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Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics

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Summary

1. This study addresses the issue of structure in sperm whale (*Physeter macrocephalus* Linnaeus) populations and whether it is geographically based.

2. During a survey around the South Pacific Ocean, we collected sloughed skin for genetic analyses, recorded coda vocalizations, and photographed fluke markings.

3. Groups of female and immature sperm whales had characteristic mitochondrial haplotypes, coda repertoires, and fluke-mark patterns, but there was no clear geographical structure in any of these attributes.

4. However, similarities of coda repertoire and mitochondrial haplotype distribution were significantly correlated among pairs of groups in a manner that was not geographically based. There was also a significant canonical correlation coefficient between coda repertoire and fluke-mark patterns.

5. These results suggest that attributes (such as vocal repertoire and techniques of predator defence) which are acquired matrilineally, and probably culturally, are conserved during the fission and dispersal of groups.

Key-words: coda, conserved culture, mitochondrial DNA, *Physeter macrocephalus*

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Introduction

Structure within populations, whereby some individuals are more similar to each other than they are to others, is an important consideration in the ecology, evolution, management and conservation of a species (Anonymous 1980; Huston 1994; Harrison & Hastings 1996). Such structure can be based on age, stage, geography, genetic variation, cultural processes or environmental differences. Population structure is particularly important when similarities between members of the population on two or more attributes are correlated, and when the attributes relate to survival or reproduction.

Populations of cetaceans (whales and dolphins) are often strongly structured, most obviously by sex and age, but also frequently by geography, which may allow the definition of 'stocks' (Donovan 1991). Structure can show itself in ranging behaviour, foraging behaviour, social organization, genetics, morphology, acquired markings, or vocal dialects. Often, but not always, differences in these attributes are geographically based, with nearby individuals being more similar. Spatial scales of such structure vary considerably between species, and may differ between features over each of which the population is structured. Usually, however, structural patterns in different attributes are correlated: for instance, the animals least similar genetically also have least similar dialects. This could be because the attributes are directly linked (dialect is genetically controlled) or because of parallel processes (genetic and cultural drift).

A good example of a cetacean species with highly structured populations is the humpback whale (*Megaptera novaeangliae* Borowski). The mitochondrial (mtDNA) genome (Baker *et al*. 1993), the song sung by males on the breeding ground (Payne & Guinee 1983), the proportion of white on the body and flukes (Winn & Reichly 1985), and the number of scars from predators on the flukes (Katona *et al*. 1980) all show geographical variation. However, scars from predators are a product of the whales' environment, songs are culturally transmitted, and pigmentation patterns are probably largely genetically determined. Although all these structures are geographically based and generally correlated, they operate at different

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scales: songs and pigmentation patterns over ocean basins, mtDNA genomes and fluke scars over the scales of summer feeding aggregations (a few thousand km).

Killer whales (*Orcinus orca* Linnaeus) off British Columbia and Washington State are also strongly structured, but at several levels the structuring is not geographically based. 'Transient' and 'resident' forms are sympatric, but differ substantially in morphology, genetics, behaviour and vocalizations (Morton 1990; Hoelzel & Dover 1991; Baird, Abrams & Dill 1992; Barrett-Lennard, Ford & Heise 1996). Among sympatric transients there are 'pod'-specific foraging tactics, possibly corresponding to maternal lineage (Baird & Dill 1995). In residents, vocal repertoire varies between sympatric pods as well as geographically between 'communities' (Ford 1991).

This paper looks for population structure among groups of female and immature sperm whales (*Physeter macrocephalus* Linnaeus) of the South Pacific. Population structure in sperm whales was an important and contentious issue for the Scientific Committee of the International Whaling Commission during the 1970s and early 1980s, as it had the potential severely to affect management decisions (Donovan 1991). However, despite much research and debate, there was no clear consensus on the structure of sperm whale populations other than the clear differences in distribution between the highly dimorphic sexes (Rice 1989; Donovan 1991).

Female and immature sperm whales travel in groups of about 20 animals (Whitehead, Waters & Lyrholm 1991). A group seems generally to consist of one or more matrilines, some of which stay together for periods of days, and others of which may be much more permanent companions (Whitehead *et al.* 1991; Richard *et al.* 1996a). Generally one matriline appears numerically to dominate the group (Richard *et al.* 1996a). Males disperse from these groups of females and immatures at about 6 years of age (Best 1979; Richard *et al.* 1996a).

In 1992–93 the sperm whales of the South Pacific were surveyed (Fig. 1). For each group encountered, an attempt was made to record 'coda' vocalizations, collect sloughed skin for genetic analysis, and photograph tail flukes for the identification of individuals through marking patterns, as well as quantification of the degree of marking.

Codas are patterned series of 2 to > 20 clicks made by socializing sperm whales, and often arranged into exchanges (Watkins & Schevill 1977). Codas can be classified into nearly discrete categories based on the number of clicks they contain and the temporal patterning of the clicks (Weilgart & Whitehead 1993, 1997).

The trailing edges of sperm whale flukes are marked with nicks, scallops, waves, toothmark scars and holes and may have missing pieces (Whitehead 1990). We think that most of these marks are the result of environmental factors and thus, that the degree and type of marking on an individual's pair of flukes may be related to its experiences, particularly with predators (Dufault & Whitehead 1995a, b, 1998).

Separate analyses of the genetic, vocalization and marking data from the present study's South Pacific survey showed similar patterns: within groups there was significant similarity of mitochondrial genome (Dillon 1996), nuclear genotype as indicated by microsatellites (K. Richard, unpublished data), coda repertoire (Weilgart & Whitehead 1997) and fluke markings (Dufault & Whitehead 1998). Thus, the population is strongly structured at the level of the group. However, geographically based structures among groups in these attributes seemed weak (coda repertoire and fluke marks) or non-existent (genetic markers). This paper looks beyond the level of the social group, trying to relate mitochondrial haplotypes, coda repertoires and marking patterns to each other and to geography.

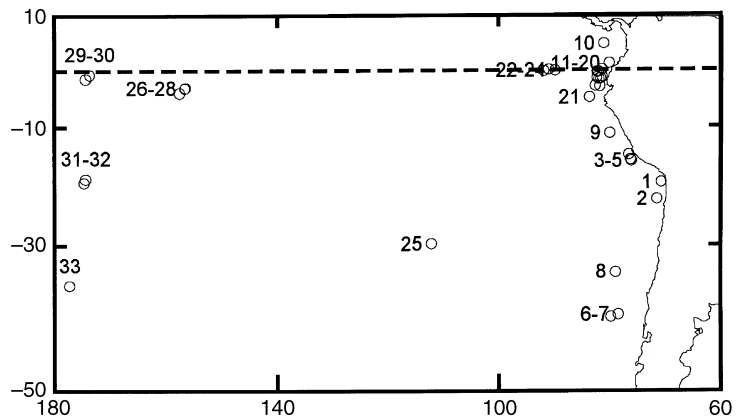

Fig. 1. South Pacific Ocean showing positions of encounters with sperm whale groups labelled by group index number. The dashed line indicates the equator.

Methods

FIELD METHODS

Between June 1992 and April 1993 sperm whale concentrations were surveyed in the South Pacific from the 12·5 m auxiliary cutter *Balaena*. The route was designed to cross many of the sperm whale 'grounds' shown in Townsend's (1935) charts of the kills by 19th century American sperm whalers. Additional data, from studies off the Galápagos Islands in 1989 and 1991, and off mainland Ecuador in 1991 are also used.

While over water deeper than 1000 m, a towed omnidirectional hydrophone [modified Benthos AQ-21B (Falmouth, MA, USA) on 30 m of cable] was monitored every 30 min for the distinctive clicks of sperm whales (Backus & Schevill 1966). If sperm whale clicks were sufficiently loud and the weather was favourable (wind less than ≈ 17 knots $= \approx 9$ m s^{-1}), a bearing was obtained on the clicks using a custom-made directional hydrophone (cf. Whitehead & Gordon 1986). Whales were then tracked visually and acoustically (using the directional hydrophone) for 0·5–3 days. This allowed the boat to stay within about 2 km of groups of sperm whales during most of the tracking time.

Groups consisted principally of female sperm whales and their young, but were sometimes briefly accompanied by large mature males (Whitehead & Waters 1990).

Whenever possible, whales were approached to within 30–100 m in order to photograph the ventral side of their tail flukes for individual identification (Arnbom 1987) and marking pattern analysis (Dufault & Whitehead 1998).

Pieces of sloughed skin floating in the wake of whales were collected and used as a source of DNA (Whitehead *et al*. 1990; Amos *et al*. 1992). Many of these pieces could be linked to specific, photographically identified individuals when animals were photographed by themselves, as the skin sinks (Dillon 1996; Richard *et al*. 1996a).

Whenever whales were socializing near the surface, as well as periodically throughout the tracking time, the hydrophone was monitored for the presence of codas. If present and clear with good signal to noise ratio, codas were recorded using a reel-to-reel tape recorder (Nagra IV-SJ) and preamplifier (Ithaco 453). While recording codas the boat was usually within 300 m of the whales.

ANALYSIS OF IDENTIFICATION PHOTOGRAPHS AND MARK-TYPE ANALYSIS

Photographic negatives showing sperm whale flukes were viewed on a light table with an 8 × magnifying loupe. Arnbom's (1987) 'Q' value, an integer ranging from 1 to 5, was assigned to each negative based on the quality of the image (Dufault & Whitehead 1993). Individuals were identified from these photographs and compared with a catalogue using standard techniques (Arnbom 1987; Whitehead 1990).

The best photograph of each individual was digitized (using a CalComp digitizing tablet) into a computer catalogue which stores coordinates of the characteristic markings along the trailing edge of the fluke, and checks for matches between flukes (Whitehead 1990). The mark types considered were nicks, distinct nicks, scallops, waves, missing portions, toothmark scars, and holes as defined by Whitehead (1990). A computer program (Dufault & Whitehead 1993) was used to generate a count for each of the mark types for each identified individual using the digitized information.

For each group the mean number was calculated of each of the seven mark types possessed by identified members of the group (with at least one photograph of $Q \geqslant 4$)as shown on their best quality photograph (Table 1).

DEFINITION OF GROUPS

The photographic identifications of individuals allowed us to assign fluke photographs, coda recording sessions and genetic samples to particular groups (Weilgart & Whitehead, 1997). All data from a particular day were assumed to be from the same group. If n_A whales were identified from good quality ($Q \geqslant 3$) photographs on day A and n_B on day B, with m_{AB} common to the 2 days, then data from the 2 days were considered to be from the same group if:

$$m_{AB} > 0{\cdot}25 \cdot \text{Minimum } \{n_A, n_B\}.$$

As about half the whales in the group being followed were identified each day (Whitehead, Waters & Lyrholm 1992), we expected that if the same group was being followed then:

$$m_{AB} = \approx 0{\cdot}5 \cdot \text{Minimum } \{n_A, n_B\}.$$

Thirty-three such groups were distinguished (with identification numbers 1–33, see Table 1).

GENETIC ANALYSES

The sperm whale mitochondrial control region was amplified as described by Dillon & Wright (1993). Sequencing primers were $tRNA^{Thr}$ [one of the polymerase chain reaction (PCR) primers] and an internal primer that anneals to 'block a' of the sperm whale control region (Dillon & Wright 1993). With these primers, ≈ 500 bp of the sperm whale control region were sequenced. We are confident of our mtDNA sequences for several reasons, including the fact that we re-amplified and re-sequenced in excess of 15 000 bp. This included samples from the same individual (determined by photographic identifications) collected on different days, with no discrepancies observed. Sequences were aligned and variable nucle-

Table 1. Summary of data for sperm whale groups studied in South Pacific: proportions of long, short, regular and plus-one (+1) codas recorded; mean number of nicks, distinct nicks (D-ni), scallops (Scal), waves, missing portions (Miss), toothmark scars, and holes; and distribution of mitochondrial haplotypes (3#4 = 3 individuals with mtDNA haplotype #4). – = insufficient, or no, data available

	Coda class proportions				Mean number of marks							
ID	Long	Short	Reg.	+1	Nick	D-ni	Scal	Wave	Miss	Scar	Hole	mtDNA haplotypes
01	–	–	–	–	3·76	1·00	1·94	5·94	0·29	0·00	0·18	2#3
02	0·127	0·419	0·191	0·005	2·00	0·75	1·25	5·75	0·00	0·00	0·25	–
03	0·038	0·024	0·024	0·103	6·09	1·27	2·64	4·18	0·00	0·00	0·18	–
04	0·048	0·580	0·223	0·053	3·56	0·75	0·44	6·13	0·06	0·00	0·06	1#1, 6#3
05	0·069	0·844	0·007	0·014	11·43	1·57	1·43	5·86	0·14	4·43	0·29	–
06	0·040	0·508	0·628	0·000	3·75	1·88	0·38	5·38	0·13	0·00	0·25	–
07	0·103	0·484	0·611	0·000	–	–	–	–	–	–	–	–
08	–	–	–	–	4·00	1·00	0·44	5·76	0·16	0·12	0·12	1#1, 1#2, 2#3, 1#7, 1#9
09	–	–	–	–	6·33	2·44	3·33	6·00	0·22	0·00	0·22	1#1, 2#4, 1#5
10	0·000	0·922	0·420	0·002	2·00	0·50	1·25	7·25	0·00	0·00	0·00	–
11	–	–	–	–	3·64	1·91	2·09	5·41	0·27	0·00	0·00	3#1
12	–	–	–	–	3·00	1·23	1·50	3·91	0·27	0·00	0·00	1#3, 1#6
13	–	–	–	–	5·39	1·65	1·22	3·57	0·13	0·00	0·39	3#1, 1#2, 13#3, 1#11
14	–	–	–	–	4·53	1·56	1·79	4·02	0·33	0·00	0·26	2#1
15	–	–	–	–	3·31	1·75	1·25	2·00	0·06	0·00	0·06	–
16	–	–	–	–	4·00	2·26	0·61	3·96	0·13	0·00	0·22	1#1, 17#2, 2#3
17	–	–	–	–	4·83	2·74	0·65	3·17	0·30	0·00	0·17	2#1
18	0·031	0·859	0·326	0·012	4·17	1·13	1·65	6·43	0·26	0·00	0·04	–
19	–	–	–	–	4·47	1·97	1·53	4·09	0·56	0·00	0·18	9#1, 4#2, 1#6, 3#10, 4#12
20	0·210	0·054	0·023	0·628	4·63	1·12	1·37	5·02	0·19	0·47	0·02	–
21	0·169	0·662	0·058	0·008	3·44	1·36	1·88	3·76	0·16	0·00	0·16	–
22	–	–	–	–	3·73	1·43	1·50	5·27	0·23	0·00	0·23	6#3, 1#7, 2#9
23	–	–	–	–	–	–	–	–	–	–	–	4#1
24	–	–	–	–	1·94	1·13	1·44	3·44	0·13	0·06	0·00	–
25	0·064	0·300	0·039	0·037	–	–	–	–	–	–	–	–
26	0·031	0·852	0·284	0·025	5·48	1·74	1·19	6·84	0·45	0·00	0·29	1#1, 2#2, 1#8
27	0·008	0·928	0·235	0·008	3·00	0·25	2·00	7·50	0·25	0·00	0·00	4#1
28	0·106	0·681	0·418	0·000	2·75	1·35	0·85	4·80	0·30	0·00	0·30	5#5, 1#6
29	0·059	0·839	0·248	0·034	4·18	1·27	1·45	8·09	0·36	0·00	0·36	2#1, 1#2, 1#12
30	0·254	0·461	0·292	0·024	–	–	–	–	–	–	–	–
31	–	–	–	–	3·96	1·92	0·83	7·96	1·00	0·13	0·13	–
32	0·388	0·261	0·004	0·019	3·90	1·70	2·20	5·90	0·50	0·00	0·00	–
33	0·068	0·702	0·188	0·021	–	–	–	–	–	–	–	1#1, 2#3, 2#6, 1#7

otide positions identified. All sequence differences were transition substitutions, making sequence alignment straightforward. Based on the sequence at these positions, 12 mtDNA haplotypes were defined (Dillon 1996), which are referred to here as #1–#12.

For subsequent analysis only samples were used which we could be confident were from different individuals. Such samples were distinguished from all other samples in their group by one or more of the following criteria: all samples in the group were linked to photographic individual identifications; samples were from distinct individuals as determined by microsatellite genetic analyses (Richard, Whitehead & Wright 1996b); or (very occasionally) samples could not be from the same individual for logistic reasons, such as samples collected from whales who were at the surface at the same time, but separated by 100 m or more.

For each group the distribution of typed haplotypes was tabulated (Table 1). Only groups with at least two typed individuals were considered for subsequent analysis. Results were almost identical when this restriction was tightened so that only groups with at least four typed individuals were included.

ANALYSIS OF CODAS

The acoustic analysis of codas is described in detail by Weilgart & Whitehead (1993, 1997). Each coda was assigned to one of 30 coda types based on the number of clicks contained in it and their temporal patterning (Weilgart & Whitehead 1993). Categories were classified into four overlapping classes: *short* codas (<5 clicks), *long* codas (>6 clicks), *regular* codas (equally spaced intervals between clicks), and *plus-one* codas (double interval between last two clicks in coda). Coda repertoires were then constructed for each group using the total proportions of codas of

each type measured (coda type repertoire), and the proportions of all codas recorded from the group which were short, long, regular or plus-one (coda class repertoire).

DISTANCES BETWEEN SPERM WHALE GROUPS

Where data were available, up to six dissimilarity measures were calculated between pairs of groups:

1. *Distance*: geographical distance (rhumb line) between encounter positions of the groups in km – emphasizes large-scale effects.

2. *Log-distance*: natural logarithm of geographical distance – considers both large- and small-scale effects.

3. *Gene-distance*: 1 minus probability that a randomly chosen member of the first group has the same mtDNA haplotype as a randomly chosen member of the second group:

$$1 - \Sigma\, X_i \cdot Y_i/[\Sigma\, X_i \cdot \Sigma\, Y_i]$$

where X_i and Y_i are, respectively, the number of individuals in the two groups with haplotype i. Unlike most genetic distances (Nei 1972) this measure does not consider the degree of similarity of different haplotypes. The present study adopted a measure based on probability of shared haplotype between members of different groups because we are interested in population processes (principally the fission of matrilines) operating over much shorter time scales than the evolution of mtDNA haplotypes.

4. *Coda-type-distance*: 1 minus Spearman correlation coefficient between coda type repertoires of two groups. Coda-type-distance is small if the ranking of the different coda types according to frequency of use is similar for the two groups, and high if the groups use the coda types with very different relative frequencies.

5. *Coda-class-distance*: Squareroot of the Penrose distance (Penrose 1953) over four coda classes:

$$\sqrt{\Sigma(X_i - Y_i)^2/4 \cdot V_i}$$

where X_i and Y_i are, respectively, the proportion of codas of class i recorded from the two groups, and V_i is the variance among groups in the proportion of codas of class i. Coda-class-distance is small if the proportional usage of the four coda classes is similar for the two groups.

6. *Mark-distance*: Square root of the Penrose distance over seven mark types (mean number of marks per individual in group):

$$\sqrt{\Sigma(X_i - Y_i)^2/7 \cdot V_i}$$

where X_i and Y_i are, respectively, the mean number of marks of type i on the flukes of individuals from the two groups, and V_i is the variance among groups in the mean number of marks of type i. Thus, mark-distance between two groups is small if the members of the groups have similar numbers of each mark type.

STATISTICAL ANALYSIS

The relationships between groups on the different measures were displayed using plots in which groups with similar values are generally plotted close together, and those with dissimilar values apart: geographical distances are shown by a map (Fig. 1); genetic dissimilarities and coda type dissimilarities by means of non-metric multidimensional scaling plots; and coda class dissimilarities and mark-type dissimilarities by two-dimensional metric scaling of the Penrose distances of these measures using principal coordinates analysis (equivalent to principal components analysis of the correlation matrix).

Each set of dissimilarities between pairs of groups formed a dissimilarity matrix. The strength of the association between two dissimilarity matrices was measured by the matrix correlation (the product-moment, or Pearson, correlation between corresponding elements in the two matrices, ignoring the diagonal elements). Associations between dissimilarity matrices were tested using the Mantel test (Mantel 1967), in which the null hypothesis is that there is no relationship between the measures. When performing Mantel tests between dissimilarity matrices, each matrix was edited to remove groups missing from either matrix. Significance levels of Mantel tests were calculated using 1000 Monte Carlo permutations, as recommended by Manly (1992), and checked against the normal distribution approximation given by Mantel (1967); the two methods gave very similar results.

When Mantel tests showed significant correlation between two non-geographical distance matrices, we also calculated, and tested, partial matrix correlations controlling for the logarithm of geographical distance using the methods of Smouse, Long & Sokal (1986).

We also examined relationships between pairs of those attributes which could be expressed as a multivariate data matrix of not too high dimension (geographical position, coda class, and mark types) using canonical correlation analysis. This tests the hypothesis that there is a significant correlation between linear combinations of the variables of each attribute (e.g., $0{\cdot}5 \cdot$ latitude $- 0{\cdot}4 \cdot$ longitude is significantly correlated with $0{\cdot}1 \cdot X_1 + 0{\cdot}3 \cdot X_2 \ldots$, where X_1 is the proportion of short codas, X_2 the proportion of long codas, etc.).

Results

The geographical distances, genetic dissimilarities, coda repertoire dissimilarities, and mark-type dissimilarities between groups are displayed in Figs 1–5. These two-dimensional displays are generally good representations of the distance matrices: the stress of the multi-dimensional scaling plots was quite low (0·15 for the genetic data in Fig. 2, and 0·16 for the coda type dissimilarities in Fig. 3), and the first two

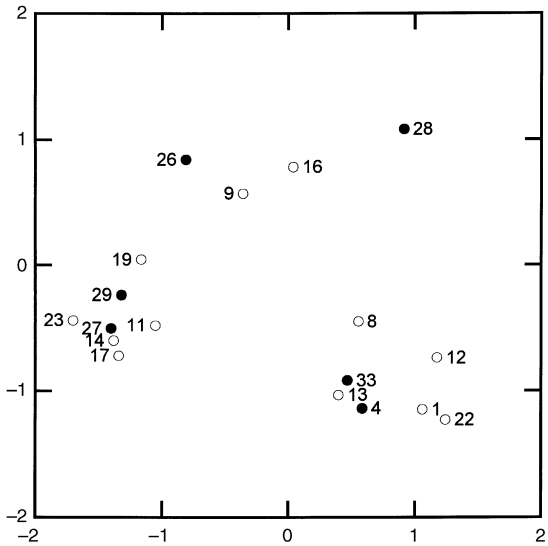

Fig. 2. Representation of groups according to similarity of distributions of mtDNA haplotypes (gene-distance) using two-dimensional non-metric multi-dimensional scaling. Groups for which there are both genetic and coda repertoire data are represented by ●. Symbols are slightly staggered so that they do not overlap.

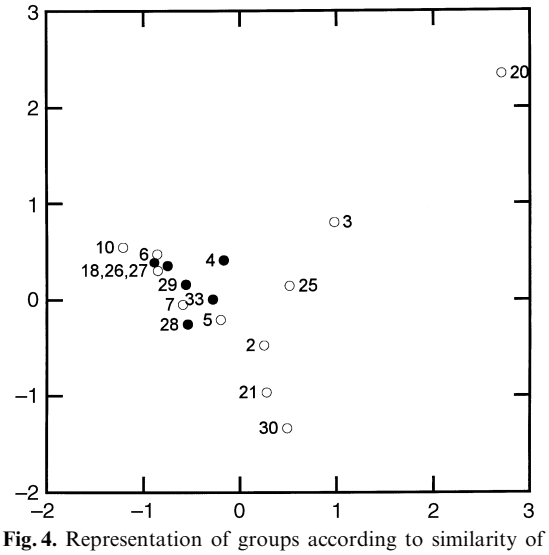

Fig. 4. Representation of groups according to similarity of distributions of coda classes (coda-class-distance) using two-dimensional metric scaling (the first two principal components). Groups for which there are both genetic and coda repertoire data are represented by ●.

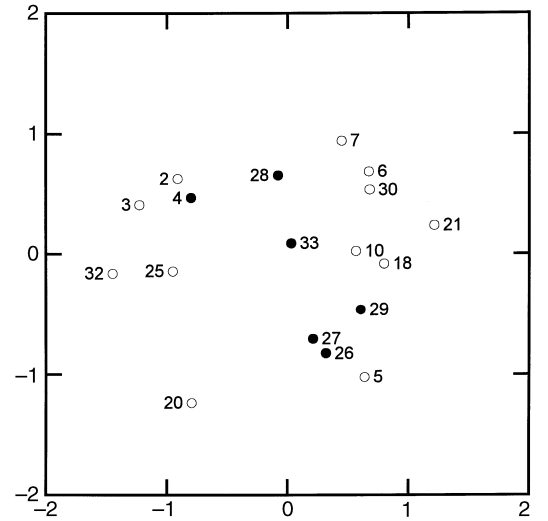

Fig. 3. Representation of groups according to similarity of distributions of coda types (coda-type-distance) using two-dimensional non-metric multi-dimensional scaling. Groups for which there are both genetic and coda repertoire data are represented by ●.

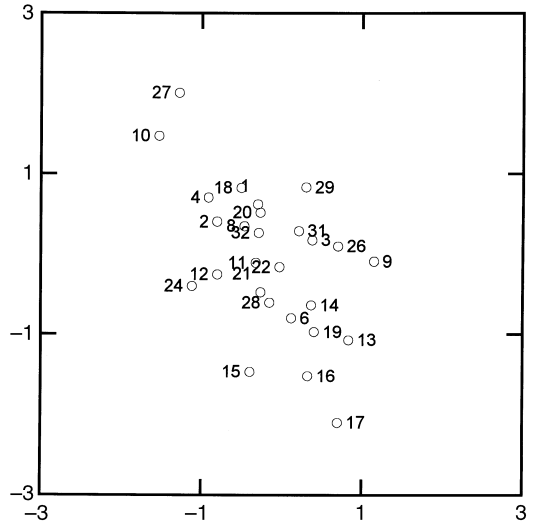

Fig. 5. Representation of groups according to similarity of fluke markings (mark-distance) using two-dimensional metric scaling (the first two principal components).

principal components of the coda class data (Fig. 4) account for 73% of the original variance. However, they only account for 50% of the mark-type variance, so Fig. 5 is not as good a representation of the mark dissimilarities as are the previous figures of their measures. Both the non-metric multi-dimensional scaling plots (Figs 2 and 3), for genetic and coda type dissimilarities, show 'horse-shoe' patterns characteristic of ordinations in which units can be arranged along a dominant gradient and non-neighbouring units are nearly equally dissimilar (in this case sharing few haplotypes or coda types).

Matrix correlations between geographical distances and genetic, coda and mark-type dissimilarities were low, and Mantel tests were non-significant (Table 2) indicating a lack of geographically based structure in these measures among sperm whales of the South Pacific. There were no significant canonical correlation coefficients between geographical position (latitude and longitude) and coda classes ($r = 0{\cdot}672$, $P = 0{\cdot}17$) or geographical position and mark type ($r = 0{\cdot}77$, $P = 0{\cdot}06$). The lack of geographical structure in the attributes examined is also suggested by little obvious concordance between the map of

Table 2. Matrix correlations of geographical distances and dissimilarities between pairs of groups based on mtDNA, coda repertoires and fluke markings (significance values from Mantel tests in parentheses)

	Log-distance	Distance
Gene-distance	0·06 (0·25)	0·09 (0·19)
Coda-type-distance	0·02 (0·37)	−0·06 (0·75)
Coda-class-distance	0·03 (0·35)	−0·03 (0·57)
Mark-type-distance	0·16 (0·12)	0·15 (0·15)

Table 4. Canonical loadings (correlations between original variables and canonical variates) of first canonical correlation between mark types and coda class repertoire ($r = 0{\cdot}998$, $P = 0{\cdot}021$)

Coda class		Mark type	
Short	0·544	Small nicks	−0·414
Long	0·156	Distinct nicks	0·285
Regular	0·335	Scallops	−0·312
Plus-one	−0·134	Waves	0·116
		Missing pieces	0·564
		Scars	−0·232
		Holes	−0·091

encounter positions (Fig. 1) and the displays of these measures (Figs 2–5).

There was little relationship between mark types and genetic or coda repertoire measures as indicated by matrix correlations and Mantel tests (Table 3). However, canonical correlation analysis suggested a significant relationship between mark type and coda class ($r = 0{\cdot}998$, $P = 0{\cdot}021$, for first canonical correlation; other canonical correlations non-significant; significance values from Monte Carlo analysis with 5000 permutations of coda class matrix). The canonical loadings which describe the relationship between mark type and coda class are given in Table 4. It seems that, generally, flukes of individuals in groups which predominantly use short codas have more missing pieces and fewer small nicks.

There were also strong and significant positive correlations between the matrices of genetic dissimilarity and both coda-type and coda-class dissimilarities (Table 3). Thus, groups with dominant mitochondrial haplotypes in common generally possessed similar coda repertoires. This can be seen when comparing the genetic dissimilarities displayed in Fig. 2 with the coda repertoire dissimilarity plots in Figs 3 and 4. Symbols representing the six groups for which both coda and genetic data were available are filled in. Clusters of groups (such as 26, 27 and 29) are common to both the genetic and coda repertoire plots. Some of the clusters transcend geography; for instance, groups 4 and 33 are plotted fairly closely on all three figures (as they make predominantly short codas, and haplotype #3 is common), but group 4 is from the eastern Pacific and group 33 from the western Pacific (Fig. 1, Table 1).

The independence of the coda-gene relationship from geographical distance was formalized by use of partial matrix correlations. When corrected for the logarithm of geographical distance, genetic dissimilarity has a partial matrix correlation coefficient of 0·63 ($P = 0{\cdot}03$) with coda-type dissimilarity, and 0·67 ($P = 0{\cdot}02$) with coda-class dissimilarity.

Discussion

Some of the results of this work are unexpected. With only a few exceptions (Machin 1974), most previous studies of population structure in sperm whales suggested that whales in different parts of an ocean were systematically different, for instance in morphology (Veinger 1980) or genetics (Wada 1980). Patterns of these apparent differences were never very clear, and it may be that many of these statistically significant results would have disappeared if the similarity of animals within groups had been considered. However, it was expected to find some geographically based population structure, and that any correlations between genetic, acoustic and marking measures would largely reflect these geographical patterns, as is the case with humpback whales.

The lack of any substantial, or statistically significant, correlations between measures in the present study and geographical distance could result from imprecision in the measures. However, in each case, group-specific effects were clearly shown by the same data (Dufault & Whitehead 1998; Dillon 1996; Weilgart & Whitehead, 1997), and there were strong and significant correlations between genetic distance and

Table 3. Matrix correlations of dissimilarities between pairs of groups based on mtDNA, coda repertoires and fluke markings (significance values from Mantel tests in parentheses)

	Gene-distance	Coda-type-distance	Coda-class-distance
Gene-distance	–		
Coda-type-distance	0·63 (0·01)	–	
Coda-class-distance	0·67 (0·01)	0·55 (0·00)	–
Mark-type-distance	−0·08 (0·79)	0·02 (0·42)	−0·06 (0·48)

both measures of coda repertoire dissimilarity (Table 3). This suggests that the data are adequate to indicate clear patterns when present, and thus that there is no substantial, geographically based population structure in these genetic, acoustic and marking measures among groups of female and immature sperm whales of the South Pacific.

The present analysis does not rule out all geographically based structure. Weak geographically based structure was indicated by other analyses of the coda data: groups recorded within $\approx$1000 km of each other had significantly more similar coda class repertoires than those recorded at ranges of a few thousand km (Weilgart & Whitehead 1997). Furthermore, geographical structure may well exist in unmeasured attributes. However, this analysis indicates that such structure is relatively weak compared to the similarities within groups, and other non-geographically based structures.

The strong gene-coda correlations suggest a non-geographically based population structure whereby maternally related groups have similar coda repertoires. The small sample size – only six groups were sampled for both codas and mtDNA – and the possibility of Type I errors following a number of hypothesis tests [we follow the arguments summarized by Stewart-Oaten (1995) for avoiding multiple comparison techniques], mean that this conclusion must be accepted with some caution. However, the correlation was strong and significant when considering each of two quite different measures of coda repertoire, and does not appear to be dependent on fortuitously placed data from one or two groups.

This seems to imply that coda repertoire is conserved matrilineally. Such a phenomenon could perhaps occur if dialect were genetically determined, although this would be very unusual (Catchpole & Slater 1995). Attributes of communicative vocalizations of other cetaceans seem to be culturally acquired, as indicated by their ability to mimic sounds (Tyack 1986; Janik & Slater 1997), and it is likely that the same is true for sperm whales. Therefore, the correlations between mtDNA haplotype and coda repertoire are, we think, best explained by parallel processes of matrilineal inheritance of coda repertoire (culturally) and mtDNA haplotype. As female sperm whales generally migrate only distances of 1000 km or so over periods of about 10 years (Best 1979; Dufault & Whitehead 1995c), for coda repertoire to be correlated with mtDNA haplotype over the large scales of an ocean basin, coda repertoire must be well conserved within matrilines, and when matrilines split. This is similar to the situation with the 'resident' killer whales around Vancouver Island, where sympatric or nearly sympatric matrilineal groups maintain traditional vocal repertoires, which are, at least partially, conserved when groups split (Ford 1989). However, in sperm whales these processes seem to be operating over much larger spatial scales.

The statistically significant canonical correlation between mark type and coda repertoire is difficult to interpret as there is little information about how the marks are acquired. Perhaps certain coda repertoires are more attractive to predators (as the major canonical loading on mark type is with missing pieces on the fluke). Alternatively, and perhaps more plausibly, culturally inherited behaviour which changes the susceptibility of animals to marks could be passed matrilineally in parallel with coda repertoire. One possibility could be different techniques of group defence against predators. Some groups of female sperm whales have been observed to defend themselves communally by facing the predators (Arnbom *et al.* 1987), whereas others adopt the 'marguerite' formation with heads together and bodies radiating out like spokes of a wheel (Nishiwaki 1962; Weller *et al.* 1996). Groups adopting the second of these defensive formations would seem more likely to accumulate marks on their flukes.

In conclusion, this study emphasizes the significance of matrilines in sperm whale society, suggesting that the characteristic attributes of matrilineal groups are conserved, probably often culturally, after a group splits and its constituents have dispersed over large geographical areas. It also indicates that the discovery of additional unusual and interesting aspects of population structure in sperm whales is likely to result from further analyses of more data and additional characters.

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