# Vocal clans in sperm whales (*Physeter macrocephalus*)

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Cultural transmission may be a significant source of variation in the behaviour of whales and dolphins, especially as regards their vocal signals. We studied variation in the vocal output of 'codas' by sperm whale social groups. Codas are patterns of clicks used by female sperm whales in social circumstances. The coda repertoires of all known social units ($n = 18$, each consisting of about 11 females and immatures with long-term relationships) and 61 out of 64 groups (about two social units moving together for periods of days) that were recorded in the South Pacific and Caribbean between 1985 and 2000 can be reliably allocated into six acoustic 'clans', five in the Pacific and one in the Caribbean. Clans have ranges that span thousands of kilometres, are sympatric, contain many thousands of whales and most probably result from cultural transmission of vocal patterns. Units seem to form groups preferentially with other units of their own clan. We suggest that this is a rare example of sympatric cultural variation on an oceanic scale. Culture may thus be a more important determinant of sperm whale population structure than genes or geography, a finding that has major implications for our understanding of the species' behavioural and population biology.

**Keywords:** sperm whale; vocal clan; culture; population structure

## 1. INTRODUCTION

There is an ongoing debate about the existence and nature of culture—defined as group-level information or behaviour transmitted by social learning (Rendell & Whitehead 2001)—in non-humans (Galef 1992; Boesch & Tomasello 1998; McGrew 1998; Whiten *et al.* 1999). This debate has recently widened to include cases of cultural variation in the behaviour of cetaceans (Whitehead 1998; Noad *et al.* 2000; Rendell & Whitehead 2001), a group noted for its social (e.g. Connor *et al.* 2001) and cognitive (e.g. Reiss & Marino 2001) complexity. For example, killer whales (*Orcinus orca*) around Vancouver Island live in stable pods, each with its own unique, culturally transmitted, vocal dialect, within a hierarchical social structure in which pods that share some calls are grouped into vocal clans (Ford 1991; Deecke *et al.* 2000; Yurk *et al.* 2002); pods and clans remain distinct despite sympatry and regular interaction. There may also be examples of gene–culture coevolution in cetaceans that are unique outside humans. For example, also in killer whales, some have suggested that the cultural transmission of differing foraging techniques initiated the split between the so-called 'resident', fish-eating, and 'transient', mammal-eating, forms, which may be in the process of speciation (Baird *et al.* 1992; Boran & Heimlich 1999; Baird 2000). More broadly, cultural and genetic processes may have interacted to reduce mtDNA diversity greatly in matrilineal odontocetes, through neutral mitochondrial alleles hitchhiking on successful cultural traits (Whitehead 1998).

One such species is the sperm whale (*Physeter macrocephalus*), a key player in mesopelagic ecosystems, which can be found in the deep waters of every ocean (Whitehead & Weilgart 2000). This species also has a complex social structure, the most basic element of which is the long-term social 'unit' (Christal *et al.* 1998). Consisting of *ca.* 10–12 females and their immature offspring, these units may be described as generally matrilineal (Whitehead & Weilgart 2000) but individuals do sometimes transfer between units, and units may contain unrelated individuals (Christal *et al.* 1998; Mesnick 2001). These units are encountered in tropical and subtropical waters and typically form temporary 'groups' with one or more other units for a few days or so (Whitehead *et al.* 1991; Christal *et al.* 1998; Whitehead & Weilgart 2000). This terminological distinction between 'unit' and 'group' will be retained throughout the paper. Male sperm whales disperse from their natal units at a mean age of *ca.* 6 years, and gradually move to cold-water feeding grounds. In their late 20s they begin to make migrations to the tropics to mate (Whitehead & Weilgart 2000); mating is generally outside of their natal group according to genetic evidence (Lyrholm *et al.* 1999).

Codas are stereotyped sequences of 3–40 broadband clicks usually lasting less than 3 s in total (Watkins & Schevill 1977) and are generally heard from groups of socializing sperm whales (Whitehead & Weilgart 1991). Groups vary in their use of different coda types (Weilgart & Whitehead 1997) and among six groups this variation correlates with mtDNA variation (Whitehead *et al.* 1998): groups with similar coda output have similar mtDNA haplotypes. Whitehead *et al.* (1998) suggested that analogous inheritance processes through the female line produced this pattern: calves both inherit their mtDNA and learn their coda dialect from their mothers. The cultural transmission of coda dialect would have to be highly stable to produce this correlation (Whitehead *et al.* 1998). We thus suggested that sperm whales showed culture in the form of sympatric variation in vocal dialects (Rendell & Whitehead 2001). However, this interpretation

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has been challenged (Tyack 2001) because the groups that showed vocal dialects are often only temporary aggregations of two or more social units, raising the question of how temporary social entities can maintain stable cultural characteristics (Mesnick 2001; Tyack 2001).

Here, we answer this question by using codas recorded over 15 years of research on sperm whales in the South Pacific and Caribbean to investigate variation in coda usage among groups. We find strong evidence for a higher level of social structure based on variation in vocal output, somewhat similar to the acoustic clans of killer whales. Sperm whale populations may thus be structured more along cultural lines than on a geographical basis, which has major implications for our understanding of the species' behavioural and population biology.

## 2. MATERIAL AND METHODS

### (a) Coda recording

Recordings were made using one of several sets of equipment, either an Offshore Acoustics hydrophone (frequency response 6 Hz–10 kHz, ±3 dB) connected directly to a Sony TC-D5M cassette recorder, or either a Benthos AQ17 or a modified AQ21B hydrophone (frequency response 1–10 kHz, ±3 dB) connected via either Barcus-Berry 'Standard' or Ithaca 453 pre-amplifiers to a Uher 4000, Sony TC770 or Nagra IV-SJ reel-to-reel tape recorder. We measured the inter-click time intervals (the time between the onset of one click and the onset of the next click) of codas in one of two ways, either from a DSP Sona-Graph, Model 5500, or by digitizing the recordings at 44.1 kHz onto a desktop PC and extracting inter-click intervals using custom-written software for analysing sperm whale sounds (Gillespie 1997; Leaper *et al.* 2000). The resultant click intervals were then standardized to coda length, thus discarding tempo information but retaining rhythm (see Moore *et al.* (1993) for justification).

### (b) Assigning codas to units or groups

We selected codas recorded from sperm whale social units whose members were photographically identified around the Galapagos Islands during the period 1985–1999; units were defined by repeated associations (in time and space) between individuals over months and years (for details see Christal *et al.* 1998). We assigned codas in a given recording to a known social unit if at least one member of that unit was photographically identified within 2 h of the recording start time. Only photographs with a quality rating, $Q$, of three or more out of five were included (Arnbom 1987; Christal *et al.* 1998). If members of more than one known unit were identified in that same period, then the codas were assigned to a joint unit (e.g. A&B). Note that, with the exception of unit T, non-unit members were always also identified during these periods. We included only units from which we had recorded at least 25 codas; 3943 codas were included in the analysis.

We then widened our analysis to include recordings made across the South Pacific, and some made in the Caribbean, using codas assigned to groups based on photo-identification records, so that we were not restricted to known social units nor to just the Galapagos Islands. All codas recorded on a given day were assumed to have come from the same group. Codas recorded on two different days were considered to be from the same group if $m_{ab} > 0.25 \times \min\{n_a, n_b\}$, where $m_{ab}$ is the number of individuals photographed on both days, $n_a$ is the number photographed

on the first day and $n_b$ is the number photographed on the second day (as in Weilgart & Whitehead 1997). Again, we included only groups from which at least 25 codas had been recorded; 13 941 codas from 64 groups were included in this analysis, incorporating those from the unit analysis.

### (c) Repertoire comparisons

We used MATLAB, v. 12.0 for all numerical analyses. We used an averaged multivariate similarity method to compare sets of codas, based on the infinity-norm distance between two coda vectors:

$$s_{AB} = \frac{\displaystyle\sum_{i=1}^{n_A} \sum_{\substack{j=1 \\ l_j = l_i}}^{n_B} \frac{0.001}{0.001 + d_{ij}}}{n_A . n_B},$$

where $s_{AB}$ denotes the similarity between coda sets A and B, $l_i$ is the number of clicks in coda $i$ of set A, $l_j$ is the number of clicks in coda $j$ of set B and $d_{ij}$ is the maximum absolute distance (or infinity-norm) between the vectors containing the standardized inter-click intervals of the codas, $x_i$ and $x_j$ ($\|x_i - x_j\|\infty$). The similarity between two codas containing different numbers of clicks was 0. In our formula for similarity we chose the basal similarity, 0.001, as being approximately the maximum resolution of our most accurate analysis system given a median coda length of 0.93 s and a maximum time resolution of 0.001 s. This figure is also *ca.* 10% of the distance across most of the obvious clusters in the coda data (these clusters generally represent coda types) such that analysis at this resolution examines not only the use of different types, but also the variation within a given type (see Rendell & Whitehead 2003). For both the unit and the group analyses we calculated similarities between sets of codas assigned to each unit or group and entered these similarities into an average linkage cluster analysis (e.g. Manly 1994). We tested the robustness of the resultant clustering using 100 bootstrap resamples (codas resampled with replacement within sets) of the original data; for a given branch we counted the number of bootstrap resamples in which that branch was reproduced perfectly, that is, contained exactly the same groups as the original clustering.

In order to illustrate observed differences we also classified codas containing the same number of clicks using $k$-means clustering and the variance ratio criterion (VRC) (Milligan & Cooper 1985) to select an appropriate $k$. Each coda type was then given a descriptive name based on the pattern of clicks: for example, '5R' denotes a coda with five regularly spaced clicks, while '4 + 1' signifies four regularly spaced clicks followed by a longer gap before the fifth click (Weilgart & Whitehead 1997). The VRC produced unambiguous estimates of $k$ for all but the five-click codas, where the splitting of one very large cluster— the '5R' codas—led to misleading VRC values at $k > 4$. The splitting of large clusters is a known weakness of $k$-means analysis (Duda & Hart 1973), and in this case the '5R' cluster contained 84% (4111 of 4879) of all the five-click codas, such that splitting it necessarily greatly reduced the sum of squared errors on which the VRC is based. Hence, in this case, we randomly sampled ten five-click codas from each recording day and ran the VRC analysis on this subsample; in 20 out of 20 repeats of this procedure the VRC unambiguously indicated $k = 3$, so we classified the entire five-click dataset into three clusters. This classification did not split the '5R' cluster.
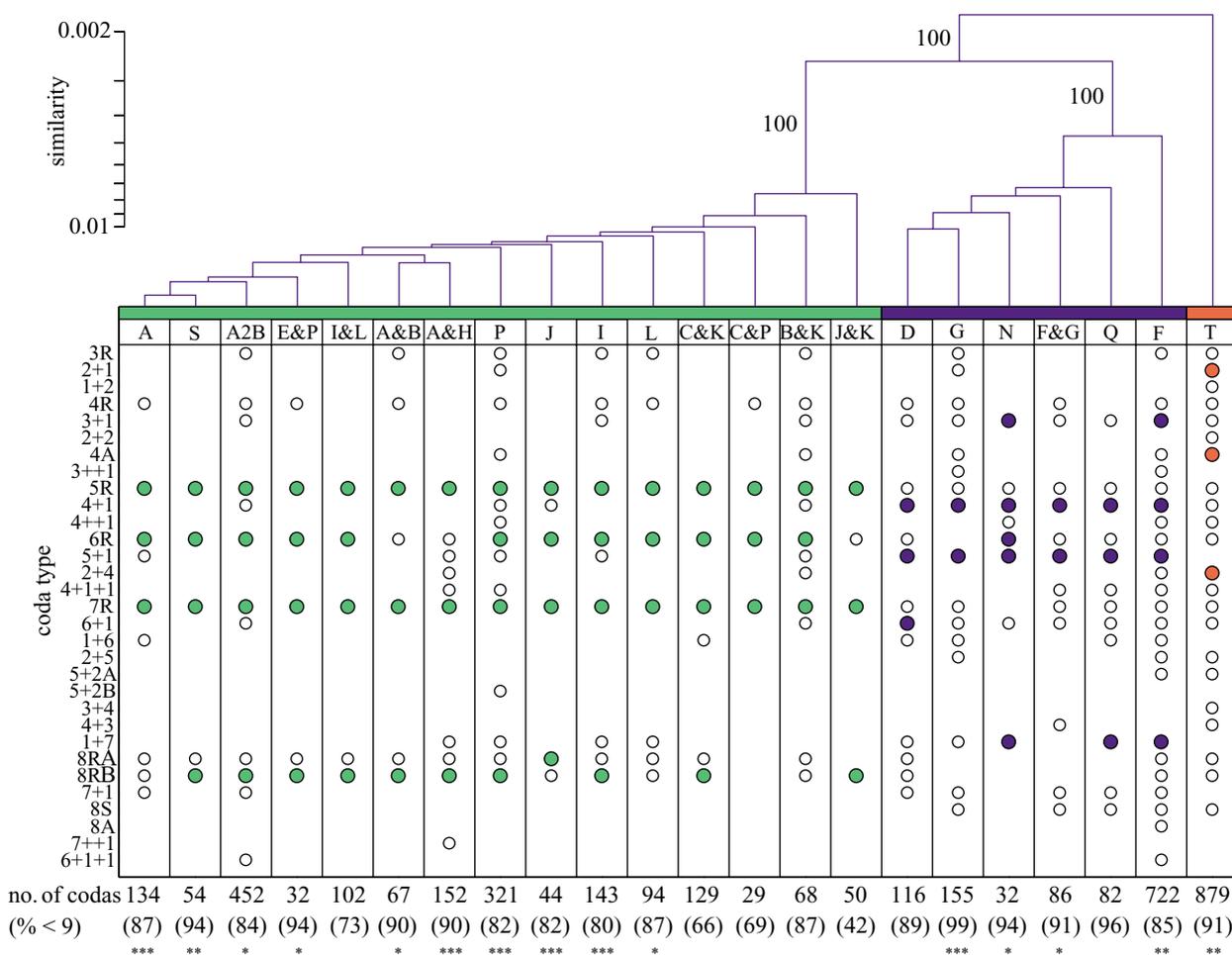
Figure 1. Coda repertoires of sperm whale groups containing known social units recorded around the Galapagos Archipelago compared using multivariate similarity (top) and *k*-means classification methods (bottom). Unit codes are retained from previous studies (Christal *et al.* 1998; Whitehead 2001); more than one code is given when members of more than one unit were identified within 2 h of recording. Numbers next to dendrogram branches are the number of bootstrap resamples in which that branch was recreated (out of 100). Circles in the classification table indicate coda types present in a unit's recorded repertoire, while filled markers indicate types that made up 10% or more of a unit's repertoire. The code ++ means an extended gap between clicks, the code S means a coda with steadily increasing click intervals and the codes A and B are used where there is no obvious feature to separate coda types. The raw data underlying the classification table can be found in electronic Appendix A available on The Royal Society's Publications Web site. Numbers below each column are the number of codas recorded from each unit and in brackets the percentage of that number with fewer than nine clicks and hence shown in the table (note that all codas are included in the hierarchical cluster analysis). Units flagged with one, two or three asterisks were recorded on more than one day; those with two asterisks had 30 or more days between the first and last recording, and those with three asterisks had more than 1 year between the first and last recording. Colours represent clan assignments: green, 'Regular'; blue, '+1'; red, short.

| | A | S | A2B | E&P | I&L | A&B | A&H | P | J | I | L | C&K | C&P | B&K | J&K | D | G | N | F&G | Q | F | T |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| no. of codas | 134 | 54 | 452 | 32 | 102 | 67 | 152 | 321 | 44 | 143 | 94 | 129 | 29 | 68 | 50 | 116 | 155 | 32 | 86 | 82 | 722 | 879 |
| (% < 9) | (87) | (94) | (84) | (94) | (73) | (90) | (90) | (82) | (82) | (80) | (87) | (66) | (69) | (87) | (42) | (89) | (99) | (94) | (91) | (96) | (85) | (91) |
| | *** | ** | * | * | | * | *** | *** | *** | *** | * | | | | | *** | * | * | | | ** | ** |

## 3. RESULTS

The coda repertoires of all social units could be assigned to one of three acoustic groupings based on coda-use patterns (figure 1). We term these groupings 'clans'. One clan made predominantly regularly spaced codas (5R, 6R, 7R), the second made predominantly codas with an extended last interval (4 + 1, 5 + 1, 6 + 1) and the third, represented here by just one unit, made predominantly short codas (containing three or four clicks). We termed these clans 'regular', '+1' and 'short', respectively. This division is apparent whether the analysis is based on discrete classification or on continuous measures, and, like all the patterns we describe here based on the infinity-norm distance, was reproduced when the analysis was repeated using Euclidean distance as a measure of dissimilarity between the inter-click interval vectors of codas containing the same number of clicks instead of the infinity-norm. The clustering was reproduced in all 100 bootstrap resamples, giving confidence that the division is not data dependent. The results are consistent across units: in cases where units were recorded grouped with one or more other identified units (e.g. A, A&B; F, F&G), they always clustered in the same clan. Clan coda use is stable over time: some units were recorded over periods of years but still retained a clear clan signal; the longest such period was for unit G, which was recorded in 1987 and 1993 with the same pattern of coda usage; data on the coda repertoires of this and the three other units recorded in different years are included in electronic Appendix A, available on The Royal Society's Publications Web site.

Units generally associated with other units of the same
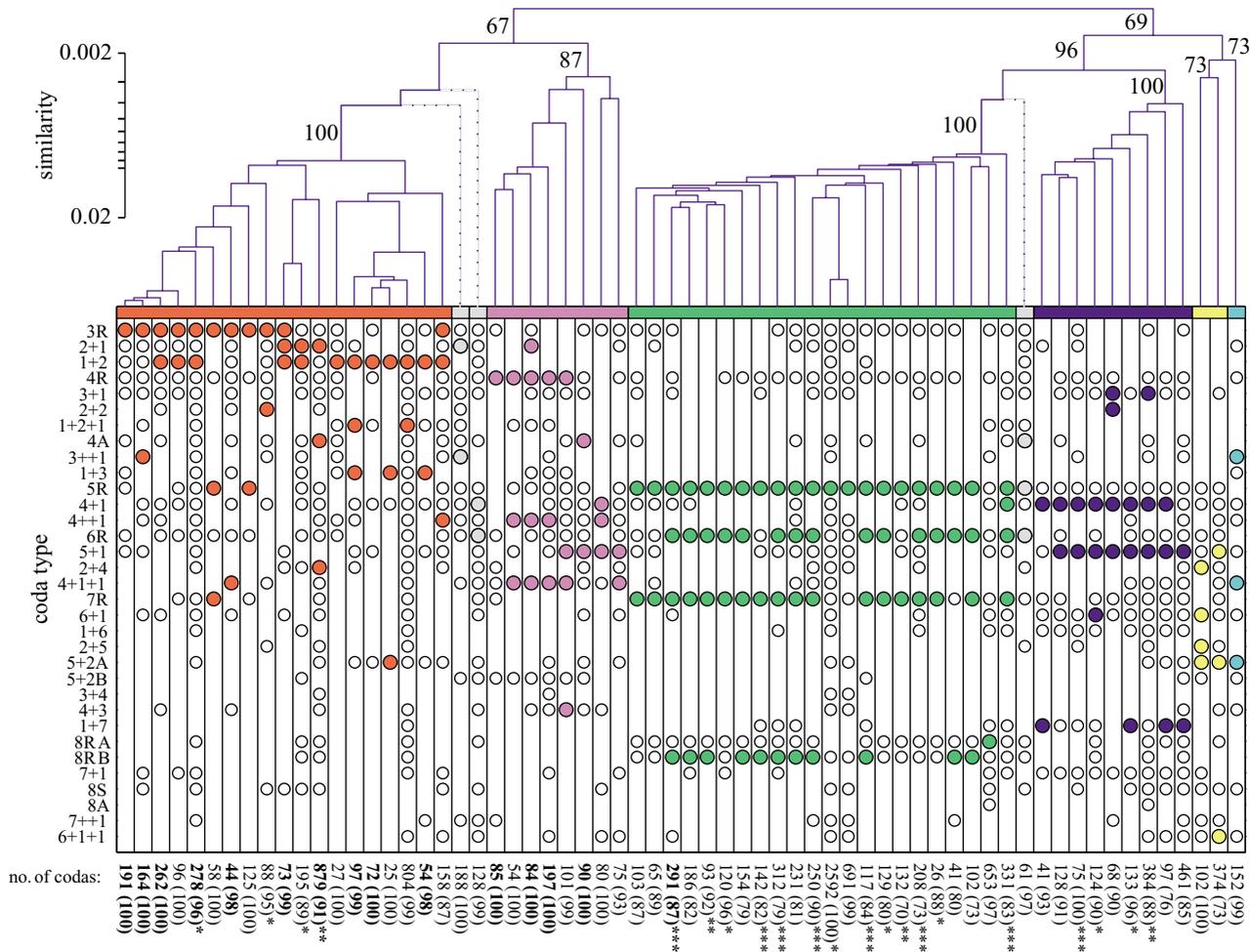
Figure 2. Coda repertoires of photographically identified sperm whale groups compared using multivariate similarity (top) and *k*-means classification methods (bottom). Grey markers and dashed lines in the dendrogram denote groups that were shown to cluster ambiguously by low bootstrap support; these groups were not assigned to a clan and were not included in the bootstrap analysis. All other notations, markers and colours are as in figure 1, with the addition of three extra clans: yellow, '+2' (the Caribbean clan); cyan, '++1/+1+1' (recorded off Tonga only); and magenta, '4+'. The raw data underlying the classification table can be found in electronic Appendix A available on The Royal Society's Publications Web site. Group data printed in bold indicate mtDNA data were available for that group (table 1).

clan. Out of 26 encounters in which members of different units were identified within 2 h of each other, only one involved units from different clans (23 were between 'regular' clan units, and two were between '+1' clan units). This was on 27 April 1993 when two members of unit G ('+1 clan') were identified between 06.32 and 06.35, eight members of unit L ('regular' clan) between 06.48 and 07.46, and 12 members of unit G between 08.10 and 12.50, including the two first sighted. A recording made at 11.26, assigned to unit G using our method, gave a clear '+1' signal; given that this unit had been assigned to the '+1' clan by independent recordings on other dates, the consistency of results here provides some *post-hoc* justification of our 2 h criterion for assigning codas to groups or units. Unit L was assigned to the 'regular' clan based on recordings from other dates. Members of other units were identified throughout this time, but for at least 1 h on this day members of units from different clans were within a few kilometres of one another.

The clan structure is reproduced in a similar analysis of groups across the South Pacific and Caribbean (figure 2). Although data on unit membership are generally not avail-

able for these groups, we assume that the general pattern found in the Galapagos, where groups consist of temporary associations of long-term social units, applies across the Pacific. We also assume that clan signatures recorded from these groups are, as in the Galapagos data, an accurate reflection of the clan membership of the underlying units. Additional groups belonging to each of the Galapagos clans (particularly the 'short' clan) were identified. However, there is also evidence of two more clans in the Pacific, bringing the total to five, and a distinct clan recorded only in the Caribbean (figures 2 and 3). The most common of these we termed '4+' because the dominant coda types were based on a root of four regular clicks (e.g. 4R, 4 ++ 1, 4 + 1 + 1). The fifth Pacific clan (++1/+1+1) is represented by a single group. We termed the Caribbean clan '+2' because of the '5 + 2A' and '6 + 1 + 1' types commonly used. These terms are for descriptive purposes only and do not necessarily represent the most important differences between clans. Three out of the 64 groups had ambiguous clan membership: in bootstrap samples they were often assigned to different clans. Hence, we excluded these groups from the boots-
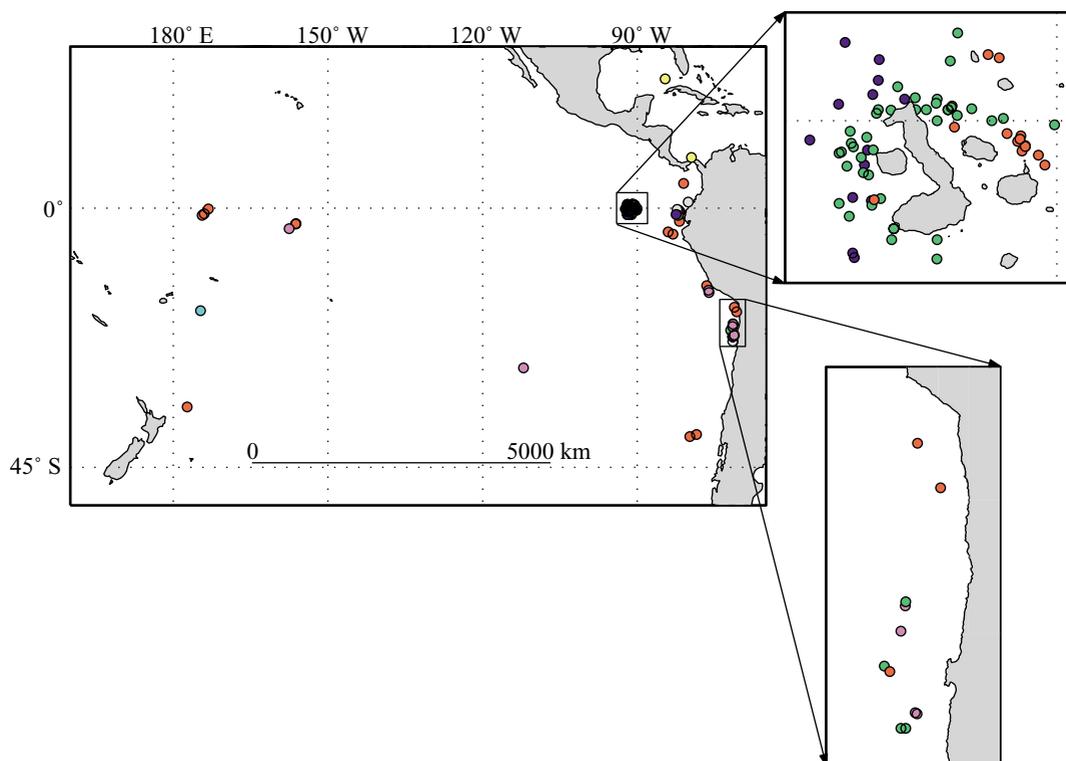
Figure 3. Clan distribution. Each point on the map indicates the nearest fix to the first recording time for each day a group was recorded. Green, regular; blue, +1; yellow, +2; cyan, ++1/+1+1; red, short; magenta, 4+; grey, unassigned.

trap analyses reported here, which give high support (at least 73%) to the clusters found at the clan level.

Clans are sympatric across huge geographical ranges (figure 3). While there are differences in these ranges, no Pacific clan is restricted to a single area except for the '++1/+1+1' clan that was recorded just once near Tonga (where our sampling effort was least). For example, the 'regular' and '+1' clans are found only in the eastern Pacific, with the '+1' clan occurring only in the tropics (although it may extend further north than our effort), while the '4+' and 'short' clans both span the entire South Pacific.

## 4. DISCUSSION

The analyses reveal a picture of sympatric vocal variation that has implications for our understanding of sperm whale society. Results are consistent with those of previous studies that found large between-group variations in coda usage overlying a weaker geographical variation (Weilgart & Whitehead 1997), but add a very significant factor: the vocal clan. We suggest that variation in vocal behaviour between clans is cultural, based on social learning rather than genetic variation or ecological differences plus individual learning (Boesch 1996) for the following reasons. First, variation cannot be caused by ecology plus individual learning, because clans are sympatric. Second, available genetic data point to male dispersal and female philopatry (Lyrholm *et al.* 1999) and are inconsistent with within-group mating, making genetic inheritance unlikely, although we do not know whether there is gene flow between clans. Several mitochondrial haplotypes are shared between clans, showing that the clans are not

matrilineally monophyletic (table 1; mtDNA data from previous studies (Whitehead *et al.* 1998)). Individuals in the same clan, but different groups, were no more likely to have the same haplotype (19%) than individuals in different clans (17%). Thus, albeit with a small sample (15 groups from three clans), we can not reject the null hypothesis that clans are undifferentiated in mtDNA. Further evidence of gene flow between clans is given by social-unit dynamics: between 1985 and 1987 one individual from unit C, belonging to the 'regular' clan, transferred to unit D, belonging to the '+1' clan (Christal *et al.* 1998).

In answer to previous criticisms asking how labile day-to-day aggregations of sperm whales can maintain stable cultural characteristics (Mesnick 2001; Tyack 2001), we therefore suggest that cultural variation, in the form of coda usage dialects, is maintained primarily at the level of the clan rather than the level of the group or unit. Previous findings of dialects at the group level are explained by units forming groups predominantly with other units of their own clan. Clans may thus represent a higher-level social structure essentially unobservable over the short time periods for which we can follow sperm whales in the field. The closest parallel to this, from where we took the term 'clan', are the acoustic clans of killer whales, based on discrete pulsed calls (Ford 1991), with the important difference that killer whale clans do not share call types in the way that sperm whale clans do. Killer whale clans are also more geographically restricted, spanning about 1000 km (Ford *et al.* 2000) rather than the sperm whales' 10 000 km (figure 3), and contain fewer members, about 100 (Ford *et al.* 2000) rather than the 10 000 suggested by the number of clans in the South Pacific and global

Table 1. Mitochondrial haplotypes present in clans for which data are available.
($N_i$ and $N_g$ are the number of individuals and the number of groups sampled from each clan, respectively. $H$ is the number of haplotypes present. Data are number of samples with a given haplotype.)

| clan | $N_i$ | $N_g$ | haplotype code | | | | | | | | | | $H$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | no. 1 | no. 2 | no. 3 | no. 5 | no. 6 | no. 7 | no. 8 | no. 11 | no. 12 | no. 13 | |
| 4+ | 15 | 4 | 1 | | 7 | 5 | 1 | 1 | | | | | 5 |
| regular | 19 | 1 | 18 | | | | | | | | | 1 | 2 |
| short | 67 | 10 | 18 | 23 | 17 | | 2 | 1 | 1 | 1 | 1 | 3 | 9 |

sperm whale densities (Whitehead 2002). The striking conclusion is that there are only five clans present in our extensive South Pacific sample, although the relatively low sampling effort in the western Pacific means that there may well be other undiscovered clans in that region. We are aware of no similar phenomena on this oceanic scale, where stable cultural groupings persist despite being largely sympatric.

The function of codas is unknown, and the function, if any, of coda dialects is thus a matter of speculation. However, we do know that members of sperm whale groups will take considerable risks to help group-mates under predatory attack (Pitman *et al.* 2001) and also provide allomaternal care of calves within groups (Whitehead 1996). We suggest that coda dialect performs a signature function in this context, allowing units to identify other units of the same clan within a highly mobile sperm whale society (c.f. Tyack & Sayigh 1997) and perhaps mediating seemingly altruistic exchanges such as communal defence and allomaternal care. It is important to know whether clan signatures form boundaries to these exchanges; if they do, then sperm whale clans would be among the largest cooperative groups known outside humans. The erection of social boundaries through vocal variation is considered important in human evolution and social behaviour (Nettle 1999) and may be paralleled here in sperm whales. Thus, we suggest that clan signatures may give sperm whales a cultural identity that is of great importance to their individual survival and reproduction. Playback experiments are an obvious way of assessing how clan signatures affect social interactions in sperm whales.

The next research priority is to establish how clan structure relates to genetic population structure. Genetic and other studies have found little evidence for population structure in sperm whales at scales below ocean basins (Dufault *et al.* 1999; Lyrholm *et al.* 1999). Sperm whale populations may be most clearly structured culturally, in which case coda recordings may be an easy way of mapping their population structure worldwide. This is particularly important at a time when sperm whale populations are threatened by the resumption of commercial whaling as well as, potentially, by other anthropogenic effects such as climate change. It is therefore of obvious interest to investigate whether other, non-vocal, behavioural traits are correlated with clan structure, particularly aspects of behaviour with direct fitness consequences, as, in this case, anthropogenic effects may affect clans in different ways. Finally, if there is variation in ecologically important behaviour as well as gene differences between clans, this would potentially allow culture to drive genetic evolution at the level of the clan.

## REFERENCES

Arnbom, T. 1987 Individual identification of sperm whales. *Rep. Int. Whaling Commission* **37**, 201–204.

Baird, R. W. 2000 The killer whale: foraging specializations and group hunting. In *Cetacean societies: field studies of dolphins and whales* (ed. J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 127–153. University of Chicago Press.

Baird, R. W., Abrams, P. A. & Dill, L. M. 1992 Possible indirect interactions between transient and resident killer whales: implications for the evolution of foraging specializations in the genus *Orcinus*. *Oecologia* **89**, 125–132.

Boesch, C. 1996 The emergence of cultures among wild chimpanzees. *Proc. Br. Acad.* **88**, 251–268.

Boesch, C. & Tomasello, M. 1998 Chimpanzee and human cultures. *Curr. Anthropol.* **39**, 591–614.

Boran, J. R. & Heimlich, S. L. 1999 Social learning in cetaceans: hunting, hearing and hierarchies. In *Mammalian social learning: comparative and ecological perspectives*, vol. 73 (ed. H. O. Box & K. R. Gibson), pp. 282–307. Cambridge University Press.

Christal, J., Whitehead, H. & Lettevall, E. 1998 Sperm whale social units: variation and change. *Can. J. Zool.* **76**, 1431–1440.

Connor, R. C., Heithaus, M. R. & Barre, L. M. 2001 Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proc. R. Soc. Lond.* B **268**, 263–267. (DOI 10.1098/rspb.2000.1357.)

Deecke, V. B., Ford, J. K. B. & Spong, P. 2000 Dialect change in resident killer whales: implications for vocal learning and cultural transmission. *Anim. Behav.* **40**, 629–638.

Duda, R. O. & Hart, P. E. 1973 *Pattern classification and scene analysis*. New York: Wiley.

Dufault, S., Whitehead, H. & Dillion, M. 1999 An examination of the current knowledge on the stock structure of sperm whales (*Physter macrocephalus*) worldwide. *J. Cetacean Res. Mngmt* **1**, 1–10.

Ford, J. K. B. 1991 Vocal traditions among resident killer

whales (*Orcinus orca*) in coastal waters of British Columbia. *Can. J. Zool.* **69**, 1454–1483.

Ford, J. K. B., Ellis, G. M. & Balcomb, K. C. 2000 *Killer whales*. Vancouver, British Columbia: UBC Press.

Galef, B. G. 1992 The question of animal culture. *Hum. Nature* **3**, 157–178.

Gillespie, D. 1997 An acoustic survey for sperm whales in the Southern Ocean sanctuary conducted from the *R/V Aurora Australis*. *Rep. Int. Whaling Commission* **47**, 897–908.

Leaper, R., Gillespie, D. & Papastavrou, V. 2000 Results of passive acoustic surveys for odontocetes in the Southern Ocean. *J. Cetacean Res. Mngmt* **2**, 187–196.

Lyrholm, T., Leimar, O., Johanneson, B. & Gyllensten, U. 1999 Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. *Proc. R. Soc. Lond.* B **266**, 347–354. (DOI 10.1098/rspb.1999.0644.)

McGrew, W. C. 1998 Culture in nonhuman primates? *A. Rev. Anthropol.* **27**, 301–328.

Manly, B. F. J. 1994 *Multivariate statistical methods*. New York: Chapman & Hall.

Mesnick, S. L. 2001 Genetic relatedness in sperm whales: evidence and cultural implications. *Behav. Brain Sci.* **24**, 346–347.

Milligan, G. W. & Cooper, M. C. 1985 An examination of procedures for determining the number of clusters in a dataset. *Psychometrika* **50**, 159–179.

Moore, K. E., Watkins, W. A. & Tyack, P. L. 1993 Pattern similarity in shared codas from sperm whales (*Physeter catodon*). *Mar. Mammal Sci.* **9**, 1–9.

Nettle, D. 1999 Language variation and the evolution of societies. In *The evolution of culture* (ed. R. I. M. Dunbar, C. Knight & C. Power), pp. 214–227. Piscataway, NJ: Rutgers University 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. (DOI 10.1038/35046199.)

Pitman, R. L., Ballance, L. T., Mesnick, S. L. & Chivers, S. J. 2001 Killer whale predation on sperm whales: observations and implications. *Mar. Mammal Sci.* **17**, 494–507.

Reiss, D. & Marino, L. 2001 Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proc. Natl Acad. Sci. USA* **98**, 5937–5942.

Rendell, L. E. & Whitehead, H. 2001 Culture in whales and dolphins. *Behav. Brain Sci.* **24**, 309–382.

Rendell, L. E. & Whitehead, H. 2003 Comparing repertoires of sperm whales: a multiple methods approach. *Bioacoustics* (In the press.)

Tyack, P. 2001 Cetacean culture: humans of the sea. *Behav. Brain Sci.* **24**, 358–359.

Tyack, P. L. & Sayigh, L. S. 1997 Vocal learning in cetaceans. In *Social influences on vocal development* (ed. C. T. Snowdon & M. Hausberger), pp. 208–233. Cambridge University Press.

Watkins, W. A. & Schevill, W. E. 1977 Sperm whale codas. *J. Acoustical Soc. Am.* **62**, 1486–1490.

Weilgart, L. & Whitehead, H. 1997 Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behav. Ecol. Sociobiol.* **40**, 277–285.

Whitehead, H. 1996 Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol.* **38**, 237–244.

Whitehead, H. 1998 Cultural selection and genetic diversity in matrilineal whales. *Science* **282**, 1708–1711.

Whitehead, H. 2001 Direct estimation of within-group heterogeneity in photo-identification of sperm whales. *Mar. Mammal Sci.* **17**, 718–728.

Whitehead, H. 2002 Estimates of the current global population size and historical trajectory for sperm whales. *Mar. Ecol. Prog. Ser.* **242**, 295–304.

Whitehead, H. & Weilgart, L. 1991 Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. *Behaviour* **118**, 275–296.

Whitehead, H. & Weilgart, L. 2000 The sperm whale: social females and roving males. In *Cetacean societies: field studies of dolphins and whale* (ed. J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 154–172. University of Chicago Press.

Whitehead, H., Waters, S. & Lyrholm, T. 1991 Social organization in female sperm whales and their offspring: constant companions and casual acquaintances. *Behav. Ecol. Sociobiol.* **29**, 385–389.

Whitehead, H., Dillon, M., Dufault, S., Weilgart, L. & Wright, J. 1998 Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics. *J. Anim. Ecol.* **67**, 253–262.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E., Wrangham, R. W. & Boesch, C. 1999 Chimpanzee cultures. *Nature* **399**, 682–685.

Yurk, H., Barrett-Lennard, L., Ford, J. K. B. & Matkin, C. O. 2002 Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Anim. Behav.* **63**, 1103–1119.