*) call type production. — Ethology 114: 599-606.

Ford, J.K.B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. — Can. J. Zool. 69: 1454-1483.

Ford, J.K.B. (2002). Killer whales. — In: The encyclopedia of marine mammals (Perrin, W.F., Würsig, B. & Thewissen, J.G.M., eds). Academic Press, New York, NY, p. 669-676.

Ford, J.K.B. & Ellis, G.M. (2006). Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. — Mar. Ecol. Prog. Ser. 316: 185-199.

Foster, E.A., Franks, D.W., Morrell, L.J., Balcomb, K.C., Parsons, K.M., van Ginneken, A. & Croft, D.P. (2012). Social network correlates of food availability in an endangered population of killer whales, *Orcinus orca*. — Anim. Behav. 83: 731-736.

Ginsberg, J.R. & Young, T.P. (1992). Measuring association between individuals or groups in behavioural studies. — Anim. Behav. 44: 377-379.

Greenhill, S.J., Currie, T.E. & Gray, R.D. (2009). Does horizontal transmission invalidate cultural phylogenies? — Proc. Roy. Soc. Lond. B: Biol. Sci. 276: 2299-2306.

Itakura, F. (1975). Minimum prediction residual principle applied to speech recognition. — IEEE Trans. Acoust. Speech Signal Process. 51: 67-72.

Ivkovich, T.V., Filatova, O.A., Burdin, A.M., Sato, H. & Hoyt, E. (2010). The social organization of resident-type killer whales (*Orcinus orca*) in Avacha Gulf, Northwest Pacific, as revealed through association patterns and acoustic similarity. — Mamm. Biol. 75: 198-210.

Laland, K.N. & Galef, B.G. (2009). The question of animal culture. — Harvard University Press, Cambridge, MA.

López, B.D. & Shirai, J.A.B. (2008). Marine aquaculture and bottlenose dolphins (*Tursiops truncatus*) social structure. — Behav. Ecol. Sociobiol. 62: 887-894.

Mann, J., Stanton, M.A., Patterson, E.M., Bienenstock, E.J. & Singh, L.O. (2012). Social networks reveal cultural behaviour in tool-using dolphins. — Nature Commun. 3: 980.

Nylander, J.A., Ronquist, F., Huelsenbeck, J.P. & Nieves-Aldrey, J.L. (2004). Bayesian phylogenetic analysis of combined data. — Syst. Biol. 53: 47-67.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H. & Wagner, H. (2016). vegan: community ecology package. R package version 2.3-5. — R Foundation for Statistical Computing, Vienna. Available online at http://CRAN.R-project.org/package=vegan.

Parsons, K.M., Durban, J.W., Burdin, A.M., Burkanov, V.N., Pitman, R.L., Barlow, J., Barrett-Lennard, L.G., LeDuc, R.G., Robertson, K.M., Matkin, C.O. & Wade, P.R. (2013). Geographic patterns of genetic differentiation among killer whales in the northern North Pacific. — J. Hered. 104: 737-754.

R Core Team (2014). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna. Available online at http://www.R-project.org/.

Rendell, L. & Whitehead, H. (2001). Culture in whales and dolphins. — Behav. Brain Sci. 24: 309-324.

Sargeant, B.L., Mann, J., Berggren, P. & Krützen, M. (2005). Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). — Can. J. Zool. 83: 1400-1410.

Schnell, G.D., Watt, D.J. & Douglas, M.E. (1985). Statistical comparison of proximity matrices: applications in animal behaviour. — Anim. Behav. 33: 239-253.

Shapiro, A.D., Tyack, P.L. & Seneff, S. (2011). Comparing call-based versus subunit-based methods for categorizing Norwegian killer whale, *Orcinus orca*, vocalizations. — Anim. Behav. 81: 377-386.

Tarasyan, K.K., Filatova, O.A., Burdin, A.M., Hoyt, E. & Sato, H. (2005). Keys for the status of killer whales in Eastern Kamchatka, Russia: foraging ecology and acoustic behaviour. — Biosphere Conserv. 6: 73-83.

Venables, W.N. & Ripley, B.D. (2002). Modern applied statistics with S, 4th edn. — Springer, New York, NY.

Whitehead, H. (2008). Analyzing animal societies: quantitative methods for vertebrate social analysis. — University of Chicago Press, Chicago, IL.

Whitehead, H. (2009). SOCPROG: programs for analyzing social structure (version 2.4). — Dalhousie University, Halifax, NS.

Williams, R. & Lusseau, D. (2006). A killer whale social network is vulnerable to targeted removals. — Biol. Lett. 2: 497-500.