



Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska

H. YURK*†§, L. BARRETT-LENNARD†§, J. K. B. FORD*‡ & C. O. MATKINS§

*Department of Zoology, University of British Columbia

†Marine Mammal Research, Vancouver Aquarium Marine Science Centre

‡Fisheries and Oceans Canada, Pacific Biological Station

§North Gulf Oceanic Society

(Received 20 February 2001; initial acceptance 20 April 2001;
final acceptance 13 November 2001; MS. number: A8997R)

Cultural lineages are based on learned social traditions that are stable for several generations. When cultural lineages also reflect common ancestry and/or are shared by individuals that live together they are called clans. The existence of clans among killer whales has been previously proposed but has not been confirmed. Here, we show that clans exist among resident type killer whales, *Orcinus orca*, in southern Alaska. Resident killer whales live in stable matrilineal groups from which emigration of either sex has not been observed. Matrilineal groups that associate regularly ($\geq 50\%$ observation time) are called pods. Pods are believed to consist of closely related matrilineal groups and share a unique repertoire of discrete call types. Pods that share parts of their repertoire form what Ford (1991, *Canadian Journal of Zoology*, **69**, 1454–1483) called an acoustic clan. Here, we identified discrete call types of seven pods from southern Alaska, using a method based on human discrimination of distinct aural and visual (spectrogram) differences. Mitochondrial DNA of members of each pod was also analysed. The repertoires of the seven pods were compared and two acoustically distinct groups of pods were identified. Each group was monomorphic for a different mitochondrial D-loop haplotype. Nevertheless, pods from different clans associated frequently. It thus appears that the acoustic similarities within groups, which we presume to be cultural, reflect common ancestry, and that these groups therefore meet the above definition of clans. We also argue that a combination of cultural drift and selection are the main mechanisms for the maintenance of clans.

© 2002 The Association for the Study of Animal Behaviour. Published by Elsevier Science Ltd. All rights reserved.

Traditions and Cultural Lineages

Traditions are expressions of conserved information that are not coded genetically but learned socially and are stable for several generations (Munding 1980; Cavalli-Sforza & Feldman 1981). Cultural lineages are characterized by traditions, and commonly identify groups of individuals that inhabit the same area and/or belong to a consanguineal kin group (Murdock 1960). One advantage of culturally transmitted information over genetically transmitted information is that traditions can respond more rapidly than genetically formed traits in

response to changes in the environment (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). However, traditions can also be maintained for long periods if they remain advantageous for individuals of a group, subpopulation or population (Munding 1980). Unique social traditions can develop by a process of cultural drift and selection of behavioural traits that distinguish groups, while migration between groups is sufficiently low in frequency. The stability of those traits then allows individuals to use them as cultural identifiers of relatedness between groups as well as individuals.

Traditions can generally be divided into several categories (e.g. those that involve physical manipulation of objects, those that can be regarded as social customs or those that involve vocalizations). Social customs such as complex greeting ceremonies and physical manipulation, such as tool use are common in apes, such as chimpanzees, *Pan troglodytes* (Whiten et al. 1999) and humans. A well-known example of a tradition that involves physical manipulation but is outside the hominid family is that of the potato-washing Japanese macaques, *Macaca fuscata*

Correspondence: H. Yurk; Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada (email: yurk@zoology.ubc.ca). L. Barrett-Lennard is at the Marine Mammal Research Department, Vancouver Aquarium Marine Science Centre, P.O. Box 3232, Vancouver, BC V6B 3X8, Canada. J. Ford is at the Pacific Biological Station of Fisheries and Oceans Canada, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada. C. Matkin is at the North Gulf Oceanic Society, 60920 Mary Allen Avenue, P.O. Box 15244, Homer, AK 99603, U.S.A.

(Kawamura 1959). The behaviour was invented by an individual female macaque in 1958, and spread over a period of two years first to related members of the troop and later to nonrelatives (Nishida 1987). The best-described examples of vocal traditions in animals are the commonly found structured song repertoires of birds (Lynch 1996; Payne 1996), and the rare group or subpopulation-specific dialects of some mammals, such as humans and certain cetaceans (Payne & Guinee 1983; Ford 1991; Weilgart & Whitehead 1997). Vocal traditions of songbirds contain recognizable themes, phrases and notes (Marler & Tamura 1962; Slater & Ince 1979), elements that are also used by male humpback whales, *Megaptera noveangliae*, to structure their song types and themes (Payne et al. 1983). Further examples of vocal traditions are discrete call type repertoires produced by killer whales (Ford 1991), and discrete temporal patterns in click vocalizations of sperm whales, *Physeter macrocephalus* (Weilgart & Whitehead 1997).

The specific vocal traditions of sympatric living or neighbouring groups or subpopulations of mammals are called dialects (Conner 1982; Ford 2002) (no single definition for dialects exists for birds). Vocal repertoire differences resulting from isolation between groups or subpopulations should be called geographically varying repertoires because they most likely resulted only from passive cultural or genetic drift due to that isolation (Conner 1982; Lynch 1996). The majority of mammalian dialects are learned within a social group by copying signals of a parent or other kin group member or through acoustic interaction between nonrelated individuals that are familiar with each other (Mundinger 1980; Conner 1982; Ford 2002). The humpback song, which is a tradition learned socially by males on the breeding ground, is an example of a vocal tradition that is not a dialect. Novel songs produced by singers new to a particular breeding ground appear to spread rapidly through a population. Moreover, existent songs appear to disappear quickly when new songs are introduced (Noad et al. 2000). Therefore, the song does not identify a group or subpopulation.

A vocal tradition is by definition a learned behaviour. However, even when mammalian dialects are learned, the question of how are they learned, vocally or contextually, is still important (Janik & Slater 1997). Potentially, dialects could arise from vocalizations whose acoustic structure is determined completely by genetic templates (Marler 1997). The calls could then either be the result of maturational processes of the individual, or the template usage could be learned contextually making the dialect a socially learned pattern. However, as Janik & Slater (1997) point out, the vocalizations comprising the dialect would not be learned vocally. An individual producing the same vocalizations as other members of the group would do so because of a learned social custom and every individual could potentially still produce all of the vocalizations typical for a population or species.

Dialects of resident type killer whales appear to be learned vocally. Killer whales copy calls of distantly related conspecifics in captivity (Bain 1989; Ford 1991), and also mimic calls in the wild. These mimicked calls are

easily recognizable as such by human observers and therefore possibly easily recognizable as mimics by other killer whales (Ford 1991). Dialects appear to be strongly associated with the recognition process of social groups within the hierarchical social organization of these whales (Bigg et al. 1990), implying that the vocalizations are also learned socially by selectively copying signals of group members.

Resident Killer Whales: Social Structure, Vocalizations and Relatedness

The structure of the resident killer whale population is characterized by the social and acoustic associations of groups of animals that are closely related by matrilineal descent (matrilines). Neither males nor females are known to disperse from their matriline (Barrett-Lennard 2000). Whales of the same matriline use specific call types as vocal signatures of their matriline (Ford 1991; Deecke et al. 2000; Miller & Bain 2000). Groups of matrilines that associate at least 50% of the observation time are called pods (Bigg et al. 1990). Matrilines within a pod are more closely related than matrilines of different pods (Barrett-Lennard 2000). Resident pods from southern Alaska are sighted regularly throughout the summer in Prince William Sound and the fjords of the Kenai Peninsula (Fig. 1) (Matkin & Saulitis 1997).

Vocalizations of residents fall into three categories, clicks, whistles and calls. Clicks are heard in 95% of all recordings of residents, and appear to be used by whales in the detection and pursuit of prey, as well as during social encounters (Barrett-Lennard et al. 1996). Whistles are mainly heard during social interactions when the whales are close to each other (Ford 1989; Thomsen et al. 2001). After echolocation clicks, discrete calls are the most common type of vocalization (Ford 1989) (Fig. 2). Discrete calls are heard in approximately 90% of all recordings, typically in situations where the whales are spread out foraging or when two or more pods meet. Ford (1989) suggested that the discrete calls of resident killer whales serve as signals for maintaining contact between matrilines or pod members. Some discrete call types appear as two or more stable variants. Pods share a repertoire dialect of 7–17 discrete calls and call variants, which appear to be stable over several generations (Ford 1991).

Bigg et al. (1990) and Ford (1991) suggested that pod fission and variation in discrete calls occurs gradually over several generations. According to this hypothesis, newly formed sister pods initially spend a significant amount of time together and share most of the calls of their ancestral pod. Over time, because of copying errors of calls between generations and fewer contacts between sister pods, calls change progressively and repertoires diverge. Ford (1991) termed pods that share parts of their repertoires acoustic clans. In keeping with this hypothesis, Barrett-Lennard (2000) showed that pods with very similar repertoires are more closely related than pods that share only few calls. Ford (1991) concluded that

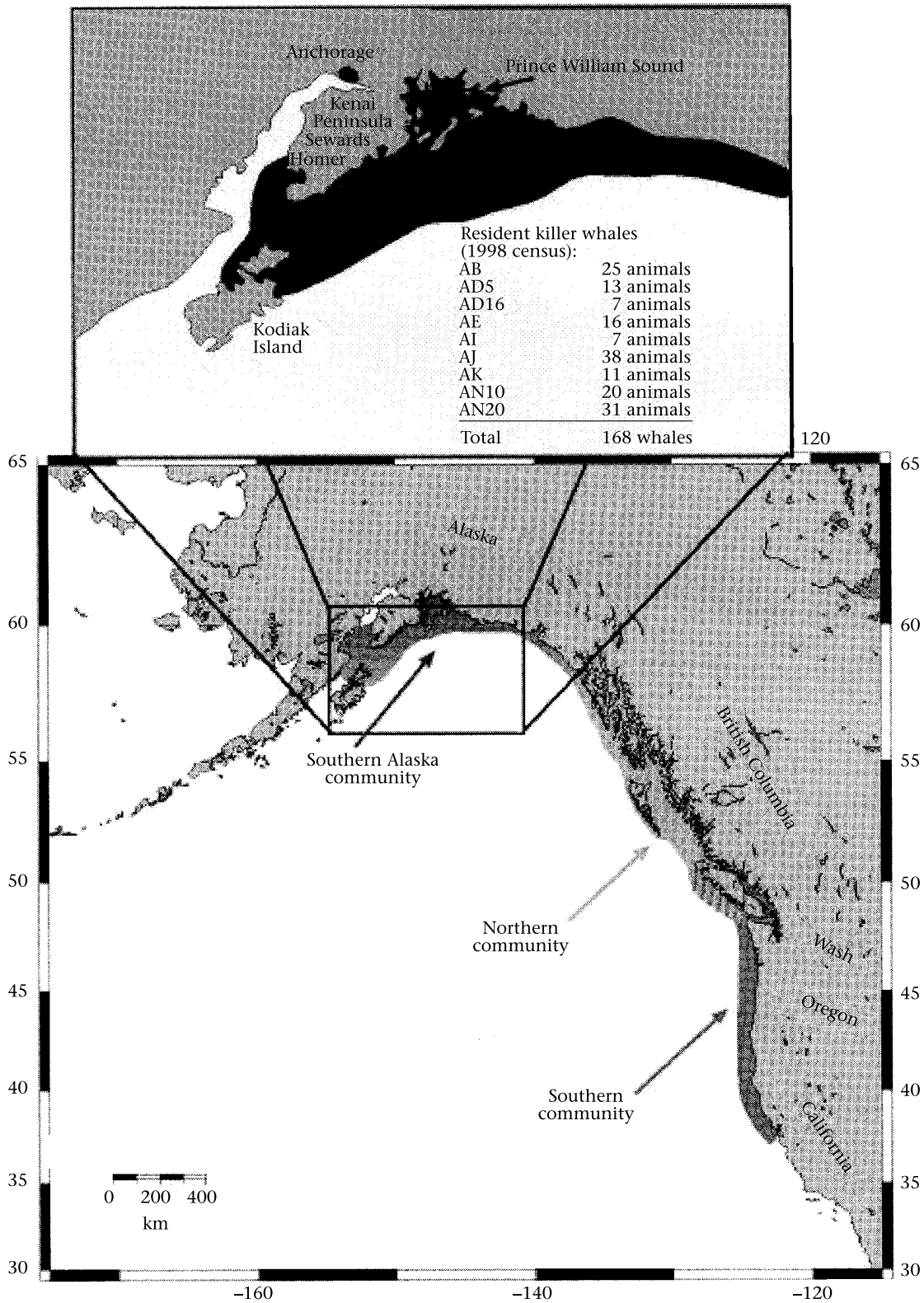


Figure 1. Distribution of the seven resident killer whale pods in Prince William Sound and adjacent waters during late spring/summer and early autumn. Distribution ranges of resident killer whales in the eastern North Pacific.

pods that share large amounts of their call repertoire have split more recently than pods that have fewer calls in common.

The aims of our study were to investigate whether acoustic clans as mentioned by Ford (1991), hereafter called vocal clans because of their basis in vocalizations,

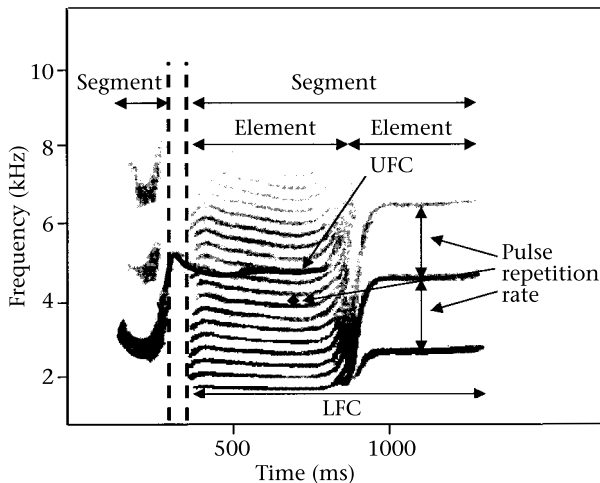


Figure 2. Spectrographic examples of a discrete call (AKS02). Calls often consist of two components, (1) a lower-frequency component, LFC (duration 0.5–2 s; pulse repetition rate 0.2–2.5 kHz), and (2) an upper-frequency component, UFC (duration 0.5–2.5 s; frequency range 4–8 kHz). Abrupt shifts of the pulse frequency in the lower-frequency component distinguish elements. Elements differ from call segments, which are characteristically separated by silent intervals.

exist among southern Alaskan resident killer whales. Furthermore, if vocally similar groups of pods are true clans, then vocal clans should be parallel cultural and genetic lineages. To test this hypothesis, we compared a representative sample of discrete calls produced by the seven pods in the study population (Matkin et al. 1999) and determined whether the variation in discrete call use among pods matched up with results of a pre-existing genetic study of maternal relatedness patterns among the same pods. The genetic study (by L.B.-L.) and the call repertoire assessments (by H.Y.) were performed independently and were blind to each other's results.

METHODS

Acoustic Analysis

Recordings were made by a number of different observers (see Acknowledgments for details), and were analysed following the protocols of Ford 1984, Saulitis (1995) and Strager (1995). Data were collected under National Marine Fisheries Service scientific research permit Nos 840 and 875–1401. Groups of whales were located in the field (Fig. 1) and photographed for individual identification from 4–11-m vessels after visually searching for them and by listening for their vocalizations with a directional hydrophone. After photographing all of the whales present, the boat was then moved 500 m ahead of the whales, and the engine was turned off. A hydrophone was then lowered over the side of the boat to a depth of 10–15 m.

The recording systems varied, but most consisted of a Celesco BC-10/ BC-50 or an Offshore Acoustics hydrophone and a Sony WM-DC6 or Marantz PMD 221 cassette-tape recorder. The frequency responses of these recording systems were approximately linear between

0.1 Hz and 8 kHz and were still useful for call identification up to 14 kHz (± 10 dB). Some recordings with wider frequency responses were made with a Bruel & Kjaer 8101 hydrophone, and a Nagra IV-SJ reel-to-reel tape recorder (0.0005–35 kHz ± 1 dB), or an Offshore Acoustics hydrophone and a TCD-D7 Sony DAT recorder (0.02 Hz–22 kHz ± 1 dB).

Recording Selection and Discrete Call Description

We only analysed recordings of a pod when it was encountered alone or at such a distance from other pods (>1 km) that the calls could be attributed unequivocally to that group. Vocalizations were recorded during a wide range of observable behaviours, such as travelling (slow and fast), feeding, resting (milling at surface) and socializing (pod gatherings) as described by Ford (1984). All recordings meeting the above criterion (single pod recording) were used to describe the call repertoire of a pod. Table 1 shows the number of single pod recordings analysed.

We inspected recordings for the presence of calls by listening to tapes while monitoring real-time spectrograms of the acoustic signals using a Kay Elemetrics DSP Sona-Graph, Model 5500. A sample of recognized calls (minimum of 100 per pod) was digitized and further analysed spectrographically using Canary 1.2.4 sound analysis software (Cornell Laboratory of Ornithology, Ithaca, New York, U.S.A., 1998). The calls used for spectrographic analysis were digitized at a 44.1 kHz sampling rate with a 16-bit sample size. The spectrographic analysis was done using Fast-Fourier Transformations (FFT) with sizes of 1024 points for each analysed time series. Spectrograms were produced using an 87.5% overlap of analysed time series. Resulting spectrograms had a time resolution of 2.9 ms and frequency resolution of 43 Hz.

Calls are stereotyped vocalizations of 0.25–2.5-s duration (Schevill & Watkins 1966) that are often composed of two components. Following Miller & Bain (2000), components with lower sound frequency (lowest band in spectrogram at 0.5–3.5 kHz) were called lower-frequency components (LFC, see Fig. 2), and components with higher sound frequency (lowest band always above 3.5 kHz) were called upper-frequency components (UFC, see Fig. 2). LFCs consist of rapidly produced broadband pulses that overlap to produce the equivalent of sine wave tones. The distance between spectrogram bands reflects pulse repetition rate (Watkins 1967), although intensity differences due to superpositioning of pulse tones may reduce the number of bands in the spectrogram. For example, when the pulse rate is a 2ⁿ multiple of the pulse frequency, the harmonics of the pulse frequency will show up as stronger bands in the spectrogram, and bands in between may disappear completely. Both the pulse repetition rate and pulse frequency are usually modulated over the duration of the call (Fig. 2). UFCs often have no sidebands but have true harmonic bands and can then be better described as narrow band signals, such as whistles, produced simultaneously to LFCs (Fig. 2, see also call type AKS05 in Fig. 4a). Furthermore, many LFCs of calls can be divided into elements separated by rapid shifts in

Table 1. Number of pod encounters with recordings analysed for six pods (AB through AK) for each year and the number of biopsy samples collected from these pods

Year	AB	AI	AJ	AN	AD	AE	AK	Number of recordings/ year
1984	9	3	1	4	4	3	2	26
1985	4	0	0	4	2	4	1	15
1986	0	0	0	1	1	1	0	3
1988	0	0	0	0	0	0	1	1
1989	2	0	0	1	0	0	3	6
1990	1	3	4	2	1	2	2	15
1991	0	3	1	2	1	3	4	14
1992	3	2	0	1	0	2	1	9
1993	0	0	0	0	1	1	0	2
1994	0	1	1	0	0	0	0	2
1996	1	2	1	0	0	3	0	7
1997	0	2	2	5	4	3	2	18
1998	1	0	0	0	1	0	1	3
1999	0	0	0	0	1	0	0	1
Total number of recordings	21	16	10	20	16	22	17	122
Total number of biopsies	14	6	12	8	15	12	8	

Actual recording duration differed among encounters, as did vocal activity.

pulse repetition rates (Fig. 2, see also call type AKS11 in Fig. 4b). Some calls also may be segmented, with segments separated from each other by silent intervals (Fig. 2; see also call type AKS21 in Fig. 4b).

Call Type Categorization

We categorized call types by ear and by visual inspection of the sound spectrogram. Categorization was based on the distinctive audible characteristics of the calls, which appeared as distinguishing structural differences in the frequency/time contours of a call's spectrogram. Particular attention was given to call duration, segmentation, element structure of LFCs and the existence of UFCs (Fig. 2). A similar method was described by Ford & Fisher (1982) and Ford (1984). Ford (1984) found no significant difference between the categorization of killer whale calls based on a statistical comparison of certain sound parameters and the categorization using aural and spectrographic comparison. Bain (1986), comparing sound and visual appearance of calls, obtained similar call categories from two captive killer whales of the same population that Ford (1984) described. Deecke et al. (1999) compared the results of call similarity analyses from neural networks with those made by humans that had been trained to distinguish between calls and found no significant difference in the results of the types of analyses.

Our categorization method differed slightly from the one Ford (1984) used to define stable call variants. Our definition of a call variant was based on contour variations within elements and not on occurrence of elements within a call. Calls that had different numbers of elements but were otherwise similar were categorized as two distinct call types. This allowed for a greater structural resolution of call types in the categorization process.

Call types can be described by their gestalt (Katz 1950; Deecke et al. 1999), where gestalt means that acoustic similarities and differences of calls can be distinguished by humans without previous experience in categorizing calls. Furthermore, gestalt differences and similarities can be more effectively described by humans that are trained to distinguish between call types by listening to a great number of different calls (Deecke et al. 1999). To test whether our call type categorizations could be reproduced by others, we gave samples of categorized calls to two groups of human observers.

Group A consisted of 17 individuals unfamiliar with either killer whale or other cetacean vocalizations, and group B consisted of seven individuals who had experience in categorizing killer whale and/or other cetacean vocalizations. Each individual was asked to find the most similar call to a sample call among four similar sounding calls (Fig. 3). Aside from detecting similar sounding calls, observers were asked to find similarity based on (1) similar call duration, (2) the existence of the same number of components (if possible), (3) an equal number of segments and elements, and (4) similar contour modulations within elements (Fig. 3). Calls were presented in two test sequences consisting of 10 calls each. First, individuals from groups A and B both evaluated the same test sequence. In the second test sequence, group A individuals evaluated calls with equal degrees of similarity to the first sequence, while group B individuals were given call samples with higher degrees of similarity (e.g. different call type variants of the sample call were presented together with different call types among the four choices). In total, 12 call types were evaluated by both groups to identify possible effects of experience on call type categorization. Different examples of the same call types were used in more than one evaluation to minimize influences of variation in different recordings of calls. Results were arcsine square-root transformed and mean

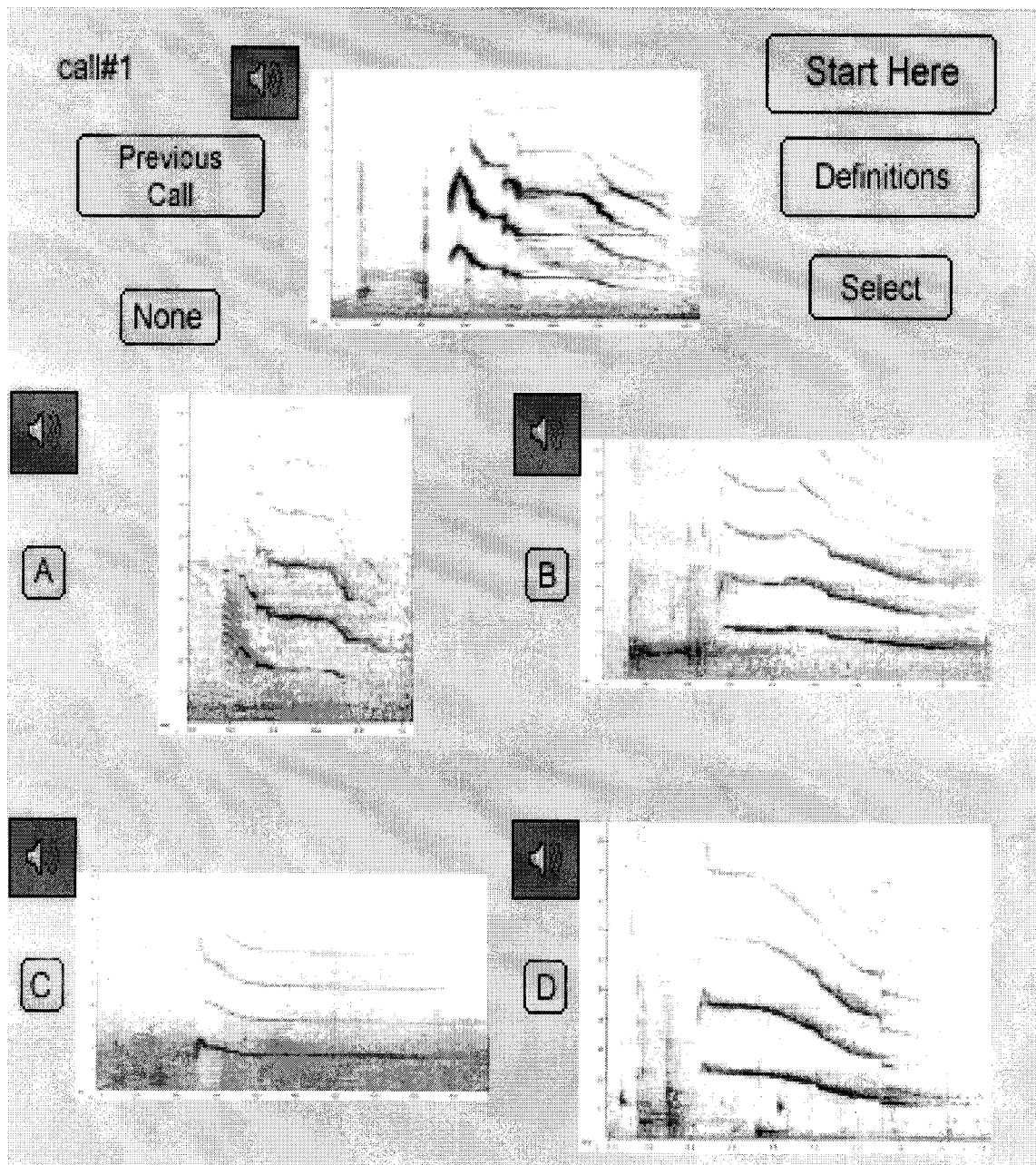


Figure 3. Example frame of the call type re-evaluations conducted by 17 inexperienced and seven experienced observers. The observers were asked to determine which sound and spectrogram of the four call samples in the lower part of the frame were most similar to that of the call at the top of the frame.

differences between observer groups tested using a paired Student *t* test.

Discrete call types were named alphanumerically using the prefix AKS to designate that the calls were from southern Alaskan resident killer whales. Numbers reflect the order in which the calls were identified and are otherwise arbitrary. The subscripts (e.g. i, ii, iii, etc.) that are used in combination with the AKS, and number denomination of some call types indicate the existence of call type variants (Table 2). We considered maximum repertoire size to be reached when no new call types appeared after new recordings of a pod made in two

consecutive years were added to the analysis. Based on this re-evaluation of our call categories we placed all calls in a particular call type category.

Call Type Sharing

We obtained a measure of the similarity of call type repertoires or dialects for each pair of pods from an index based on the degree of call type sharing. This index was derived from Dice's coefficient of association (Ford 1991), which normalizes the data to account for differences in repertoire size:

Table 2. List of all identified call types (AKS01–AKS29) of southern Alaskan residents and their variants (i–iv) in alphanumerical order

Pod	AB	AI	AJ	AN	AD	AE	AK
No. matriline	11	1	8	13	6	5	2
No. whales*	25	7	38	51	24	16	11
<hr/>							
AKS01 i					×		×
ii					×		×
iii					×		
AKS02 i						×	
ii						×	
AKS03					×	×	×
AKS04 i					×	×	
ii					×	×	×
AKS05					×	×	×
AKS06						×	
AKS07					×		
AKS08					×		
AKS09 i					×	×	×
ii					×		×
AKS10 i	×			×			
ii	×	×	×	×			
AKS11 i	×	×	×	×			
ii	×	×	×	×			
AKS12	×						
AKS13	×	×		×			
AKS14	×	×		×			
AKS15 i	×	×	×	×			
ii	×	×	×	×			
AKS17 i	×	×		×			
ii	×	×		×			
iii	×	×		×			
iv				×			
v				×			
AKS18	×	×	×	×			
AKS20				×			
AKS21	×	×		×			
AKS22	×	×		×			
AKS23			×				
AKS24 i			×				
ii			×				
AKS25	×	×	×				
AKS27			×				
AKS28			×				
AKS29			×				
Total	16	14	13	15	11	8	7

An × in the appropriate column indicates call types produced by an individual pod. Pods that share call types are grouped together.

*Number of whales per pod is based on the 1998 census.

$$\text{Index of similarity} = \frac{2N_c}{R_1 + R_2}$$

where N_c is the total number of call types and subtypes shared, and R_1 and R_2 are the repertoire sizes (call types plus subtypes) of the two pods. We used the index values, which ranged between 0 and 1, to calculate a hierarchical structure of acoustic similarity, which we displayed in the form of a dendrogram by means of average link cluster analysis.

Genetic Analysis

Skin biopsies were collected (by L.B.-L. and C.M.) for DNA analysis using lightweight darts projected with

a pneumatic rifle (Barrett-Lennard et al. 1996). We approached whales slowly on a gradually converging course and then travelled parallel to them at a distance of 10–15 m. After taking identification photographs of the entire group, we selected a whale to biopsy that we could identify visually and that had not been biopsied previously. We fired the darts at a region of the back approximately 1 m behind the dorsal fin and 50 cm below the dorsal ridge. The darts were designed to excise and retain a 0.5-g plug of skin and blubber, and to bounce off the whale and float. We rephotographed the darted whale if possible to confirm its identity and retrieved the darts from the water. We attempted to sample at least one member of each matriline. The collection of skin samples was covered under National Marine Fisheries Service permits Nos 840 and 875–1401. The number of biopsies that were collected from different pods is also presented in Table 1.

Skin tissue from the biopsy samples was ground finely in a ground-glass tissue grinder and digested with Proteinase K for 24 h at 54 °C. DNA was then purified using phenol and chloroform and precipitated with ethanol, using the procedure of Sambrook et al. (1989). The entire mitochondrial D-loop of each sample was amplified using the polymerase chain reaction and sequenced using an Applied Biosystems 377 automated DNA sequencer. The sequences were aligned using the program Clustal-W (Thompson et al. 1994), and differences between sequences were detected manually by comparing their output graphs from the automated sequencer. Further details of this procedure can be found in Barrett-Lennard (2000).

RESULTS

Call Type Repertoire Analysis

Different observers made 848 recordings concurrent with photographic identification of killer whales between 1984 and 1999 (Table 1). We analysed 112 single pod recordings that were distributed over the whole recording period (Table 1). The number of recording sessions per pod ranged from 16 to 22 with durations of sessions ranging from 5 to 135 min. A minimum of 5 h of recording was inspected for each pod. In total, 9000 calls were categorized by ear and visual inspection of spectrograms.

The energy distribution within the call spectrum usually allowed good spectrographic representation of frequencies from 0.5 to 14 kHz. The lower-frequency components (LFCs) ranged in frequency from 0.5 to 3.5 kHz, while the lowest band or fundamental frequency of the upper-frequency components (UFCs) ranged from 4 to 11 kHz (Fig. 2). However, UFCs appeared to be more directional than LFCs. Occasionally, we observed the appearance or disappearance of the upper-frequency components in calls made by whales that suddenly changed direction in front of the hydrophone. A call that showed UFCs in the majority of samples was labelled as always containing the component.

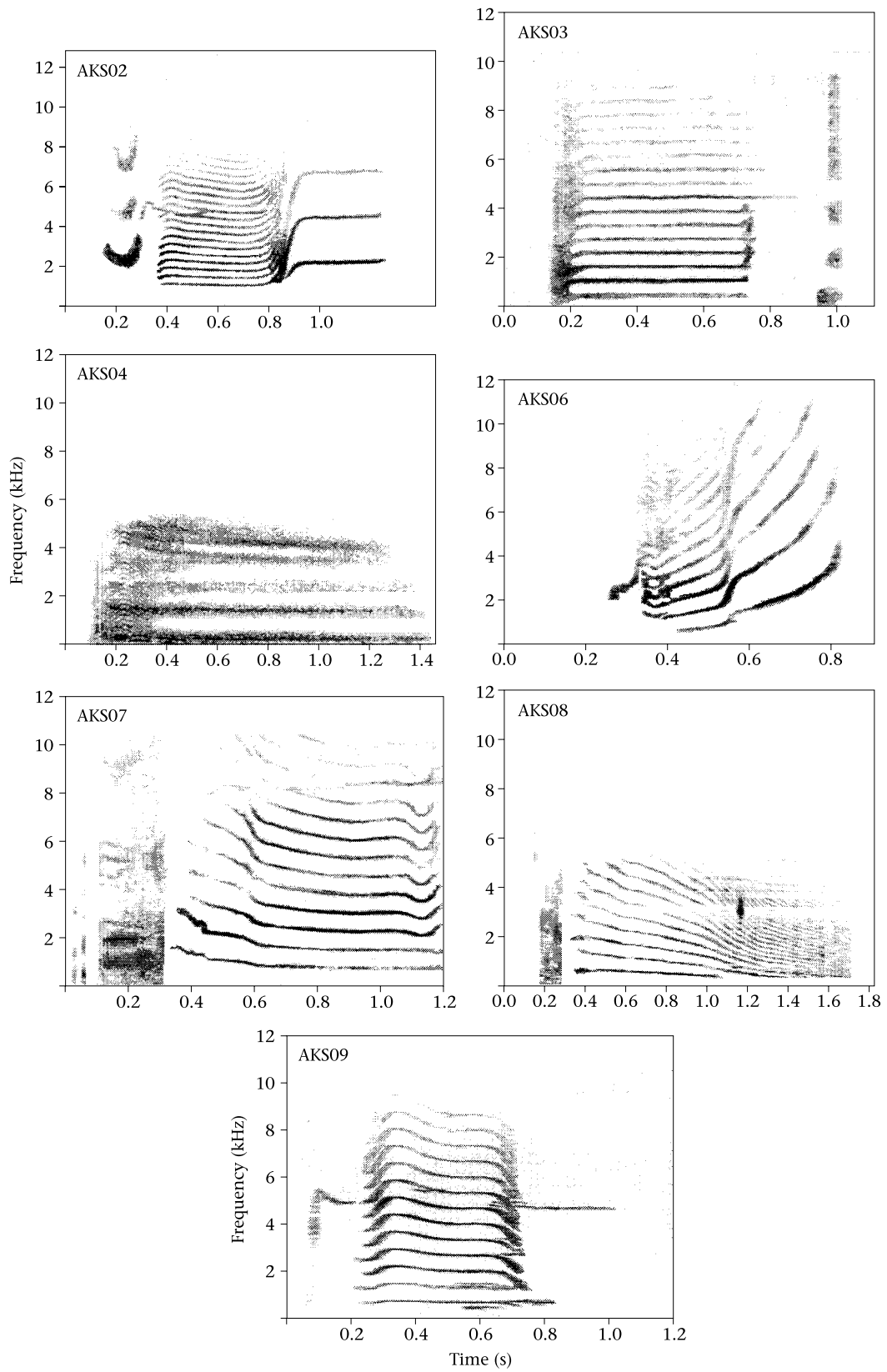


Figure 4. (a)

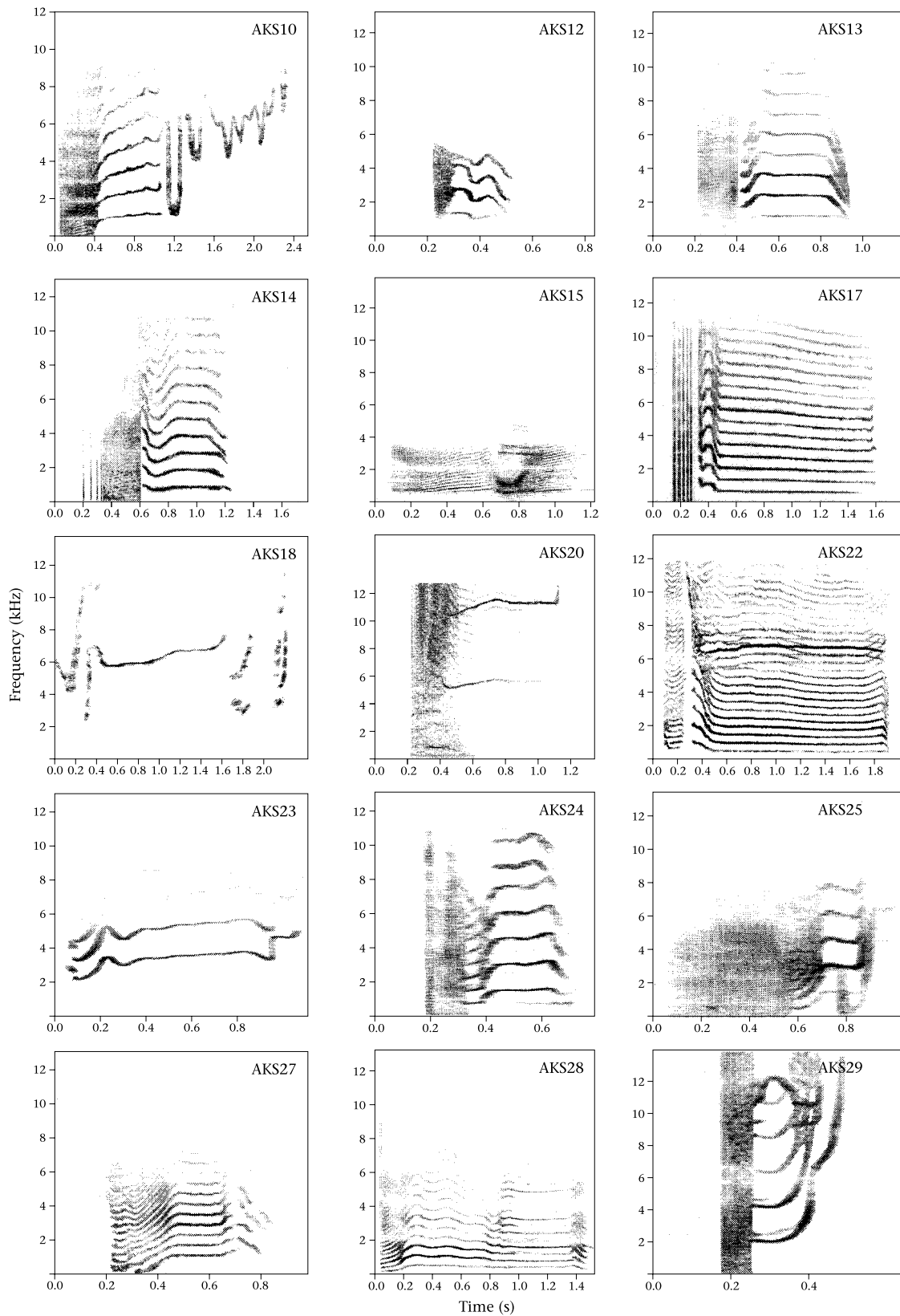


Figure 4. (b)

Figure 4. (a) Spectrographic examples of call types that were used by the AD, AK and AE pods of AD clan, with the exception of call types AKS01 and AKS05, which are displayed in Fig. 5. (b) Spectrographic examples of call types produced by the AB, AI, AJ and AN pods of the AB clan, with the exception of call types AKS11 and AKS21, which are displayed in Fig. 5. See Table 2 for a listing of all call types that were shared between AD clan pods and AB clan pods, respectively.

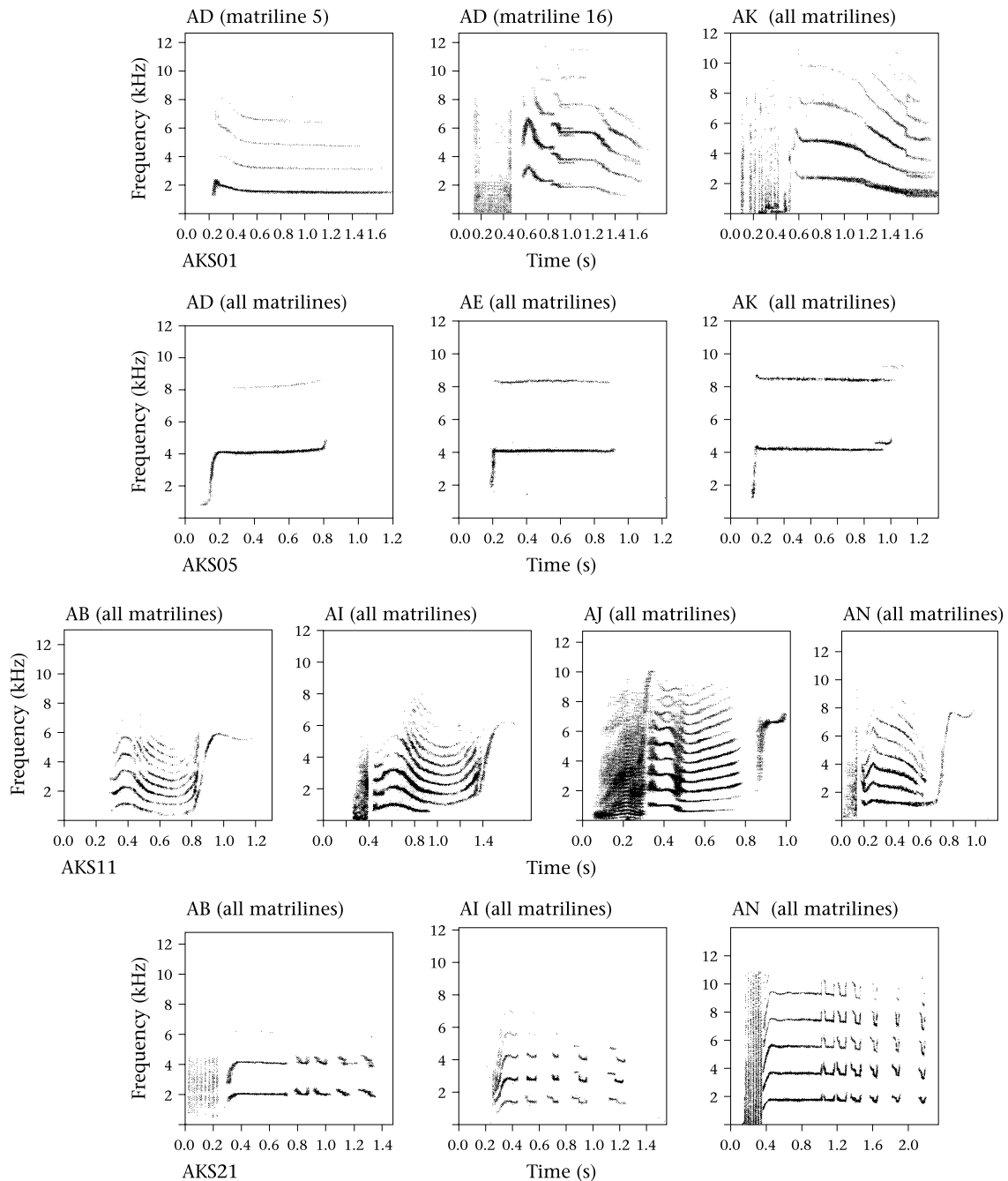


Figure 5. Spectrographic examples of call types AKS01, AKS05, AKS11 and AKS21 shared by members of AB and AD clan.

Call Type Categorization

Most call types could easily be distinguished and categorized by ear. For those that appeared to be aurally similar, differences existed in most of the following acoustic variables taken from the spectrogram: duration of calls, number and duration of segments and elements, existence of UFCs, as well as pulse repetition rates of LFCs (Fig. 2).

The seven pods AB, AD, AE, AI, AJ, AK and AN produced 26 distinct call types (Figs 4, 5). Three types (AKS16, -19

and -26) that were aurally considered call types could not be differentiated from other call types based on the spectrograms. These three types also occurred in only one or two of the recording sessions and were eliminated from further analysis. Nine of the 26 distinct types showed more than one stable variant. One had five stable variants, one had three variants and seven had two variants, making a total of 39 discrete calls. Table 2 lists all discrete calls and the pods that produced them. AN pod and AD pod recently split into four pods called AN10, AN20, AD5 and AD16, respectively (Matkin et al. 1999). However, the

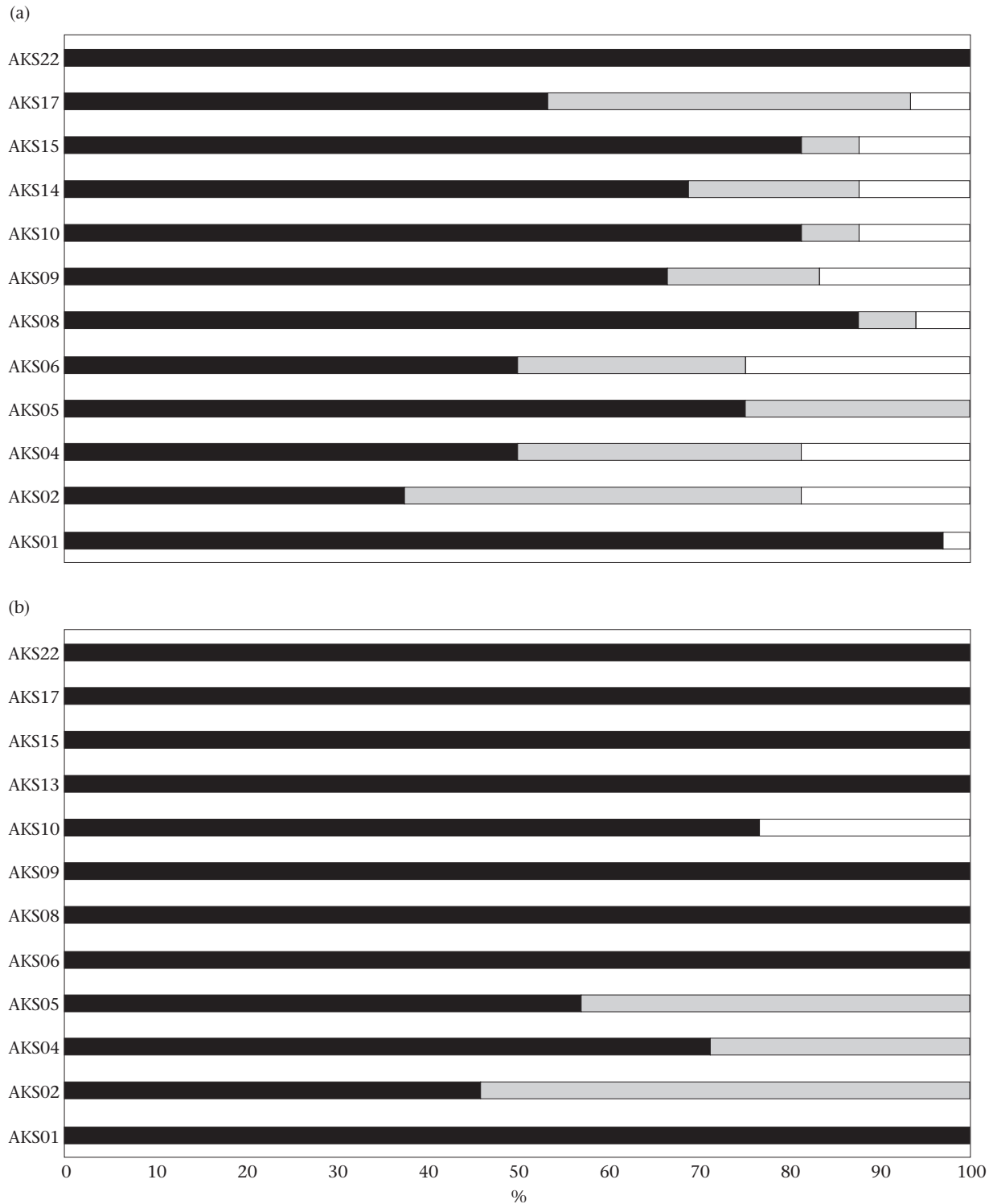


Figure 6. Results of the call type evaluations by (a) 17 observers without previous experience and (b) seven observers with previous experience with cetacean vocalizations. ■: Agreement; □: disagreement; □: indifference.

majority of recordings were made when these pods were still travelling in close association with each other. Therefore, we used the original pods in our analysis.

The interobserver consistency of call type categorization is usually very high (Bain 1986; Deecke et al. 1999). The evaluations done here showed that on average

71% (geometric $\bar{X} \pm SD = 68 \pm 20\%$) of the inexperienced evaluators agreed with our call type definitions and 88% (geometric $\bar{X} \pm SD = 85 \pm 20\%$) of the experienced evaluators did (Fig. 6). The mean difference of 17% between the two groups was significant (paired t test: $t_{11} = 2.84$, $P = 0.02$). The discrepancies between our call

type classifications and those of the experienced evaluators always involved the same three call types (AKS02, -04 and -05), while agreement was 100% for most other types. Given the number of choices presented to the observers, the probability that a call type was considered similar by chance was 25%. The lowest value of agreement was 46% for AKS02, while agreement for AKS04 and -05 was 72 and 57%, respectively (Fig. 6). All three values were considerably higher than expected by chance. Furthermore, two of the choices for similar call types to the reference AKS02 call were not produced by Alaskan residents, but were included in the experiment because they appeared to be close matches due to their similar frequency contour to the tested call type. Therefore, while the probability of erroneous categorization may be considerable for call types that exist in different subpopulations, it appears to be low for call types produced within the same subpopulation.

Call Type Description

More than one segment was found in nine call types: AKS01, -02, -03, -11, -14, -17, -18, -21 and -22 (Figs 2, 4, 5). In all cases except one (AKS02), the initial segment was characterized by low pulse repetition rates that sounded like a buzz and therefore could have been confused with strings of echolocation clicks. However, unlike echolocation clicks, these buzzes always preceded another sound segment by less than 0.1 s. The initial segment of AKS02 was a tonal segment that appeared to be part of the low-frequency component of the call (Fig. 2). However, the spectrographic representations in no case revealed a connection between this segment and the rest of the LFC (Fig. 2). In five of the nine call types (AKS01, -03, -11, -17 and -22), the number of elements of the second segment and/or the pulse repetition rates slightly varied among pods (Figs 4, 5). Call types 13 and 14 did not vary greatly in either element structure or contour modulation between pods AB and AI, but these call types of AB and AI pods did differ from AKS13 and -14 produced by the AN pod (Fig. 4b).

Call types AKS10 and AKS21 were characterized by a high number of elements (AKS10, Fig. 4b) or segments (AKS21, Fig. 5), relative to other calls. AKS10 was the longest call (>2.5 s) with the highest number of elements (up to six) and had the most contour variations per element among pods of all call types. AKS21 was characterized by two to six segments with almost identical contours (Fig. 5).

Four call types (AKS03, -09, -11 and -22) had distinct pairs of LFCs and UFCs (Figs 4, 5). Others, such as AKS05 (Fig. 5) and AKS18 (Fig. 4b), consisted mainly of single UFCs, and therefore appeared acoustically more similar to whistles than to any pulsed call. Temporal spacing of contour modulations of the lowest band of AKS18 was distinctly different among pods (Fig. 4b).

Call types AKS04 and AKS15 were characterized by small degrees of variation in pulse repetition rates (AKS04: 900–1200 Hz; AKS15: 300–700 Hz) and low peak frequency ranges (AKS04: 300–500 Hz; AKS15: 500–700 Hz) among pods. These two call types were recorded

predominantly in situations when the majority of the whales in a group were resting.

AKS02 (Fig. 2) produced by AE pod was one of the nine call types not shared by whales from more than one pod. The other eight call types were AKS06, also of AE pod, AKS07 and AKS08 of AD pod, AKS20, -23, -24, -27, 28 and -29, all of AJ pod. All of these calls showed a distinct number of elements and distinct contour variations, which made it easy to distinguish between them, at least among call types produced by Alaskan residents.

Call Type Variants

Call types varied predominantly in the number of segments and elements and/or showed consistent differences in the contour variation of call elements among pods (Fig. 5).

Calls that were characterized by simple contour modulations, usually down-sweeping contours (e.g. AKS17 and AKS01; Figs 4b, 5), produced more variants than calls that were structurally more complex (e.g. AKS22 or AKS03; Fig. 4a, b) or consisted of single UFCs (AKS05 and AKS18, Fig. 4a, b). Generally, a pod only used one call variant. Therefore, call variants could often be used to distinguish pods. However, in three cases, more than one call variant was used by a single pod: AKS01 in AD pod, AKS02 in AE pod, and AKS24 in AJ pod. These pods were characterized by matriline that often swam alone (AD5 and AD16) and/or that shared few calls with other pods (AE and AJ). Differences between call type variants are distinguishable based on their gestalt, because 70% of all experienced observers agreed with our choices of seven call type variants. Furthermore, this number increased to over 85% for those observers with previous experience in killer whale call type categorization ($N=3$).

Relationship between Repertoire Sizes and Group Sizes

The mean number of call types given by each pod was 12 ($\bar{X} \pm SE = 12.14 \pm 3.67$, $N=7$), and the median 13 (Table 2). AK pod used the least (seven) while AB pod used the most (17) number of call types. We did not detect any differences in the numbers of call types produced by different matriline of the same pod. The number of call types produced per pod was not closely correlated with the numbers of whales in that pod (Pearson correlation: $r_6=0.438$, $P=0.33$). Similarly, the number of matriline within a pod was not correlated with repertoire size, although there was a nonsignificant tendency (Fig. 7; $r_6=0.618$, $P=0.14$). Regression residuals were approximately normally distributed. If the AI pod, which started splitting from the AB pod during the early 1980s, was combined with the AB pod, the correlation between matriline number per pod and repertoire size increased ($r_5=0.932$, $P=0.007$).

Call Sharing

Forty-eight per cent of the discrete calls identified ($N=8000$) were shared by more than one resident pod,

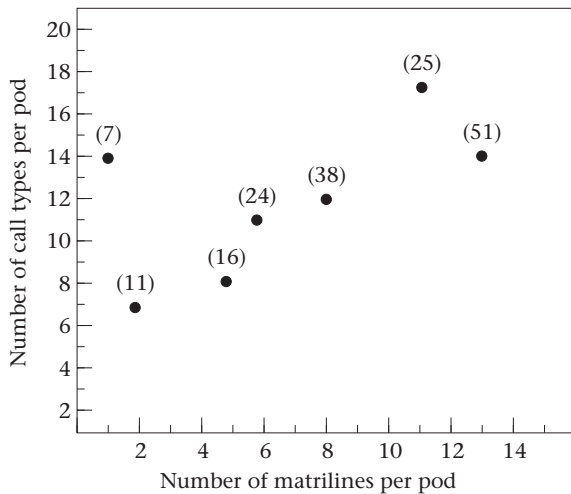


Figure 7. Comparison between pod repertoire size and number of matriline per pod. The numbers in parentheses represent the number of whales per matriline based on the 1998 census.

Table 3. Acoustic similarity between pod repertoires based on the index of similarity Ford (1991), where 1 means the repertoires of two pods were identical and 0 means the two pods did not share any call

	AB	AI	AJ	AN	AD	AE
AI	0.903					
AJ	0.533	0.519				
AN	0.75	0.759	0.429			
AD	0	0	0	0		
AE	0	0	0	0	0.444	
AK	0	0	0	0	0.824	0.533

and pods shared between 53 and 100% of their call type repertoires with other pods (Table 2). Although all seven pods shared calls with at least two other pods, the pattern of sharing revealed two distinct clusters of pods. AB, AI, AJ and AN pods shared calls, as did AD, AE and AK pods, but no calls were shared between these two groups of pods. Similar to Ford (1991), we defined pods that shared calls as a vocal clan. Therefore, we defined two vocal clans among southern Alaskan resident killer whales: AB, AI, AJ and AN pods belong to the AB clan; and AD, AE and AK pods belong to the AD clan.

We calculated the degree of repertoire similarity between pairs of pods of each clan using the index of similarity (Ford 1991). Because pods from different clans did not share any calls, the similarity between them was 0 (Table 3). The repertoires of AB, AI and AN pods within AB clan were more similar to each other than they were to the repertoire of the AJ pod. Similarly, AD and AK pods within the AD clan had more shared calls than either had with the AE pod. The results of the repertoire analysis are displayed in the form of a dendrogram by means of average link cluster analysis (Fig. 8).

Genetic Analysis

Eighty-two photographically identified resident whales from southern Alaska were biopsied. The complete

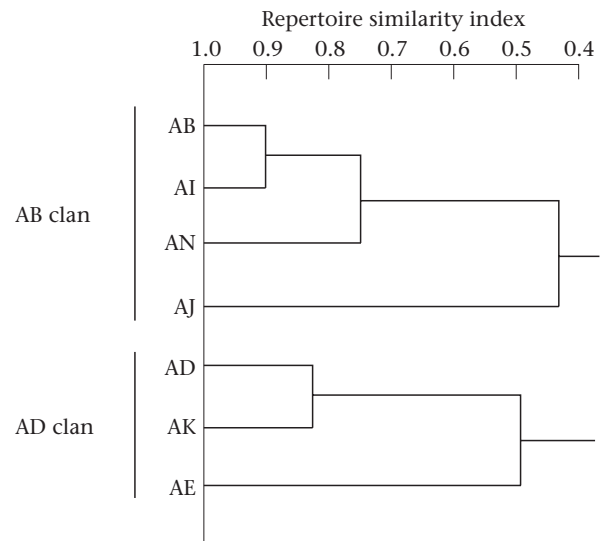


Figure 8. Degree of repertoire similarity between pods based on a single-cluster dendrogram of acoustic similarity.

Table 4. Mitochondrial D-loop haplotype distinctions of AB and AD clans in comparison to other resident killer whale clans in the eastern North Pacific

Clan	Number of biopsied whales	Community	D-loop haplotype
AB	44	Southern Alaska	NR
AD	38	Southern Alaska	SR
A	75	Northern British Columbia	NR
G	34	Northern British Columbia	NR
R	17	Northern British Columbia	NR
J	8	Southern British Columbia	SR

NR: Northern Resident type; SR: Southern Resident type.

mitochondrial D-loop sequence was determined for 40 of these whales, including one individual from each set of mothers and known offspring. All the sequenced whales in the four pods belonging to the AB clan had the same mitochondrial D-loop haplotype (Table 4). This haplotype has also been found in all biopsied killer whales ($N=126$) of the Northern Resident (NR) community, which inhabits most of British Columbia and the southern tip of Alaska (Fig. 1). In contrast, all whales in the three pods of the AD clan showed a mitochondrial haplotype that has also been found in all biopsied whales ($N=8$) of the Southern Resident (SR) community (Table 4), which is usually sighted in southern British Columbia, Canada and Washington State, U.S.A. and occasionally further south (Fig. 1).

DISCUSSION

Our study is the first to provide direct evidence that the vocal clans of resident killer whales, which Ford (1991) described as acoustic clans, are maternal lineages. One could argue that the call type categorization method that

we used to define clans is less objective than one that uses statistically significant differences among sound variables to make discriminations. However, the ability of our discrimination method to detect acoustic differences between maternal lineages is proof that it provides biologically meaningful categorizations. This discrimination method has also been used in the categorization of discrete acoustic structures in bird and humpback whale songs, such as notes, phrases and themes, and has proven to be highly reliable in detecting overall similarities and differences among these structural parts within and between songs (Marler & Tamura 1962; Payne & McVay 1971).

Call Type Transmission and Evolution of Clans

Our results and those of Barrett-Lennard (2000) show that maternal relatedness is reflected in call sharing among resident killer whales. Ford (1991) proposed such a system of call sharing but had no access to genetic data.

Call types could be inherited vertically from their parents (genetically or culturally) or learned from all members of the group, which implies at least some form of horizontal/oblique transmission (Deecke et al. 2000). Furthermore, call types could be culturally selected to identify the group.

All members of the matriline use the same set of calls (Ford 1991; Miller & Bain 2000), and mating usually takes place between pods (Barrett-Lennard 2000). Paternal genetic inheritance can be ruled out, because it would produce different repertoires for individuals of the same pod. Maternal genetic inheritance of call types either through mitochondrial DNA, maternal sex chromosomes, or through genomic imprinting is also unlikely, because many call types are highly complex. Genomic imprinting has been reported to influence the transmission of certain social behaviours (Spencer et al. 1999). However, we could not find any evidence in the literature that structural modifications that enable organisms to produce complex behaviours have been encoded by mtDNA, or imprinted.

Although call learning in killer whales has not yet been demonstrated in a controlled experiment (Janik & Slater 1997), observations of captive killer whales with different regional ancestry (Bain 1989; Ford 1991) have shown that whales regularly imitate calls of their tankmates, and young whales copy calls preferentially from close relatives (Bowles et al. 1988). Learning is also the most likely mechanism for true vocal mimicry (Ford 1991), and horizontal or oblique transmission of calls among wild killer whales (Deecke et al. 2000). Therefore, the most parsimonious explanation for the existence of vocal clans is that killer whale calls are socially learned from maternally related individuals.

The genetic differentiation of clans is best explained by a lack of dispersal of females (Barrett-Lennard 2000). Consequently, the differences in repertoires among dialect groups within each clan could either be the passive result of gradual pod splitting and call divergence over time (genetic separation followed by genetic or

cultural drift, Bigg et al. 1990), the result of cultural selection on repertoires after separation, or both.

Ford (1991) proposed a number of potential mechanisms for repertoire divergence such as cultural drift, vertical cultural transmission from mother to offspring, cultural diffusion and innovation. Cultural drift is the passive result of pod fission, and would be caused by copying errors during the transmission process. New calls should form, and old ones lost, at a somewhat constant rate that would correspond to the change in number of matriline per pod. Repertoire size would tend to increase very gradually with the increase in number of matriline of the pod. For example, AI03 matriline of AI pod (7 whales: 4 males, 2 females, 1 juvenile), which is believed to have split from AB pod during the first half of the 1980s (Matkin et al. 1999), consistently shared 14 of the 17 calls from the AB pod repertoire. Therefore, AI03 differs in 18% of its repertoire from AB pod, a number that is consistent with drift. However, this 18% difference is based solely on call losses. No new call type or variant has yet been invented. Concurrently, the 12 matriline that comprised AB pod in 1984 declined from around 50 members to 25 members and eight matriline in 1998 (Matkin et al. 1999). A change in repertoire size, however, was not detected in recordings of the remaining eight matriline. Drift should produce slightly different repertoires between matriline, if call use varies between matriline, as has been shown for some matriline in the Northern Residents (Deecke et al. 2000; Miller & Bain 2000). If cultural drift is the only cause for vocal change, there should have been at least some repertoire change in the AB pod, which lost four complete matriline or 33% of its original number of matriline. Furthermore, it appears that certain call types change more quickly than others (Deecke et al. 2000). Therefore, cultural drift alone cannot explain all the observed differences in repertoires.

If vertical cultural transmission from mother to offspring were the only mechanism responsible for the transmission of call types, one should also see minor variations among calls produced by different matriline. However, as Deecke et al. (2000) have shown such variation only occurs in structurally simpler call types, while complex call types remain highly similar among matriline of the same pod. Therefore, vertical cultural transmission also cannot be the only mechanism for the observed repertoire differences.

Cultural diffusion results either from dispersal of whales between matriline or the sharing of calls between matriline that are not closely related. Dispersal has not been observed in over 25 years of study on resident killer whales in British Columbia (Ford et al. 2000). Call mimicry between not closely related matriline has been observed (Ford 1991). However, no call transfer has been observed for either resident killer whale clans in British Columbia or Alaska. Call innovation, although the most plausible cause for major divergence in resident killer whale repertoires, also has yet to be observed.

Considering reports of variation in call frequency among matriline of the same dialect group (Ford 1991; Miller & Bain 2000), our findings are in support of a transmission process based on both cultural drift in call

structure and selection on repertoire difference and similarity. Repertoire difference could be readily achieved by selectively dropping calls and changing the frequency of others during matriline fission, while similarity is maintained by keeping the majority of calls stable, while only allowing certain call structures to change gradually over time. Such gradual processes have been detected in call types of the Northern Residents (Ford 1991; Deecke et al. 2000; Miller & Bain 2000). Deecke et al. (2000) proposed a cultural drift model for the change they observed. However, they could not determine whether this change was neutral with regard to loss or invention of call structure, and also failed to detect a similar gradual change for another call type. Barrett-Lennard (2000) provided support for cultural selection of call repertoires by showing that an inbreeding avoidance function of group-specific dialects is the most parsimonious explanation for the observed mating patterns in the Northern Residents. Mating is virtually absent within pods, rare within clans, and common between clans. Acoustic differences between clans could therefore be the result of both types of cultural evolution: (1) call type selection for parts of the repertoire, presumably calls that are complex in structure and difficult to produce and learn, and (2) drift for those calls that are easier to produce and learn.

Possible Functions of Clans

If calls are learned selectively from their mothers within the matriline, females could determine their degree of relatedness to prospective mates. Any males that attempted to cheat by using different calls could easily be unveiled, because females could determine the relatedness of a male based not only on his own calls, but on those used by his matriline (Barrett-Lennard 2000). Since male killer whales have not been observed to form male coalitions that coerce females into mating (Connor et al. 2000), males probably depend on female choice for their mating success. Cultural lineages based on calls learned in the matriline serve to associate males strongly with their mothers. Mating success of males therefore could depend on the status of the matriline within a clan or community. Males of matrilineages that are highly successful in matters of survival and reproduction might be chosen preferably as mating partners (Barrett-Lennard 2000).

A similar example of gene/culture lineages is found among certain human populations. The Tsimshian of the coast of British Columbia and Alaska were historically organized in four named clans. The names were shared with two other societies, the Haida and the Tlingit (Garfield 1939). Before the Tsimshian came in contact with Europeans, each clan had several names that were the sole property of that clan. Children of marriages between members of different clans carried a maternal clan name with an addition that indicated the clan of the father. Clan names thereby always reflected degrees of relatedness and were used to avoid marriage between close relatives (Garfield 1939).

With the exception of a Southern Alaskan Resident call type (AKS02) from the AD clan that was very similar to a Northern Resident R-clan call type (N 32ii), all other call

types were used only within their respective clans. The two clans (AD and R) that used similar call types have adjacent ranges but have not been observed associating with each other. Therefore, call type transmission appears to take place solely within clans, and call type exchange between clans is negligible, if it occurs at all. The two vocal clans within the Southern Alaskan Residents have different mitochondrial DNA haplotypes, while the three clans of the Northern Residents share the same haplotype. This indicates that call repertoires evolve faster than mitochondrial DNA, because female exchange between matrilineages, pods, or clans is very rare or nonexistent (Barrett-Lennard 2000), thereby pointing towards the same maternal ancestor of the three vocal clans among Northern Residents. Furthermore, the two vocal clans of the southern Alaskan subpopulation, which clearly are distinct cultural and genetic lineages, may have joined to form a breeding population after both clans migrated into the area.

Another possible function of clans could be to help kin survive. One of the main food sources of resident killer whales is salmon, particularly chinook, *Oryzias tshawytsch* (Ford et al. 1998) and coho, *O. kisutch* (Saulitis et al. 1993). Large-brained animals, such as killer whales, potentially have the ability to store fluctuating temporal and spatial information in their memory. Long-lived females can positively affect the survival of their relatives by using such an ability to store information on the seasonal distribution of salmon.

The evolution of parallel cultural and genetic lineages in resident killer whales shows similarities to the development of parallel lineages in humans. In humans and in resident killer whales the similarities of vocalizations within genetically distinct lineages is in sharp contrast to distinct vocal differences among lineages (Barbujani 1991). Human languages, which might have evolved through a process of dialect divergences (Hill 1978), also show geographical distinctiveness. However, different dialects can also coexist in the same area, as seen by the African American vernacular versus standard American English.

Killer whale dialects identify maternal relatedness. Because resident killer whales do not appear to leave their natal group, this lowers the rate by which dialects change over time. The change of dialects is probably a result of cultural drift. However, cultural selection on a group level that would regulate how dialects change over time cannot be ruled out as an alternative explanation.

Acknowledgments

We thank the many observers who made recordings and took photographs of killer whales. In particular, recordings by Eva Saulitis, Kathy Heise and Kirsten Englund contributed useful data. We thank Graeme Ellis for identifying killer whales that were photographed parallel to recordings. We also thank the Oil Spill Recovery Institute and the Exxon Valdez Oil Spill Trustee Council for providing funding. We thank the Vancouver Aquarium Marine Science Centre for the use of their Acoustic Laboratory, and the BC Wild Killer Whale Adoption

Program for financial support to H.Y. and L.B.L. L.B.L. and H.Y. were also supported by the National Science and Engineering Research Council of Canada (NSERC), the Science Council of British Columbia (SCBC) and the University of British Columbia. We thank David Bain, Volker Deecke, Kathy Heise, Sally Otto, Jamie Smith, Andrew Trites, Hal Whitehead and one anonymous referee for helpful comments.

References

- Bain, D. E. 1986. Acoustic behavior of *Orcinus*: sequences, periodicity, behavioral correlates and an automated technique for call classification. In: *Behavioral Biology of Killer Whales* (Ed. by B. C. Kirkeveld & J. S. Lockard), pp. 335–371. New York: Alan R. Liss.
- Bain, D. E. 1989. An evaluation of evolutionary processes: studies of natural selection, dispersal, and cultural evolution in killer whales (*Orcinus orca*). Ph.D. thesis, University of California, Santa Cruz.
- Barbujani, G. 1991. What do languages tell us about human microevolution? *Trends in Ecology and Evolution*, **6**, 151–156.
- Barrett-Lennard, L. G. 2000. Population structure and mating patterns of killer whales, *Orcinus orca*, as revealed by DNA analysis. Ph.D. thesis in Zoology, University of British Columbia, Vancouver.
- Barrett-Lennard, L. G., Ford, J. K. B. & Heise, K. A. 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour*, **51**, 553–565.
- Barrett-Lennard, L. G., Smith, T. G. & Ellis, G. M. 1996. A cetacean biopsy system using lightweight pneumatic darts, and its effect on the behavior of killer whales. *Marine Mammal Science*, **12**, 14–27.
- Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B. & Balcomb, K. C., III. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission, Special Issue*, **12**, 383–405.
- Bowles, A. E., Young, W. G. & Asper, E. D. 1988. Ontogeny of stereotyped calling of a killer whale calf during her first year. *Rit Fiskideildar*, **11**, 251–275.
- Boyd, R. & Richerson, P. J. 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.
- Cavalli-Sforza, L. L. & Feldman, M. W. 1981. *Cultural Transmission and Evolution: a Quantitative Approach*. Princeton, New Jersey: Princeton University Press.
- Conner, D. A. 1982. Dialects versus geographic variation in mammalian vocalizations. *Animal Behaviour*, **30**, 297–298.
- Connor, R. C., Read, A. J. & Wrangham, R. 2000. Male reproductive strategies and social bonds. In: *Cetacean Societies* (Ed. by R. C. Connor, J. Mann, P. L. Tyack & H. Whitehead), pp. 247–269. Chicago: University of Chicago Press.
- Deecke, V. B., Ford, J. K. B. & Spong, P. 1999. Quantifying complex patterns of bioacoustic variation: use of a neural network to compare killer whale (*Orcinus orca*) dialects. *Journal of the Acoustical Society of America*, **105**, 1–9.
- Deecke, V. B., Ford, J. K. B. & Spong, P. 2000. Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Animal Behaviour*, **60**, 629–638.
- Ford, J. K. B. 1984. Call traditions and dialects of killer whales (*Orcinus orca*) in British Columbia. Ph.D. thesis. University of British Columbia, Vancouver.
- Ford, J. K. B. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, **67**, 727–745.
- Ford, J. K. B. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, **69**, 1454–1483.
- Ford, J. K. B. 2002. Dialects. In: *The Encyclopedia of Marine Mammals* (Ed. by W. F. Perrin, B. Würsig & J. G. M. Thewissen), pp. 322–323. New York: Academic Press.
- Ford, J. K. B. & Fisher, H. D. 1982. Killer whale (*Orcinus orca*) dialects as an indicator of stocks in British Columbia. *Report of the International Whaling Commission*, **32**, 671–679.
- Ford, J. K. B., Ellis, G. M. & Balcomb, B. C. 2000. *Killer Whales*. Vancouver, British Columbia: UBC Press.
- Ford, J. K. B., Ellis, G. M., Barrett-Lennard, L. G., Morton, A. B., Palm, R. S. & Balcomb, K. C., III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, **76**, 1456–1471.
- Garfield, V. E. 1939. *Tsimishian Clan and Society*. Seattle: University of Washington Press.
- Hill, J. 1978. Apes and language. *Annual Review of Anthropology*, **7**, 89–112.
- Janik, V. M. & Slater, P. J. B. 1997. Vocal learning in mammals. *Advances in the study of behaviour*, **26**, 59–99.
- Katz, D. 1950. *Gestalt Psychology, Its Nature and Significance*. New York: Ronald Press.
- Kawamura, S. 1959. The process of sub-culture propagation among Japanese macaques. *Primates*, **2**, 43–60.
- Lynch, A. 1996. Population memetics of bird song. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. M. Kroodsma), pp. 181–197. Ithaca, New York: Comstock.
- Marler, P. 1997. Three models of song learning: evidence from behavior. *Journal of Neurobiology*, **50**, 501–516.
- Marler, P. & Tamura, M. 1962. Song 'dialects' in three populations of white-crowned sparrows. *Condor*, **64**, 368–377.
- Matkin, C. & Saulitis, E. 1997. *Killer Whale, Orcinus orca*. Anchorage, Alaska: Exxon Valdez Oil Spill Trustee Council.
- Matkin, C. O., Ellis, G. M., Olesiuk, P. & Saulitis, E. L. 1999. Association patterns and inferred genealogies of resident killer whales, *Orcinus orca*, in Prince William Sound. *Fisheries Bulletin*, **97**, 900–919.
- Miller, P. J. O. & Bain, D. E. 2000. Within-pod variation in the sound production of a pod of killer whales, *Orcinus orca*. *Animal Behaviour*, **60**, 617–628.
- Mundinger, P. C. 1980. Animal cultures and a general theory of cultural evolution. *Ethology and Sociobiology*, **1**, 183–223.
- Murdock, G. P. 1960. *Social Structure*. New York: MacMillan.
- Nishida, T. 1987. Local traditions and cultural transmission. In: *Primate Societies* (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 462–474. Chicago: University of Chicago Press.
- Noad, M. J., Cato, D. H., Bryden, M. M., Jenner, M.-N. & Jenner, K. C. S. 2000. Cultural revolution in whale songs. *Nature*, **408**, 537.
- Payne, K., Tyack, P. & Payne, R. 1983. Progressive changes in the songs of humpback whales (*Megaptera novaeangliae*): a detailed analysis of two seasons in Hawaii. In: *Communication and Behavior of Whales. AAAS Selected Symposia Series 76* (Ed. by R. Payne), pp. 9–57. Boulder, Colorado: Westview Press.
- Payne, R. & Guinee, L. N. 1983. Humpback whale (*Megaptera novaeangliae*) songs as an indicator of "stocks". In: *Communication and Behaviour of Whales* (Ed. by R. Payne), pp. 333–358. Boulder, Colorado: Westview Press.
- Payne, R. B. 1996. Song traditions in indigo buntings: origin, improvisation, dispersal, and extinction in cultural evolution. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. M. Kroodsma), pp. 198–220. Ithaca, New York: Comstock.
- Payne, R. S. & McVay, S. 1971. Songs of humpback whales. *Science*, **173**, 585–597.
- Sambrook, J., Fritsch, E. F. & Maniatis, T. 1989. *Molecular Cloning: A Laboratory Manual*. Cold Spring Harbor, New York: Cold Spring Harbor Laboratory Press.

- Saulitis, E. L. 1993. The behaviour and vocalizations of the 'AT' group of killer whales (*Orcinus orca*) in Prince William Sound, Alaska. M.Sc. thesis, University of Alaska Fairbanks.
- Saulitis, E. L., Matkin, C., Barrett-Lennard, L. G., Heise, K. & Ellis, G. 2000. Foraging strategies of sympatric killer whale (*Orcinus orca*) populations in Prince William Sound, Alaska. *Marine Mammal Science*, **16**, 94–109.
- Schevill, W. E. & Watkins, W. A. 1966. Sound structure and directionality in *Orcinus* (killer whale). *Zoologica*, **51**, 70–76.
- Slater, P. J. B. & Ince, S. A. 1979. Cultural evolution in chaffinch song. *Behaviour*, **71**, 146–166.
- Spencer, H. G., Clark, A. G. & Feldman, M. W. 1999. Genetic conflicts and the evolutionary origin of genomic imprinting. *Trends in Ecology and Evolution*, **14**, 197–201.
- Strager, H. 1995. Pod specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in waters of Northern Norway. *Canadian Journal of Zoology*, **73**, 1037–1047.
- Thompson, J. D., Higgins, D. G. & Gibson, J. 1994. CLUSTAL-W: improving the sensibility of progressive multiple sequence alignment through sequence-weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acid Research*, **22**, 4673–4680.
- Thomsen, F., Franck, D. & Ford, J. K. B. 2001. Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Journal of the Acoustical Society of America*, **109**, 1240–1246.
- Watkins, W. A. 1967. The harmonic interval: fact or artefact in spectral analysis of pulse trains. In: *Marine Bioacoustics. Vol. 2* (Ed. by W. N. Tavolga), pp. 15–43. New York: Pergamon.
- Weilgart, L. & Whitehead, H. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology*, **40**, 277–285.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999. Cultures in chimpanzees. *Nature*, **399**, 682–685.