ANIMAL BEHAVIOUR, 2005, **70**, 191–198
doi:10.1016/j.anbehav.2005.03.001

Available online at www.sciencedirect.com
SCIENCE @ DIRECT®

Spatial and temporal variation in sperm whale coda vocalizations: stable usage and local dialects

LUKE RENDELL* & HAL WHITEHEAD†
*Sea Mammal Research Unit, School of Biology, University of St Andrews
†Department of Biology, Dalhousie University

*(Received 26 February 2004; initial acceptance 16 April 2004;
final acceptance 26 October 2004; published online 10 May 2005; MS. number: 8022R)*

Variation in vocal repertoires within species can result from various processes, from genetic drift to cultural evolution. Studying the detailed nature of such variation over time and space can provide insight into these underlying processes. The temporal stability or otherwise of vocal variants is important information in assessing the possibility of interaction between vocal variation and genetic evolution, while the geographical scale of variation can give useful clues in detailing population structure, thus providing management information. We studied variation in the vocal output of sperm whales, *Physeter macrocephalus*, which use short stereotyped click sequences called codas in social contexts, over timescales of up to 6 years and spatial scales of up to 10 000 nautical miles. We found no evidence from either correlation or regression analyses for change over time in the coda output of known social units. We did, however, find evidence for reduced similarity over distances of 200–1000 km. The apparent temporal stability of coda output suggests the possibility of evolutionary interactions. The scale of spatial variation is broadly similar to estimated home range sizes for this species, and the potential for interbreeding over such distances suggests differences between areas may represent local dialects rather than geographical variation through isolation.

© 2005 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

In many species vocal output varies over time and space. Factors affecting this variation include random genetic drift, random or directional cultural evolution (Slater 1986; Deecke et al. 2000) and local adaptation to acoustic environments or ecological niches (e.g. Nottebohm 1972; Au et al. 1985; Barrett-Lennard et al. 1996; Daniel & Blumstein 1998). In addition, the need for recognition by offspring (e.g. Charrier et al. 2001), groupmates (e.g. Boughman & Wilkinson 1998), territorial neighbours (e.g. Catchpole & Slater 1995), coadapted conspecifics (e.g. Grant & Grant 1996) or conspecifics in general (e.g. Searcy & Brenowitz 1988) can affect vocal variation. Studying the features of variation in any particular case can help us understand which of these factors might be operating. Often, the nature of variation gives important clues in assessing both the function of variation and the relation between vocal variation and social structure (Tyack & Sayigh 1997). In wide-ranging species, geographical variation can be indicative of population structure and thus provide important information for management (e.g. Stafford et al. 2001). Similarly, where vocal variation is based on cultural transmission, understanding the stability of variation is important, since stability is probably a prerequisite for significant interaction between cultural and genetic evolution (Laland 1992).

One species of particular interest in this respect is the sperm whale, *Physeter macrocephalus*, the largest of the odontocetes and one of the most abundant large whales in the postwhaling era (Whitehead 2002). Sperm whales are present in all the world's deep oceans, but one of the better-studied populations is that of the Eastern Tropical Pacific. Here, an ongoing longitudinal study has revealed a highly complex matrilineally based social structure (Whitehead & Weilgart 2000), necessitating a terminology that distinguishes between long-term social units and short-term groups. Females and their young live in social units consisting of on average 12 individuals; units are persistent over decades, but individuals occasionally transfer between units. Groups are temporary collections of two or more units that typically associate for 7–10 days before splitting back into their constituent units (Christal & Whitehead 2001). Concurrent studies of vocal behaviour

Correspondence: L. Rendell, Sea Mammal Research Unit, Gatty Marine Laboratory, School of Biology, University of St Andrews, Fife KY16 8LB, U.K. (email: ler4@st-andrews.ac.uk). H. Whitehead is at the Department of Biology, Dalhousie University, Halifax, B3H 4J1, Canada.

0003–3472/05/$30.00/0
© 2005 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

have focused on codas (Watkins & Schevill 1977): short stereotyped sequences of clicks (Fig. 1). These vocalizations are considered social in nature (rather than sensory as in echolocation clicks also made by sperm whales, Møhl et al. 2003), primarily because their production is highly correlated with periods of social behaviour (Whitehead & Weilgart 1991), although they are also heard during foraging dives (Watkins & Schevill 1977).

All known social units can be assigned to vocal clans based on the usage frequency of certain coda types (Rendell & Whitehead 2003b). For example, one clan uses primarily codas containing regularly spaced clicks, and is termed the 'Regular' clan; another uses codas that have a pause before the final click, and is termed the '+1' clan. Across the Eastern Tropical Pacific we have identified five such vocal clans, and since our observations that units overwhelmingly form groups with other units from the same clan, we have suggested that these clans form a further, higher, level of social structure (Rendell & Whitehead 2003b). These clans are sympatric and there is evidence of gene flow between them, such that their existence is best explained by cultural transmission (Rendell & Whitehead 2003b). We have also shown that, within a social unit, coda types are shared between individuals, and that several unit members contribute to coda output (Rendell & Whitehead 2004). Clans also vary in other, nonvocal, aspects of behaviour, most notably foraging success (Whitehead & Rendell 2004).

We investigated differences in coda usage and production within clans, over time and space. We first looked for evidence that coda output changes over time, using recordings of known social units. In cetaceans, cultural vocal traits vary widely in stability. The song of humpback whales, *Megaptera novaeangliae*, can change very rapidly, with complete population-level song replacement in about 2 years (Noad et al. 2000). In contrast, killer whale, *Orcinus orca*, dialects change relatively slowly, such that dialects may reliably reflect recent ancestry (Barrett-Lennard 2000; Deecke et al. 2000). The sperm whale's taxonomic position is a matter of some debate (e.g. Milinkovitch et al. 1993), but in terms of social structure it is much closer to the killer whale (Baird 2000) than the humpback, so it is of interest to know where sperm whale vocal behaviour might lie in a comparative analysis. Another reason for studying stability of vocal traits is the potential for gene–culture coevolution. Variation in vocal output in sperm whales is correlated with variation in mitochondrial DNA (Whitehead et al. 1998); the implications of this led one of us to suggest that low mtDNA diversity in sperm whales (and other matrilineal odontocetes) may be the result of gene–culture coevolution (Whitehead 1998). This proposal was based on models that used the stability of cultural traits as an important parameter, but there has been no direct study of the stability of such traits in sperm whales until now.

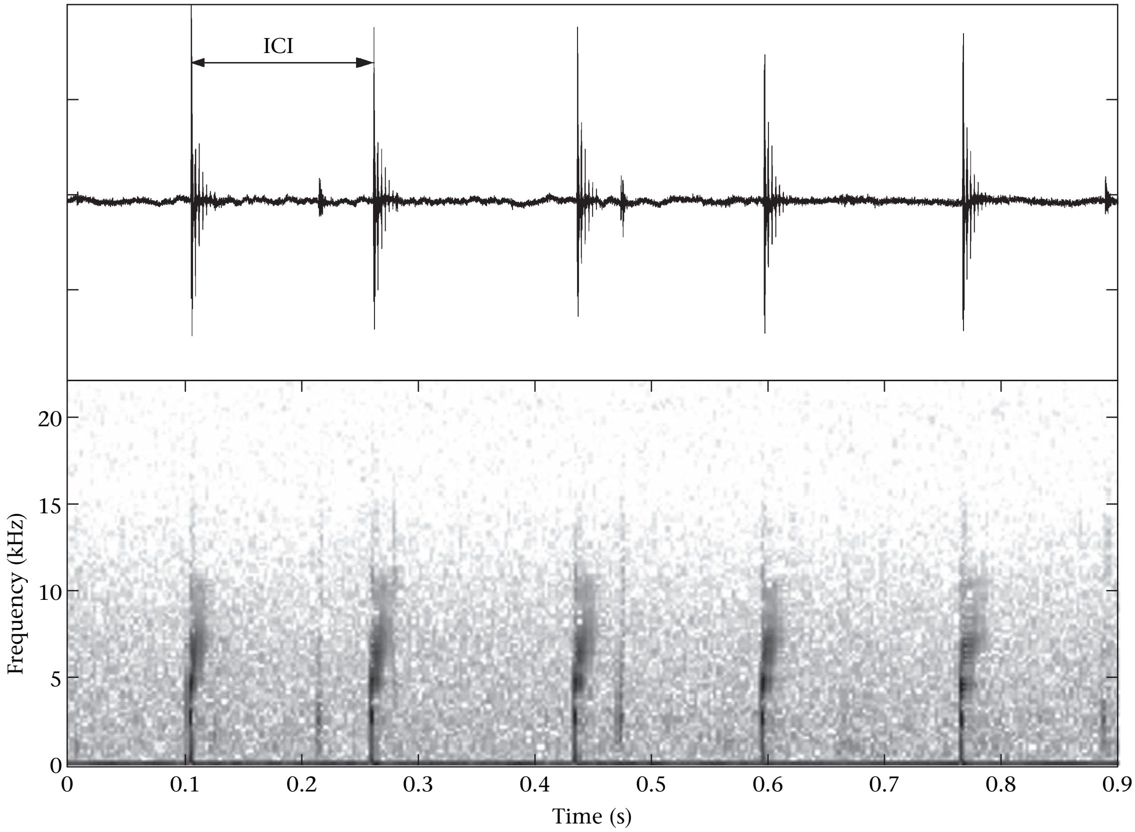

Figure 1. Waveform and sonagram of a single coda containing five clicks, illustrating the interclick interval (ICI). Sonagram based on 256 point Fast Fourier Transforms, time resolution 0.003 s.

Second, we looked for evidence of geographical variation within clans. There are many reasons to expect this; in birds adaptation to local acoustic conditions is likely to be an important determinant of signal structure (Nottebohm 1972, 1975; Handford 1981; Slabbekoorn & Peet 2003), and apparently similar variation has been noted in other cetaceans (Ding et al. 1995; Rendell et al. 1999). Geographical variation can also arise through neutral drift in signal structure in relatively isolated populations, arising through either genetic or cultural drift (e.g. Slater 1986). However, there is at least one cetacean species that maintains highly homogeneous patterns of culturally transmitted behaviour over large geographical areas: the humpback whale (Cerchio et al. 2000). In sperm whales, previous studies of geographical variation in coda output found a weak pattern overlaid and dominated by what we now know to be clan structure (Weilgart & Whitehead 1997; Rendell & Whitehead 2003b). We aimed to remove the variance in coda output attributed to clans and looked in more detail at geographical variation within clans. This information is important since geographical variation in vocal behaviour is often among the best indications we have of population structure in wide-ranging oceanic cetaceans (e.g. Stafford et al. 2001), and sperm whales are a species for which our lack of knowledge on population structure is chronic (Dufault et al. 1999).

METHODS

Data in the form of acoustic recordings and images for photoidentification were collected during periods spent following sperm whales at sea. Animals were approached under protocols approved by the Dalhousie University Committee on Laboratory Animals and designed to minimize disturbance of the focal animals. Recordings were made with a variety of equipment sets (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 modified AQ21B hydrophone (frequency response 1–10 kHz, ±3 dB) connected via either Barcus-Berry ‘Standard’ or Ithaca 453 preamplifiers to either a Uher 4000, Sony TC770 or Nagra IV-SJ reel-to-reel tape recorder) and subsequently digitized on to a desktop PC at 44.1 kHz. The acoustic and photoidentification database used here is identical to that presented in Rendell & Whitehead (2003b). We measured interclick intervals (ICIs) in codas (Fig. 1) and then standardized them to overall coda length for an analysis that focused on rhythm over tempo, the former being better conserved in codas (Moore et al. 1993). We assigned codas to type using *k*-means-based methods, and linked codas to specific units and groups based on proximity of recording to the photoidentification of known animals, as described in Rendell & Whitehead (2003a, b). For brevity, we do not repeat these methodological details here.

We compared collections of codas quantitatively using two different measures. First, we used a measure of multivariate similarity based on the infinity-norm distance between two coda vectors. This distance is simply the largest absolute difference between ICIs (interclick interval); for example two four-click codas defined by the ICIs [0.32 0.34 0.33] and [0.30 0.45 0.25] would have absolute differences of [0.02 0.11 0.08] and the infinity-norm distance is the maximum of these values, 0.11. Obviously, this can be calculated only for codas of the same length. To construct an aggregate measure of the similarity of any two sets of codas, we first calculated the distances between each coda in the reference set to all codas with the same number of clicks in the comparison set. We then converted the distance values to similarities between 1 and 0, using the formulation similarity = $b/(b + \text{distance})$, to allow for a minimum similarity value and thus prevent single comparisons of very different codas unreasonably influencing an aggregate measure. Finally, we summed these values and divided them by the total number of coda comparisons possible between the two sets, that is, the product of the number of codas in the two sets of codas; this is equivalent to an average similarity where codas containing different numbers of clicks have a similarity equal to zero. Thus, the final similarity value contains information both about how similar the codas of the same number of clicks in the two sets are and also about the extent to which codas in the two sets have the same number of clicks. This procedure can be mathematically expressed as:

$$S_{\mathrm{AB}} = \frac{\displaystyle\sum_{i=1}^{n_{\mathrm{A}}} \sum_{\substack{j=1 \\ l_j = l_i}}^{n_{\mathrm{B}}} \frac{0.001}{0.001 + d_{ij}}}{n_{\mathrm{A}} \cdot n_{\mathrm{B}}}$$

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} the maximum absolute distance (or infinity-norm) between the vectors containing the standardized interclick intervals of the codas x_i and x_j ($\|x_i - x_j\|_\infty$). We chose the value $b = 0.001$ in converting distances to similarity as being approximately the maximum resolution of our recordings digitized at 48 kHz given a median coda length of 0.93 s and a maximum time resolution of 0.001 s. Details and an analysis of the performance of this measure are given in Rendell & Whitehead (2003a). Second, we compared results from this measure with results obtained using a Spearman rank correlation between the number of times each coda type occurred in the two collections to be compared (Weilgart & Whitehead 1997). Thus, we analysed data using two measures with one independent of classification and the second based on a classification of codas (Rendell & Whitehead 2003a).

To investigate the stability of coda usage over time, we calculated, using both multivariate similarities and type–usage correlations, the similarities between the first and last days on which groups containing each known social unit were recorded (i.e. unit members were photographed within 2 h of the recording start time), provided that 25 or more codas were recorded on both days. We estimated bootstrap standard errors for these values as the standard deviation of the similarities between 1000 bootstrap resamples of the codas recorded on each day (Rendell & Whitehead 2003a). We then tested these values against the number of days between the first and last recordings, using Spearman rank correlation between similarity and days between recordings and also a linear regression analysis on the same data. If repertoires are evolving over the timescales for which data are available, such analyses would show a trend with similarity declining over longer time intervals. Note that because nonunit members were almost always present during these recordings (with the exception of one unit, designated unit T, which was always recorded alone) our data are partially confounded by variation in coda output between units. They can, however, inform us of how coda usage is changing at the clan level, since units appear to form groups primarily with other units of the same clan, and they would be likely to pick up major changes in unit-specific repertoires.

To look for evidence of geographical variation in vocal output within clans, we first selected all days on which the group recorded had been assigned to a clan (Rendell & Whitehead 2003b). Then, within each clan, we calculated the similarities between coda outputs recorded on pairs of days having no photoidentified animals in common to minimize the possibility that different groups were recorded. On average, 14 animals were identified on the days used in this analysis. Mean group size in these studies is about 24 (Whitehead 2003b), so about 58% of the animals present were identified on each day. We also calculated the geographical distance between the midday positions on those days. If there were geographical variational within clans then one would expect these data to be related: as distance increases, coda output similarity should decrease. We calculated Spearman rank correlation coefficients for each clan independently. We could not test the resultant correlation coefficients for significance, however, because this analysis used data pairwise such that individual days contributed to more than one data point, meaning that data entered into the correlation analysis were necessarily not independent. Instead, we used a *t* test assuming that each clan-specific correlation coefficient was an independent estimate of a single 'true' value, to determine the probability that this true value was negative against the null hypothesis that it was zero or positive. All tests were two tailed, and all analyses were carried out using Matlab v6.1. (MathWorks Inc., Natick, MA, U.S.A.).

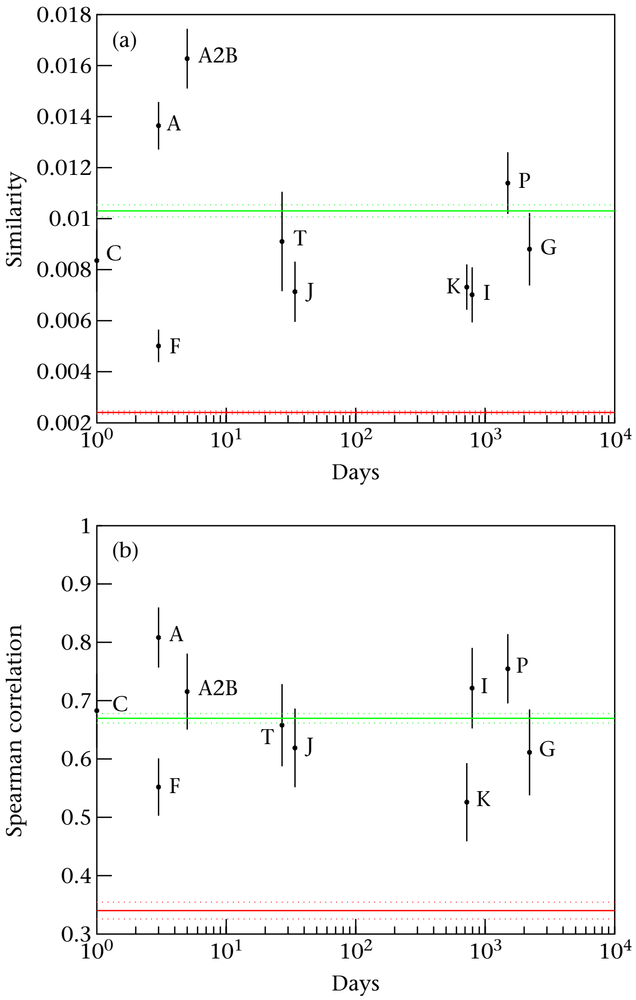

Figure 2. Similarities between the coda output on the first and last days on which groups containing each unit (indicated by letters) were recorded against the number of days between dates. Error bars are bootstrap standard errors from 1000 bootstrap resamples; straight horizontal lines indicate the mean ± 1 SE unit similarities within (upper) and between (lower) clans, respectively. (a) Using multivariate similarity, infinity-norm, $b = 0.001$; (b) using type–usage correlations based on classification of codas to types.

RESULTS

In the analysis of temporal variation, data were available for 10 different social units from three clans (Regular clan: A, A2B, C, I, J, K, P; +1 clan: F, G; Short clan: T). There was no statistical evidence for consistent changes in coda output over the timescales for which data were available (up to 2203 days, about 6 years; Fig. 2) using either multivariate similarity (infinity-norm, $b = 0.001$: $r_S = -0.04$, $P = 0.45$; linear regression: $r^2 = 0.006$, $F_{1,9} = 0.046$, $P = 0.84$) or type–usage correlation ($r_S = -0.09$, $P = 0.40$; linear regression: $r^2 = 0.004$, $F_{1,9} = 0.033$, $P = 0.86$).

There is evidence of geographical variation within clans based on data from 87 different days and four clans. Pairs closer than about 200 km (ca. 100 nautical miles) had elevated similarity, but this dropped off between 200 and 1000 km (Fig. 3). The +1 and 4+ clans had large negative correlations between distance and similarity, the Regular clan had a moderate negative correlation for the multivariate similarity method and a large negative correlation for the type–usage correlation, and the Short clan had small negative correlations for both methods; *t* tests of the combined geographical distance versus similarity or correlation values for each clan (Table 1) were significant at the 95% level for the multivariate similarity method ($t_3 = -3.765$, $P = 0.032$) but not for the type–usage correlation, although the effect was in the same direction ($t_3 = -2.539$, $P = 0.084$). Assuming the clan coefficients are normally distributed and estimate a common value, the maximum likelihood estimators for the common correlation coefficient are −0.27 (95% confidence interval, CI = [−0.41 −0.14]) and −0.27 (95% CI = [−0.56 0.02]) for the multivariate similarity and type–usage correlation measures, respectively.

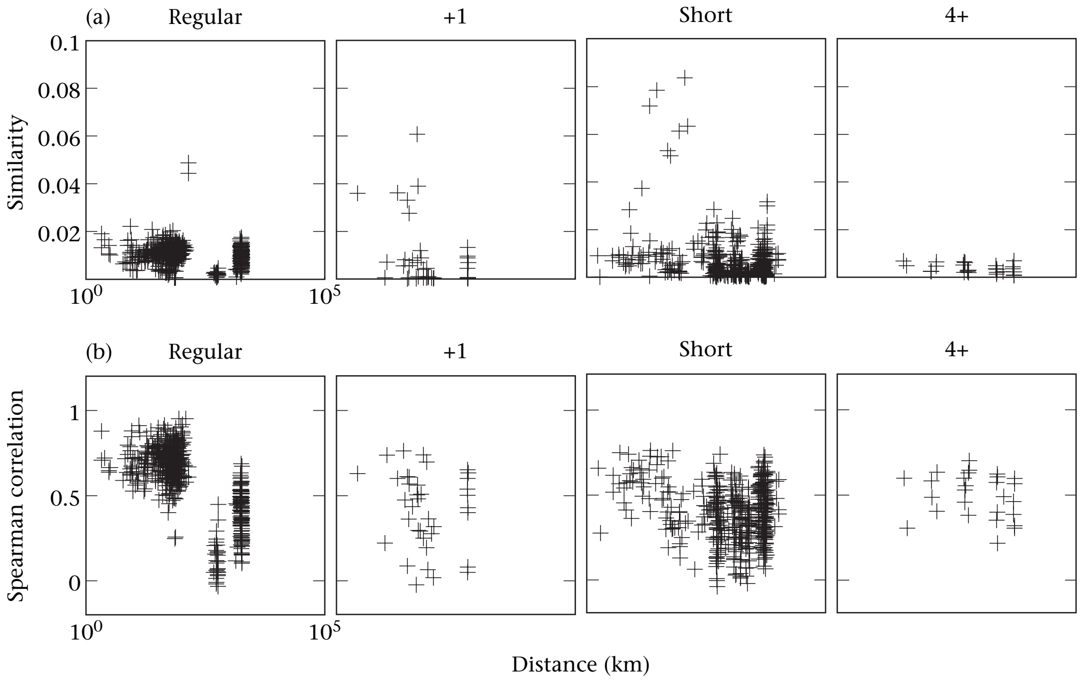

Figure 3. Similarities between the coda output of groups sharing clans (Regular, +1, short, 4+) but no individuals (according to photoidentification records) plotted pairwise against geographical distance between midday positions. (a) Using multivariate similarity, infinity-norm, $b = 0.001$; (b) using type–usage correlations based on classification of codas to types.

DISCUSSION

We found no evidence that unit coda output changed consistently over time. However, an important caveat to this result is that data are available for only a very limited timescale relative to the life span of a sperm whale. The maximum time between recordings in this analysis was about 6 years (unit G; Fig. 2), one-tenth of a female sperm whale's life span of about 60 years (Rice 1989). Hence, while the best data available on this question tell us that coda output is essentially stable over periods of about 6 years, we remain ignorant of rates of change over longer, and arguably more relevant, timescales. We also cannot remove the potential confound of other social units, which were likely to have been present for most of our recordings, and thus for variation between units affecting our ability to detect temporal change, although coda usage does not appear to vary much within clans (Rendell 2003; Rendell & Whitehead 2003b). Nevertheless, these data provide an important foundation to investigate this issue further; for comparison, Deecke et al. (2000) used a data set spanning 12 years to detect finescale structural evolution of discrete calls in killer whales, although these calls remain easily recognizable over periods of more than 30 years (Ford 1991). It is noteworthy that data in Deecke et al. (2000) also show little evidence for call change if restricted to the same timescale as our study; therefore we cannot exclude the possibility of repertoire change occurring over longer timescales. More longitudinal data are the only remedy for our ignorance in this case. Nevertheless, in the present study we were unable to find evidence for rapid change, to preclude potential interactions between culture and genetic evolution (Whitehead 1998).

Table 1. Spearman correlations between coda output similarity measures and geographical distance across groups

Clan	Multivariate similarity (b=0.001)	Type–usage correlation
Regular	−0.14	−0.58
+1	−0.33	−0.22
Short	−0.17	−0.08
4+	−0.45	−0.21
All	−0.37	−0.58

We did, however, find some evidence of geographical variation within clans, with groups of the same clan that shared no individuals generally having higher coda output similarities at ranges of less than 200 km (about 100 nautical miles; Fig. 3). All clans showed a negative trend in repertoire similarity over increasing distance, although the strength of this trend varied between clans. Such variation probably reflects high levels of intragroup variability in coda usage (Fig. 2 shows that coda usage can change markedly within a social unit over short timescales; compare units A and F for example), but may also indicate that different clans show different levels of geographical variation.

Our data are in accordance with work that found some evidence of geographical variation, albeit weak relative to clan variation (Weilgart & Whitehead 1997), although the present study is novel in that we could separate geographical effects caused by varying clan distributions from those that occur within clans. This variation could occur in two ways. First, animals may stay in one area and develop local vocal patterns (as in geographically based bird song dialects). Second, animals moving into a given area may adopt vocal patterns characteristic of that area, perhaps in response to local ecological conditions, since we know that other cetacean species can alter their vocal output in response to varying acoustic conditions (Au et al. 1985; Lesage et al. 1999). In mobile species such as cetaceans either scenario is plausible. Female sperm whales are known to range over thousands of nautical miles (Jaquet et al. 2003), but the average displacement over periods of about 5 years is nearer 740 km (400 nautical miles; Whitehead 2001). This latter distance matches the distance below which coda output similarities are elevated (Fig. 3), although the extent to which largescale movements (i.e. more than 2000 km) are a regular occurrence for individual sperm whales is still largely unknown (e.g. Dufault & Whitehead 1995). Because of these potential movements, we cannot definitively separate the possibility that the observed variation represents some form of geographical within clan 'accent' and the possibility that the variations described here represent coda output being altered according to local conditions. However, given the apparent stability of coda output (Fig. 2), the former seems more likely. Whether local 'accents' are permanent or facultative, we consider this geographical variation unlikely to take the form of direct acoustic adaptation to local sound propagation conditions, referred to as 'habitat matching' in birds (Catchpole & Slater 1995), given the structural homogeneity of the sperm whale's deep ocean habitat.

How does our observed geographical variation relate to ecological variation? Autocorrelation in oceanic ecosystems breaks down on the order of 500 km (ca. 260 nautical miles) according to fisheries data analysed by Myers et al. (1997), and it is notable that the elevated coda output similarities in Fig. 3 also fall within this range. At lower trophic levels oceans can be divided into biogeographical 'provinces' with distinct primary production properties (Sathyendranath et al. 1995; Platt & Sathyendranath 1999); in the Atlantic, these can be about 1800 km (1000 nautical miles) across (Sathyendranath et al. 1995), larger than the average ranges of sperm whales (Whitehead 2003a). Although we are aware of no such similar formal partition of the Pacific Ocean (although a biome level approach was taken by Longhurst 1998), it seems that geographical variation in coda output is broadly congruent with what we know of the spatial structure of ocean systems, although none of the above partitions relate directly to the sperm whale's major prey group, mesopelagic squid. An interesting study would relate vocal variation within a group of known animals to concurrent ecologically relevant data such as defecation rate and scattering layers, and with physical oceanographic parameters; if vocal patterns change according to local conditions, this should also be detectable longitudinally. However, a pattern of local 'accents' would be closer to what is observed in other cetacean species (e.g. Ding et al. 1995). We need to know more about sperm whale movements to clarify this issue, since there will be an upper limit to the rate of permanent range shifts for geographical variation to become established.

An important issue in considering this spatial component to vocal variation is the likelihood of animals interbreeding over the scales in question, since this establishes the distinction between geographical variation caused by genetic drift, in the case of restricted interbreeding, and the establishment of learned local dialects in the case of large amounts of interbreeding, potential or otherwise (Connor 1982). In this case, there is no clear answer, based on what we know of sperm whale reproductive biology. Males leave their natal groups at the onset of puberty, and head for polar waters: nearer the poles, schools of males contain fewer, but larger, individuals. Upon attaining an apparently size-related social maturity, males then return to the tropics where they encounter and presumably mate with groups of females (Whitehead & Weilgart 2000). Hence, there is potential for large amounts of gene flow over the spatial scales of interest. Results of genetic studies are inconsistent with mating within the natal group, and observed global homogeneity of nuclear markers indicates that males may mate successfully in areas very distant from their mother's home range (Lyrholm & Gyllensten 1998; Lyrholm et al. 1999). Thus, the potential for interbreeding over these spatial scales means that variation is best described as a form of local dialect.

In summary, we have shown that the vocal output of sperm whale clans is stable over periods of up to 6 years, although this result cannot preclude the possibility of longer term variation. We have also found evidence that there is variation within clans over geographical scales of 200–1000 km, a result that is consistent with current knowledge of sperm whale movements and ecological structure in the ocean.

Acknowledgments

We are grateful to the numerous volunteers who have helped collect data over many years of fieldwork, and Linda Weilgart, Tonya Wimmer and Erin Robinson for help analysing codas. We used software kindly donated by the International Fund for Animal Welfare for coda analysis. Fieldwork was funded by grants from the Natural Sciences and Engineering Research Council of Canada and the National Geographic Research Committee to H.W.; L.R. was supported by an Izaak Walton Killam Memorial Scholarship and a NERC Postdoctoral Fellowship. Andy Horn, Ian Mclaren, Vincent Janik, Peter Slater, Thierry Aubin and an anonymous referee gave valuable comments on the manuscript.

References

Au, W. W. L., Carder, D. A., Penner, R. H. & Scronce, B. L. 1985. Demonstration of adaptation in beluga whale (*D. leucas*) echolocation signals. *Journal of the Acoustical Society of America*, **77**, 726–730.

Baird, R. W. 2000. The killer whale: foraging specializations and group hunting. In: *Cetacean Societies: Field Studies of Dolphins and*

Whales (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 127–153. Chicago: University of Chicago Press.

Barrett-Lennard, L. 2000. Population structure and mating patterns of killer whales (*Orcinus orca*) as revealed by DNA analysis. Ph.D. thesis, University of British Columbia.

Barrett-Lennard, L. G., Ford, J. K. B. & Heise, K. A. 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour*, **51**, 553–565.

Boughman, J. W. & Wilkinson, G. S. 1998. Greater spear-nosed bats discriminate group mates by vocalizations. *Animal Behaviour*, **55**, 1717–1732.

Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.

Cerchio, S., Jacobsen, J. K. & Norris, T. F. 2000. Temporal and geographical variation in songs of humpback whales, *Megaptera novaeangliae*: synchronous change in Hawaiian and Mexican breeding assemblages. *Animal Behaviour*, **62**, 313–329.

Charrier, I., Mathevon, N. & Jouventin, P. 2001. Mother's voice recognition by seal pups. *Nature*, **412**, 873.

Christal, J. & Whitehead, H. 2001. Social affiliations within sperm whale (*Physeter macrocephalus*) groups. *Ethology*, **107**, 323–340.

Connor, D. A. 1982. Dialects versus geographic variation in mammalian vocalizations. *Animal Behaviour*, **30**, 297–298.

Daniel, J. C. & Blumstein, D. T. 1998. A test of the acoustic adaptation hypothesis in four species of marmots. *Animal Behaviour*, **56**, 1517–1528.

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

Ding, W., Wursig, B. & Evans, W. E. 1995. Whistles of bottlenose dolphins: comparisons among populations. *Aquatic Mammals*, **21**, 65–77.

Dufault, S. & Whitehead, H. 1995. The geographic stock structure of female and immature sperm whales in the South Pacific. *Reports of the International Whaling Commission*, **45**, 401–405.

Dufault, S., Whitehead, H. & Dillion, M. 1999. An examination of the current knowledge on the stock structure of sperm whales (*Physeter macrocephalus*) worldwide. *Journal of Cetacean Research and Management*, **1**, 1–10.

Ford, J. K. B. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian Journal of Zoology*, **69**, 1454–1483.

Grant, B. R. & Grant, P. R. 1996. Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution*, **50**, 2471–2487.

Handford, P. 1981. Vegetational correlates of variation in the song of *Zonotrichia capensis*. *Behavioral Ecology and Sociobiology*, **8**, 203–206.

Jaquet, N., Gendron, D. & Coakes, A. 2003. Variability of food resources and its influence on movements, residency and behaviour of sperm whales in the Gulf of California (Mexico). *Marine Mammal Science*, **19**, 545–562.

Laland, K. N. 1992. A theoretical investigation of the role of social transmission in evolution. *Ethology and Sociobiology*, **13**, 87–113.

Lesage, V., Barrette, C., Kingsley, M. C. S. & Sjare, B. 1999. The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River estuary, Canada. *Marine Mammal Science*, **15**, 65–84.

Longhurst, A. 1998. *Ecological Geography of the Sea*. London: Academic Press.

Lyrholm, T. & Gyllensten, U. 1998. Global matrilineal population structure in sperm whales as indicated by mitochondrial DNA sequences. *Proceedings of the Royal Society of London, series B*, **265**, 1679–1684.

Lyrholm, T., Leimar, O., Johanneson, B. & Gyllensten, U. 1999. Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. *Proceedings of the Royal Society of London, series B*, **266**, 347–354.

Milinkovitch, M. C., Guillermo, O. & Meyer, A. 1993. Revised phylogeny of whales suggested by mitochondrial ribosomal DNA sequences. *Nature*, **361**, 346–348.

Møhl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A. & Lund, A. 2003. The monopulsed nature of sperm whale clicks. *Journal of the Acoustical Society of America*, **114**, 1143–1154.

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

Myers, R. A., Mertz, G. & Bridon, J. 1997. Spatial scales of interannual recruitment variations of marine, anadromous and freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1400–1407.

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.

Nottebohm, F. 1972. The origins of vocal learning. *American Naturalist*, **106**, 116–140.

Nottebohm, F. 1975. Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. *American Naturalist*, **109**, 605–624.

Platt, T. & Sathyendranath, S. 1999. Spatial structure of pelagic ecosystem process in the global ocean. *Ecosystems*, **2**, 384–394.

Rendell, L. E. 2003. Cultural variation and usage of coda vocalisations by sperm whales, Physeter macrocephalus. Ph.D. thesis, Dalhousie University.

Rendell, L. E. & Whitehead, H. 2003a. Comparing repertoires of sperm whales: a multiple methods approach. *Bioacoustics*, **14**, 61–81.

Rendell, L. E. & Whitehead, H. 2003b. Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society of London, series B*, **270**, 225–231.

Rendell, L. E. & Whitehead, H. 2004. Do sperm whales share coda vocalizations? Insights into coda usage from acoustic size measurements. *Animal Behaviour*, **67**, 845–874.

Rendell, L. E., Matthews, J. N., Gordon, J. C. D. & MacDonald, D. W. 1999. Quantitative analysis of tonal calls from five odontocete species, examining interspecific and intraspecific variation. *Journal of Zoology*, **249**, 403–410.

Rice, D. W. 1989. Sperm whale, *Physeter macrocephalus*, Linnaeus, 1758. In: *Handbook of Marine Mammals* (Ed. by S. H. Ridgway & R. Harrison), pp. 177–233. London: Academic Press.

Sathyendranath, S., Longhurst, A., Caverhill, C. M. & Platt, T. 1995. Regionally and seasonally differentiated primary production in the North Atlantic. *Deep-Sea Research*, **10**, 1773–1802.

Searcy, W. A. & Brenowitz, E. A. 1988. Sexual differences in species recognition of avian song. *Nature*, **332**, 152–154.

Slabbekoorn, H. & Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature*, **424**, 267.

Slater, P. J. B. 1986. The cultural transmission of bird song. *Trends in Ecology and Evolution*, **1**, 94–97.

Stafford, K. M., Nieukirk, S. L. & Fox, C. G. 2001. Geographic and seasonal variation of blue whale calls in the North Pacific. *Journal of Cetacean Research and Management*, **3**, 65–76.

Tyack, P. L. & Sayigh, L. S. 1997. Vocal learning in cetaceans. In: *Social Influences on Vocal Development* (Ed. by C. T. Snowdon & M. Hausberger), pp. 208–233. Cambridge: Cambridge University Press.

Watkins, W. A. & Schevill, W. E. 1977. Sperm whale codas. *Journal of the Acoustical Society of America*, **62**, 1486–1490.

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

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

Whitehead, H. 2001. Analysis of animal movement using opportunistic individual identifications: application to sperm whales. *Ecology*, **82**, 1417–1432.

Whitehead, H. 2002. Estimates of the current global population size and historical trajectory for sperm whales. *Marine Ecology Progress Series*, **242**, 295–304.

Whitehead, H. 2003a. Society and culture in the deep and open ocean: the sperm whale. In: *Animal Social Complexity: Intelligence, Culture and Individualized Societies* (Ed. by F. B. M. de Waal & P. Tyack), pp. 444–464. Cambridge, Massachusetts: Harvard University Press.

Whitehead, H. 2003b. *Sperm Whales: Social Evolution in the Ocean*. Chicago: University of Chicago Press.

Whitehead, H. & Rendell, L. 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. *Journal of Animal Ecology*, **73**, 190–196.

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 Whales* (Ed. by J. Mann, R. C. Connor, P. L. Tyack & H. Whitehead), pp. 154–172. Chicago: University of Chicago Press.

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. *Journal of Animal Ecology*, **67**, 253–262.