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Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales

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Abstract Codas, which are patterned series of clicks, were recorded from female and immature sperm whales (*Physeter macrocephalus*) in a number of locations around the South Pacific Ocean and in the Caribbean Sea. Using *K*-means cluster analysis, 3,644 codas were categorized based on the number of clicks and their patterning. There were 30 resulting types of coda. The numbers of codas of the different types recorded were used to construct repertoires for each recording session, day, group of whales, place, area, and ocean. Strong group-specific dialects, which seem to persist over periods of years, were apparent, overlaid on weaker geographical variation. Significant differences in repertoire were found between the Caribbean and the Pacific Ocean. Sperm whales now join killer whales (*Orcinus orca*) as the only cetacean species in which dialects (differences in vocal repertoire among neighboring, potentially interacting groups) have been found.

Key words *Physeter macrocephalus* · Sperm whale · Dialects · Communication · Codas

Introduction

The sperm whale (*Physeter macrocephalus*) is one of the most widely distributed animals on earth. Females and

their calves are found in tropical and subtropical waters. Their distributions are concentrated onto “grounds” (Townsend 1935) which are generally related to areas of higher primary productivity (Jaquet 1996). It is not yet known to what extent these grounds contain distinct genetic or breeding units, although female sperm whales generally have smaller home ranges, about 1,000 km across, than males (Best 1979).

Female sperm whales have a life span of 60–70 years (Rice 1989) and, together with their offspring, live in matrilineal family units (Richard et al. 1996) within which there is considerable cooperative behavior, including communal care for the young (Caldwell and Caldwell 1966; Gordon 1987; Whitehead 1996). Family units, which are very stable (Whitehead et al. 1991), contain around 10–12 members, but two or more family units may move together as a group for a few days (Whitehead et al. 1991). Mature males are often solitary or are found in small, temporary associations with other males (Best 1979). Males leave their family units at about 6 years of age and are found at much higher latitudes than the family groups (Best 1979; Richard et al. 1996). During the breeding season, mature males return to warm waters and rove between groups searching for receptive females (Whitehead 1993).

The principal recognized form of acoustic communication among socializing sperm whales is the short, patterned series of clicks called a coda (Watkins and Schevill 1977). Codas are often given as exchanges between whales, and such exchanges or “conversations” seem to occur only between whales that are physically close (Watkins and Schevill 1977). Using data collected off the Galápagos Islands, Ecuador, Whitehead and Weilgart (1991) found a strong, significant correlation between sperm whale vocalizations and visually observable activities. Codas were heard most frequently when whales were tightly aggregated at the surface, moving slowly and maneuvering about one another. Weilgart and Whitehead (1993) hypothesized that codas primarily function to maintain social cohesion within groups of females following periods of dispersion during

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foraging. Codas appear to be principally used as communication among members of a group, rather than between groups, since codas do not seem to carry much beyond 600 m or so at the surface, and groups are usually separated by several kilometers.

There was remarkable similarity in coda repertoire size between sperm whales of the West Indies and the Galápagos Islands, with 28 fairly discrete coda types categorized from the West Indies (Moore et al. 1993) and 23 from the Galápagos (Weilgart and Whitehead 1993). While some coda types were common to the two areas, such as the regularly-spaced five-click coda, others were not (Moore et al. 1993; Weilgart and Whitehead 1993). Thus, in different geographical regions, there seemed to be different coda repertoires.

The purpose of our study was to examine the geographical variation in sperm whale codas more thoroughly, and to determine whether dialects occur in sperm whales. Following the distinction made by Munding (1982), we use "geographical variation" to refer to (macrogeographic) differences between populations separated by large distances which inhibit them from mixing; and "dialects" to refer to (microgeographic) differences among neighboring, potentially interbreeding or interacting populations. In sperm whales, interacting family groups do not interbreed, as breeding males are not members of these groups.

Mammals do not commonly exhibit dialects (Maeda and Masataka 1987; Mitani et al. 1992), although intraspecific local population differences in vocalizations have been shown for species such as tamarins, *Saguinus l. labiatus*, (Maeda and Masataka 1987), possibly for wild chimpanzees, *Pan troglodytes* (Mitani et al. 1992), and of course, for humans (Barbujani 1991). Killer whales (*Orcinus orca*) present a special case in which group-specific call repertoires exist among animals inhabiting the same general area, even though groups commonly also interact and mix (Ford 1991; Strager 1995). Until now, killer whales were the only cetaceans in which dialects, as defined above, have been found (Ford 1991; Strager 1995).

The study of dialects can clarify how vocal acquisition takes place. The existence of local dialects often points to vocal learning as the likely mechanism for adopting a particular sound repertoire (Kroodsma 1982). By studying dialects, we can gain insight into the social organization and pattern of association among individuals or groups, and assess the discreteness of various groupings. For instance, Ford (1991) was able to develop a genealogy of known resident killer whale groups based on the vocal traditions he observed.

In 1992–1993 we collected and analyzed data on the vocal repertoires of sperm whales during a survey of the South Pacific which included two major axes of distribution: west from Ecuador along the equator, and south from Ecuador off the west coast of South America.

Methods

Field methods

Between June 1992 and May 1993 acoustic recordings of sperm whale codas were made from a number of concentrations of whales around the South Pacific and in the Caribbean Sea from the 12.5-m auxiliary cutter *Balaena*. The route was designed to cross many of the sperm whale "grounds" shown in the charts of Townsend (1935) of the kills by 19th century American sperm whalers.

While over water deeper than 1000 m, the usual habitat for sperm whales (Rice 1989), a towed omnidirectional hydrophone (modified Benthos AQ-21B on 30 m of cable) was monitored every 30 min for the distinctive clicks of sperm whales (Backus and Schevill 1966). If sperm whale clicks were sufficiently loud and the weather was favorable (wind less than about 17 knots, 9 m/s), a bearing was obtained on the clicks using a custom-made directional hydrophone (*cf.* Whitehead and Gordon 1986). Whales were then tracked visually and acoustically (using the directional hydrophone) for 0.5–3 days. This allowed us to stay within about 2 km of groups of sperm whales during most of the tracking time. While recording codas we were usually within 300 m.

Groups consisted principally of female sperm whales and their young, but were sometimes accompanied by large mature males (Whitehead 1993).

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 Nagra IV-SJ reel-to-reel tape recorder (19 cm/s) and Ithaco 453 preamplifier. A high-pass roll-off filter in the preamplifier was used to minimize wave noise. A total of 30 h of recordings was made.

In addition, recordings made off the Galápagos Islands in 1985 and 1987 were included in the following analysis. Here, recordings were made systematically for 5 min every hour, and the best coda recordings were chosen for further detailed analysis (Weilgart and Whitehead 1993).

Acoustic analysis of codas

Tapes were played back at half-speed (9.5 cm/s) on a Technics 2-track 1500 reel-to-reel tape recorder. To examine the temporal pattern of clicks within codas, sounds were amplified using a Yamaha Natural Sound Stereo Amplifier, Model AX-500 U, and displayed on a DSP Sona-Graph, Model 5500, with NEC Multi-sync II monitor. Sounds were always monitored through headphones simultaneous to being visually displayed. Codas that could be clearly distinguished and identified (i.e. lack of confusing overlap with other codas, unambiguous presence of all clicks, and having a distinct beginning and end) were measured. The intervals between the clicks in the coda, from the beginning of one click to the beginning of the next, were measured (accurate to ± 0.01 s in recording time) from the spectral analyzer.

A subsample containing 3,644 codas from 86 recording sessions was measured. Recording sessions and sections of recording sessions were chosen for analysis so as to maximize the representation of geographic areas, sperm whale groups, and different days in each area.

Assignment of codas to coda types

All 3644 codas were assigned to coda types as follows:

1. They were first classified according to the number of clicks in the coda; i.e. "3-click codas," "7-click codas" and so on. Codas with less than 3 clicks or more than 12 were discarded, as these were rare and less easily recognizable.
2. All the codas with a given number of clicks were then characterized by the intervals between clicks relative to the total length

of the coda (e.g. for 4-click codas: "0.33, 0.33, 0.33" describes a regular coda and "0.19, 0.24, 0.57" the "plus-one" coda shown in Fig. 1). Each of these multivariate interclick interval data sets (e.g. with 5 variables for 6-click codas) was then classified into 10 clusters using *K*-means cluster analysis. A cluster contained codas with similar patterning of the clicks (e.g. Fig. 2), and *K*-means produced a clustering such that no movement of codas between clusters improved the clustering (by reducing the within-cluster sum of squares). We only used 5 initial clusters for the *K*-means analysis of the 3-click codas because of their greater simplicity.

3. Clusters containing less than 50 codas were then combined into "var" coda types (e.g. "5var") (see Fig. 2). Therefore all non-"var" coda types contained at least 50 codas, with the exception of 11- and 12-click coda types, which had less than a total of 50 codas each. Coda types (representing just one of the *K*-means clusters) were given descriptive names based on the click pattern (e.g. "6Reg" or "4 + 1 + 1"). There was a total of 30 coda types (Table 1).

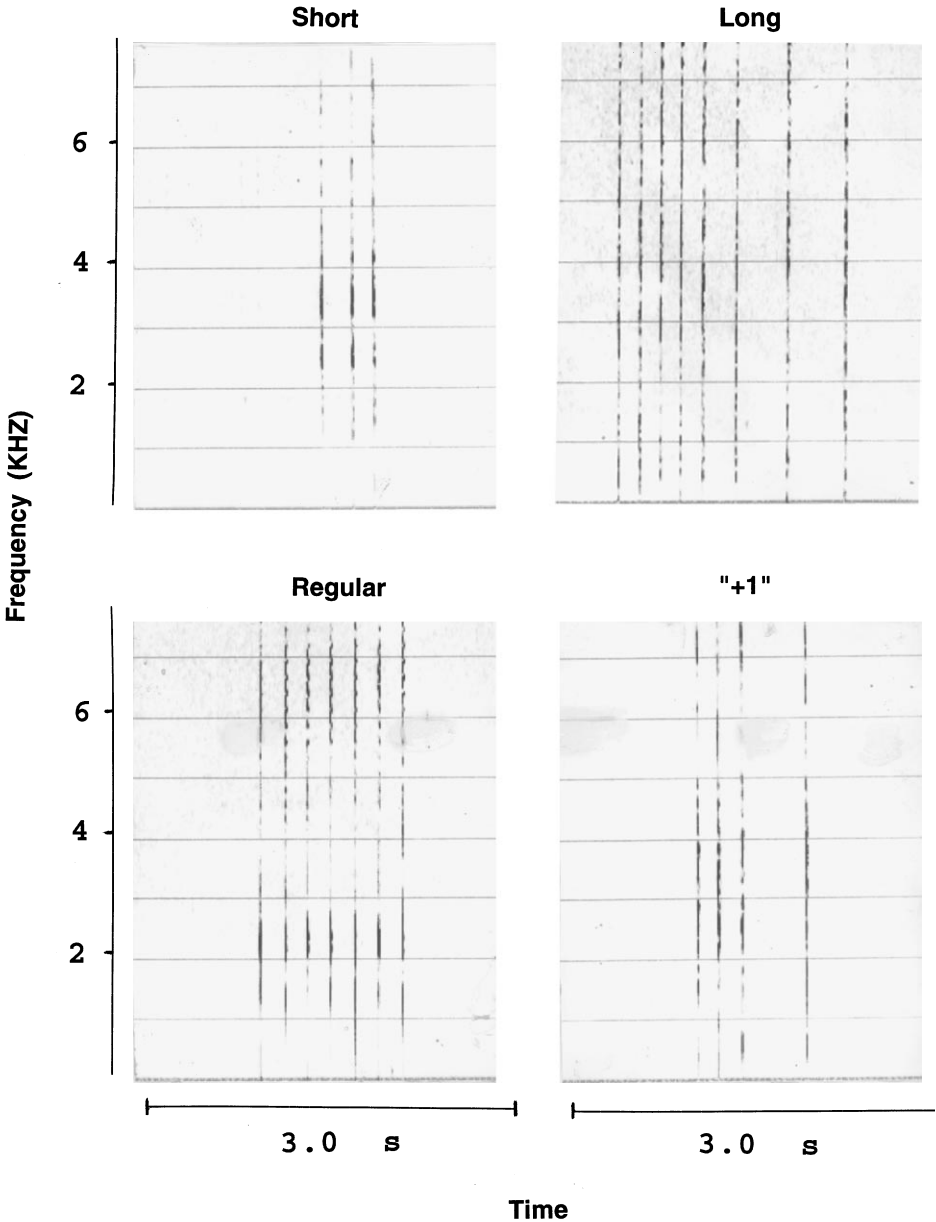
4. Codas were also classified into four classes: *short* codas (< 5 clicks), *long* codas (> 6 clicks), *regular* codas (equally spaced intervals between clicks), and *plus-one* codas (double interval between last two clicks) (Fig. 1; Table 1). These classes were not mutually exclusive.

Experimentation (using different numbers of clusters for the *K*-means procedure) with the 5-click coda data suggested that the classification procedure (*K*-means classification followed by combination of all clusters with less than 50 codas) was robust with respect to the number of clusters chosen, and their composition.

Analysis of dialects

A coda repertoire (both for the 30 coda types and 4 coda classes) for each recording session was then constructed using the numbers of codas measured of each type or class. The recording sessions were classified hierarchically as follows:

Fig. 1 Spectrograms (frequency vs. time plots) of examples of the four coda 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)



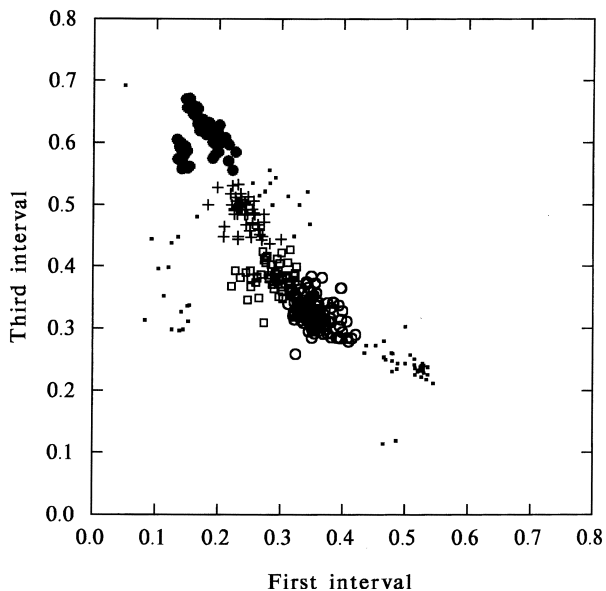


Fig. 2 Classification of four-click codas into types. Each measured coda is represented by a symbol indicating the proportional duration (relative to the total duration of the coda) of the first and last inter-click intervals. The assignment of codas to types is indicated by a symbol: ○ 4R, + 3+1, ● 3+++1, □ 4L, · 4Var

1. *Days*: recording sessions on the same day.
2. *Groups* of whales. Photographic identifications of individuals (Arnbom 1987) allowed us to assign recording sessions to

particular groups: all recording sessions on each day were assumed to be from the same group; and if n_A whales were identified from good quality (Arnbom's $Q \geq 3$) photographs on day *A*, and n_B on day *B*, with m_{AB} common to the two days, then recordings from the two days were considered to be from the same group if:

$$m_{AB} > 0.25 \cdot \text{Minimum} \{n_A, n_B\}$$

As about half the whales in the group being followed were identified each day (Whitehead et al. 1992) we expected that if the same group was being followed then $m_{AB} \sim 0.5 \cdot \text{Minimum} \{n_A, n_B\}$. In only 3/26 pairs of days with $m_{AB} \geq 1$ was:

$$0.2 < m_{AB} / \text{Minimum} \{n_A, n_B\} < 0.3$$

Thus, different days which we assigned to the same group were characterized by the presence of the same, or nearly the same, individual whales.

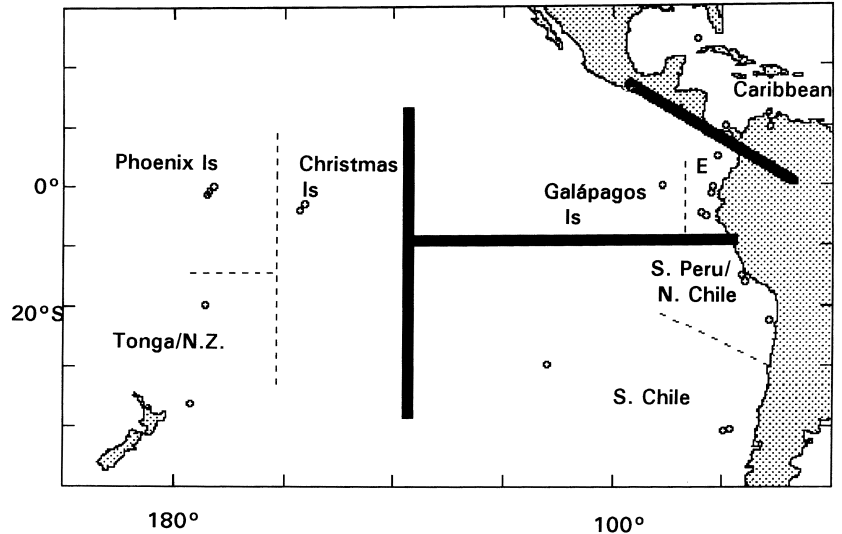
3. *Places*: geographical areas a few 1,000 km across (Table 2; Fig. 3). In two cases, small samples of codas recorded in positions isolated from other concentrations of recordings were assigned to the nearest place (New Zealand assigned to Tonga; Easter Island assigned to Southern Chile).
4. *Areas*: large geographical areas: Eastern Tropical Pacific (N of 10 °S), south-west Pacific, south-east Pacific (S of 10 °S), Caribbean Sea (Table 2; Fig. 3).
5. *Oceans*: Atlantic, Pacific.

The coda repertoire for a day was then constructed by summing repertoires for recording sessions during the day, the repertoire for a group by summing repertoires for recording sessions for that group, etc.

Table 1 The 30 coda types with an approximate representation of the modal pattern for each type (except "Var" coda types for which an example is shown), the number of codas analyzed, and their classification into 4 classes (short, long, regular and plus-one)

Name	Description	No.	Sh.	Long	Reg.	+1
"3R"		625	S		R	
"3a"		131	S			
"3b"		272	S			
"1+2"		90	S			
"2+1"		20	S			P
"4R"		209	S		R	
"3+1"		51	S			P
"3+++1"		68	S			
"4L"		69	S			
"4Var"		72	S			
"4+1"		227				P
"4+++1"		77				
"5R"		269			R	
"2+1+1+1"		53				
"5Var"		55				
"5+1"		160				P
"4+1++++1"		99				
"6R"		149			R	
"6Var"		98				
"7R"		131			R	
"5+1+++1"		56		L		
"6+1"		61		L		P
"7Var"		150		L		
"8R"		109		L	R	
"8L"		54		L		
"8Var"		98		L		
"9"		79		L		
"10"		63		L		
"11"		31		L		
"12"		18		L		

Fig. 3 Locations of recordings of sperm whale codas in the South Pacific and Caribbean, with division into areas (*thick line*), and places (*dashed line*). (E N. Peru/Ecuador)



Repertoires (numbers of each of the 30 coda types or the 4 coda classes) were compared using Spearman and Pearson correlation coefficients. Pearson correlations emphasize differences in the most heavily used categories, whereas Spearman correlations give more weight to similarities and differences among lesser used or unused categories. Moderate or high correlation coefficients (~ 0.4 – 1.0) indicate similar repertoires, and low coefficients (~ 0.0) indicate dissimilar ones. Only repertoires for which more than 10 codas were analyzed were considered. Analyses were also carried out, where possible, by lumping repertoires at different levels (e.g. comparisons between places within oceans, lumping at the level of the group).

For those groups recorded on more than one day, changes in the repertoires of groups with time were examined by plotting the repertoire similarity (Spearman correlation) between each pair of days on which the group was recorded against the time difference between the days.

To examine overall coda repertoire similarity, mean values of correlation coefficients were calculated for comparisons between all pairs of sessions with particular levels of similarity (e.g. between pairs of sessions within the same area, but different places). Standard errors were calculated using the jackknife procedure in which each session is omitted in turn from the analysis (Sokal and Rohlf 1981).

The results of analyses using data lumped by day, group, place or area were similar to those using sessions as units, and are not presented.

Tests for significant differences between units were carried out on the coda class repertoires, expressed as a proportion of the total number of codas measured. As some codas could be in two classes (e.g. short and regular), and others in none (e.g. medium length and irregular), these proportions do not necessarily add to 1.0. Tests are multivariate analyses of variance. Such tests could not be carried

out on the coda type repertoires, or at lower levels of analysis (session or day), because the size of the problem was too large for statistical packages available, although a test of group differences was possible within the Galápagos data set.

Results

Group dialects

Coda repertoires recorded from the same group, on the same or different days, were much more similar ($r_s = 0.5$ – 0.85) than those recorded from different groups in the same place ($r_s = \sim 0.15$) (Fig. 4). The correlation results, and especially the much greater within-group similarity, were consistent whether Spearman or Pearson correlations were used and whether the analysis was carried out on the 30 coda types, or the 4 coda classes. For the Galápagos data (the only place for which sufficient data were available to make such a test feasible), multivariate analysis of variance showed a highly significant difference in the use of the different classes of coda by different groups (using days as units; Table 3).

The similarity of coda type repertoire of the same group on different days ($r_s = \sim 0.6$) seems not to decline much over time periods of up to 2 years (Fig. 5), and this

Table 2 Data analyzed: in each ocean, area and place the number of recording sessions (Ses.), different days, different groups, and codas measured.

Ocean	Area	Place	Year	Ses.	Days	Groups	Codas
S. Pac.	E. Trop. Pac.	Galápagos I.	1985/7	49	25	15	1085
		N. Peru/Ecuador	1993	9	6	4	620
	S.W. Pacific	Christmas I.	1992	6	3	3	510
		Phoenix I.	1992	4	3	2	276
		Tonga/New Zealand	1992/3	4	2	2	196
	SE Pacific	S. Chile	1993	6	3	3	277
		N. Chile/S. Peru	1993	5	4	4	433
Atlantic	Caribbean	Caribbean	1992/3	3	2	2	247
Totals				86	48	37	3644

pattern was similar whether Spearman or Pearson's correlation coefficients were used, and whether coda classes or coda types were considered. Although only one comparison over 2 years (for a group recorded off the Galápagos in 1985 and 1987) is shown in Fig. 5, another Galápagos group was recorded on 1 day in 1985 and 3 days in 1987. Only six codas were measured in 1985, so these comparisons were automatically omitted from Fig. 5 (which only shows comparisons between days with at least ten codas each). However, for this group the coda type repertoire similarities between the day in 1985 and the three days in 1987 were $r_s = 0.61, 0.54, 0.54$, in line with the patterns shown in Fig. 5. Thus we consider that our data, although rather few, show no substantial changes in group dialect over periods of up to 2 years.

Geographical variation

Groups recorded in the same place had more similar coda repertoires ($r_s = \sim 0.15$), than those in the same broad area but different places ($r_s = \sim 0.02$). Groups from the same area, in turn, were marginally more similar than those in the same ocean but different areas ($r_s = \sim 0.0$), or different oceans ($r_s = \sim 0.0$) (Fig. 4). Thus, while the greatest variation in coda repertoire was accounted for by the differences between groups, there was also some geographically-based variation. Multivariate analyses of variance showed statistically significant differences in the coda class repertoire of groups in

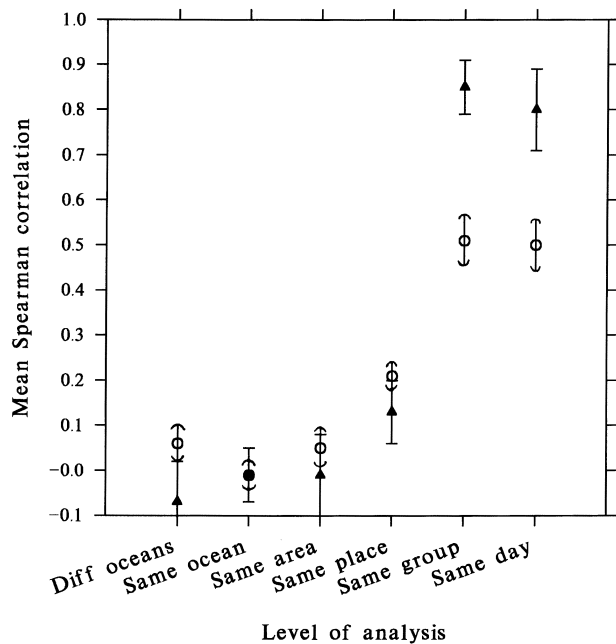


Fig. 4 Similarities of coda repertoires using 30 coda types (○) and 4 coda classes (▲) at different hierarchical levels as indicated by mean Spearman correlation coefficient (jackknife standard errors also shown)

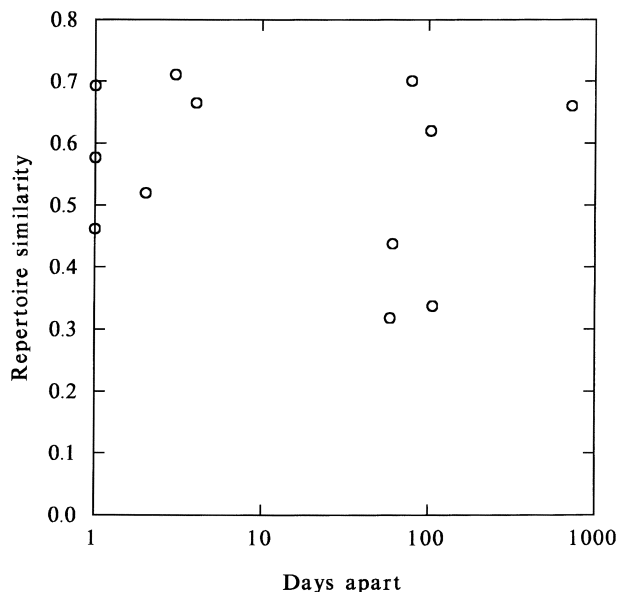


Fig. 5 Repertoire similarity (as indicated by Spearman correlation coefficient between distributions of coda types) of recordings of the same group on different days off the Galápagos Islands plotted against the number of days between the recordings

different oceans, and in different areas within the same ocean, but not between places within the same broad area (Table 3).

Nearby places sometimes, although not always, favored the same general classes of codas (Fig. 6). Short codas prevailed off Christmas Island and the Phoenix Islands which are geographically proximate in the western Pacific, but were completely absent in the Caribbean. Long codas were most common in the Caribbean, plus-one codas off Galápagos and N. Peru/Ecuador, and regular codas were heard most often in southern Chile.

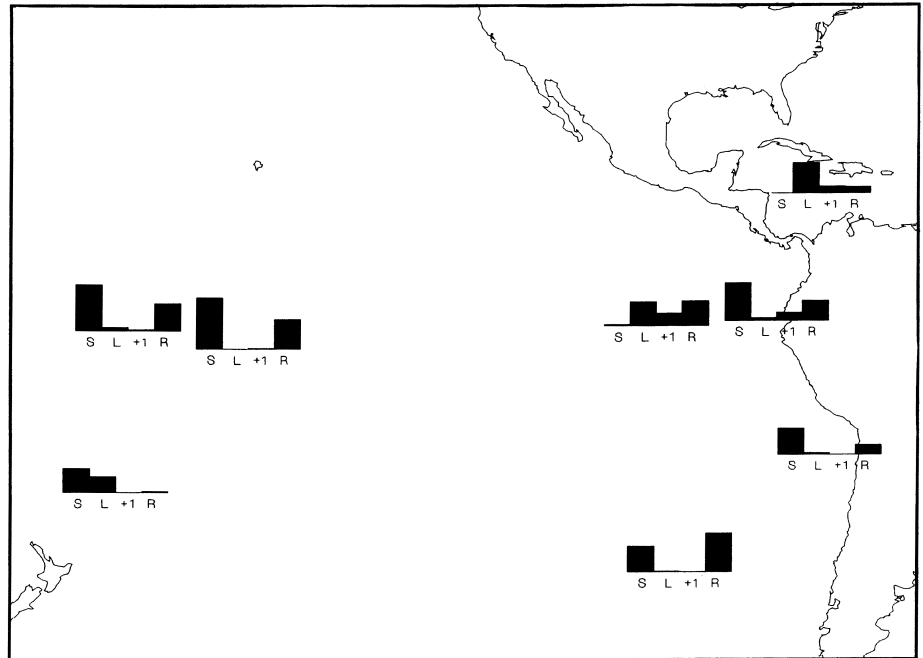
Discussion

These results show that groups of female sperm whales have distinctive vocal repertoires which seem to persist over periods of years. This is despite the fact that not all members of groups are permanent companions: groups

Table 3 Tests (Wilks' Λ nested multivariate analysis of variance) for differences between coda class repertoires at different levels of analysis

Within:	Between:	
Earth	Oceans	$\Lambda = 0.64$ $P = 0.02$
Oceans	Areas	$\Lambda = 0.47$ $P = 0.01$
Areas	Places	$\Lambda = 0.46$ $P = 0.20$
Galápagos	Groups	$\Lambda = 0.00$ $P = 0.00$

Fig. 6 Distribution of coda classes in different places in the South Pacific and Caribbean: proportion of short codas (*S*), long codas (*L*), plus-one codas (*+1*), and regular codas (*R*)



seem to generally consist of the temporary merging (over periods of a few days) of two or more stable, matrilineal family units (Whitehead et al. 1991; Richard et al. 1996). However, as most comparisons from the same groups were made within a few days of each other, groups were probably still quite stable over these time periods.

Over and above these differences in the proportional usage of coda types and classes between groups, there could be rare coda types unique to particular groups, as is the case with killer whales. Large sample sizes from several groups would be needed to show this.

We do not believe that the repertoire differences between groups can merely be accounted for by differences in group size, since this was similar among all groups, and individuals seem to use a variety of different coda types (Weilgart and Whitehead 1993). Moreover, an earlier analysis correlating coda types to specific behavioral categories visible at the surface (e.g. leaping, turning, tail slaps, etc.), showed no clear patterns of correlation (Weilgart 1990).

Repertoires distinctive to groups likely have arisen because of the strong stability of matrilineal family units and because codas primarily seem to be used for communication between members of the same group. This would hold particularly true if individuals within groups communicate principally with members of their own stable family units.

Coda repertoires in sperm whales are most likely learned from the mother or other members of the matriline, since calves appear to gradually develop the ability to produce coda-like patterns with age (Watkins et al. 1988). The smallest calves produced few repetitive click patterns but older calves used a larger number of patterned click sequences, which resembled adult codas

more closely (Watkins et al. 1988). Furthermore, genetic differences are unlikely to account for the geographical variation seen in coda repertoires since mitochondrial DNA analyses show no significant differences between sperm whale samples taken from locations throughout the South Pacific on our research voyage (Dillon 1996). Given the known ability of many cetaceans to mimic sounds (e.g. Richards et al. 1984; Reiss and McCowan 1993) and that of humpback whales (*Megaptera novaeangliae*) to learn new songs (Payne et al. 1983), it seems likely that sperm whales acquire their coda repertoire through vocal learning.

Vocal convergence among social group members has been documented in birds (Nowicki 1989; Farabaugh et al. 1994) as well as in primates (Elowson and Snowdon 1994). In these studies, call repertoires or features changed with aural exposure to new social companions. The dialects that result from such vocal adaptations may bring about a more effective and efficient means of intra-group communication or they may be simply by-products of vocal learning serving no function (Ford 1991; Catchpole and Slater 1995).

In addition to the strong group-specific dialects, these results show significant, but weaker, geographical differences in coda repertoires. In general, at smaller spatial scales (~1,000 km, places within areas) patterns are clearest using the 30 coda types (Fig. 4), whereas at larger scales (>~5,000 km, areas within oceans, and between oceans), coda type repertoires are all very dissimilar and patterns are best indicated by significant differences in usage of the four broad coda classes.

The group-specific dialects that are found in sperm whales seem most similar to those which occur in killer whales. Resident killer whale pods can have completely

discrete repertoires of calls (Ford 1991). In both sperm whales and killer whales, the repertoires are associated with social groups which not only can occupy the same range, but often interact with each other. This is unusual among non-human species, where dialect populations are usually restricted to specific locales or where there is at least no evidence of interaction between them (Ford 1991). Unlike the case with killer whales (Ford 1991), we have not yet been able to identify call types (in our case, coda types) that are unique to a particular group. We are unfortunately also not able to present as detailed a picture of the group-specific dialects, their origins, or their stability. Nevertheless, both geographical variation and dialects are apparent in sperm whale codas which, together with genetic analyses and resighting data, may shed light on the stock structure, social organization, and patterns of association.

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