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Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales

HAL WHITEHEAD and LUKE RENDELL
Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

Summary

1. The population of sperm whales (*Physeter macrocephalus*) in the South Pacific is divided into at least five sympatric vocal clans that almost certainly reflect cultural variation.
2. We investigated differences in movements and feeding success of groups from different clans off the Galápagos Islands and northern Chile, using data from 87 days spent tracking groups of known clan.
3. Groups from different clans showed different use of habitat and movement patterns. Off the Galápagos Islands, 'Plus-one' clan groups moved in relatively straight lines while 'Regular' clan groups had more convoluted tracks and a more inshore distribution, patterns which were consistent across years.
4. Groups from different clans had different defecation rates, indicating between-clan variation in feeding success. Off the Galápagos Islands, 'Plus-one' clan groups were more successful in the depauperate ENSO ('El Niño/Southern Oscillation') conditions of 1987. However, in the cooler conditions of 1989, groups of the 'Regular' clan had much higher feeding success than those of the 'Plus-one' clan.
5. Thus we suggest that cultural inheritance in sperm whales incorporates foraging strategy as well as vocal patterns, and that clan membership has fitness consequences.
6. That clans seem differentially affected by altered climate conditions has implications for the effects of global warming on sperm whales.
7. The results also support the hypothesis that culturally determined differences in fitness may have affected genetic evolution through the process of cultural hitchhiking.

Key-words: Chile, cultural hitchhiking, ENSO, Galápagos, *Physeter*.

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Introduction

Culture may be defined as information or behaviour shared by populations or subpopulations that is transmitted between individuals by some form of social learning (Rendell & Whitehead 2001a). As such, culture strongly structures human societies, for instance through dialect boundaries (Nettle 1999). While culture is also found among non-humans, for instance in chimpanzees (*Pan troglodytes*; Whiten *et al*. 1999) and songbirds (Slater 1986), in these species cultural distinctions are usually geographically based or short term, and so culture does not, on its own, structure populations. An exception is among killer whales (*Orcinus orca*), in which sympatric 'types', 'clans' and other hierarchical levels of social structure show strong cultural differences, which are consistent over time, in both vocalizations and other forms of behaviour (Yurk 2003). Thus killer whale societies are strongly structured culturally, in a manner not reported in other non-humans (Rendell & Whitehead 2001b). However, foraging specializations among individuals or groups of individuals seem to be more frequently found in apex predators whose populations are principally regulated by intraspecific competition for food (Estes *et al*. 2003).

The sperm whale (*Physeter macrocephalus* Linnaeus) is a large (11–18 m), nomadic animal distributed over almost all the world's deep oceans (Rice 1989). The sperm whale feeds principally in the mesopelagic ocean and seems to be the most significant vertebrate predator of this habitat (Clarke 1977; Whitehead 2003). It has very slow life-history processes, such as fertility (Rice 1989), indicating that intraspecific competition may be an important determinant of fitness (Horn & Rubenstein 1984). Female and immature sperm whales are typically encountered in groups of about

Correspondence: Hal Whitehead. E-mail: hwhitehe@dal.ca

20 animals in tropical and subtropical waters (Rice 1989). Many groups consist of amalgams of two or more long-term social units, each containing about 10 animals. Units remain grouped together for the order of 10 days (Whitehead, Waters, & Lyrholm 1991).

When socializing, female and immature sperm whales often make stereotypical patterns of 3-~20 clicks called codas (Watkins & Schevill 1977). The coda repertoires of each social unit that we studied off the Galápagos Islands could be allocated to one of three clans, which possess very distinctive coda repertoires (Rendell & Whitehead 2003). Units preferentially group with other units that are members of their own acoustic clan so, with very rare exceptions, groups may also be assigned unambiguously to a clan (Rendell & Whitehead 2003). Clans span large areas of the South Pacific, contain of the order of 10 000 animals, and overlap considerably in geographical extent (Rendell & Whitehead 2003). Clans are not discrete in either mitochondrial or nuclear DNA (Rendell & Whitehead 2003; Whitehead 2003) and thus provide an unusual form of large-scale cultural population structure.

Cultural differences between population segments may or may not be adaptive (Slater 1986). Clan structure would be particularly significant if, in addition to possessing distinctive vocal repertoires, clans also showed consistent differences in forms of behaviour that are likely to affect fitness more directly. Sperm whales spend most of their time deep under the water, so few elements of their behaviour are currently accessible, but both habitat use and movement are measurable and might affect fitness.

The movements of female and immature sperm whales over time scales from a few hours to a few days are related to feeding success, as indicated by observed defecation rates (an inference justified by Whitehead 1996). While movements through the water are similar for groups with good and poor feeding success, straight-line displacements over periods of hours to days are generally much less when conditions are good and defecation rates high (Whitehead 1996; Jaquet & Whitehead 1999).

We are currently unable to measure sperm whales fitness directly. However, in behavioural ecological research, foraging success is often used as a proxy for fitness (e.g. Krebs & Kacelnik 1991), and so we use observed defecation rates of sperm whales as such a proxy. Here, we look at the possible fitness consequences of clan membership by examining the differences in habitat use, movements and feeding success of sperm whales of different clans in two study areas of the south-east Pacific.

Materials and methods

We collected data on the behaviour of sperm whales from 10 to 13 m sailing vessels in various parts of the South Pacific between 1985 and 2000, but here restrict attention to the three studies in which useful data were collected from groups of more than one coda clan: off the Galápagos Islands in 1987 and 1989, and off northern Chile in 2000. The temporal and spatial distributions of effort in these studies are described in Figs 1 and 2.

The two Galápagos Islands studies provide a useful contrast because, while they were carried out at similar times of year (Fig. 1), in 1987 the waters were affected by the ENSO ('El-Niño/Southern Oscillation') phenomenon (mean measured sea-surface temperature 26 °C) while 1989 was a 'normal' cool year (mean measured sea-surface temperature 22 °C). ENSO strongly affects the biological oceanography of the eastern tropical Pacific (e.g. Arntz 1986), and reduces considerably the

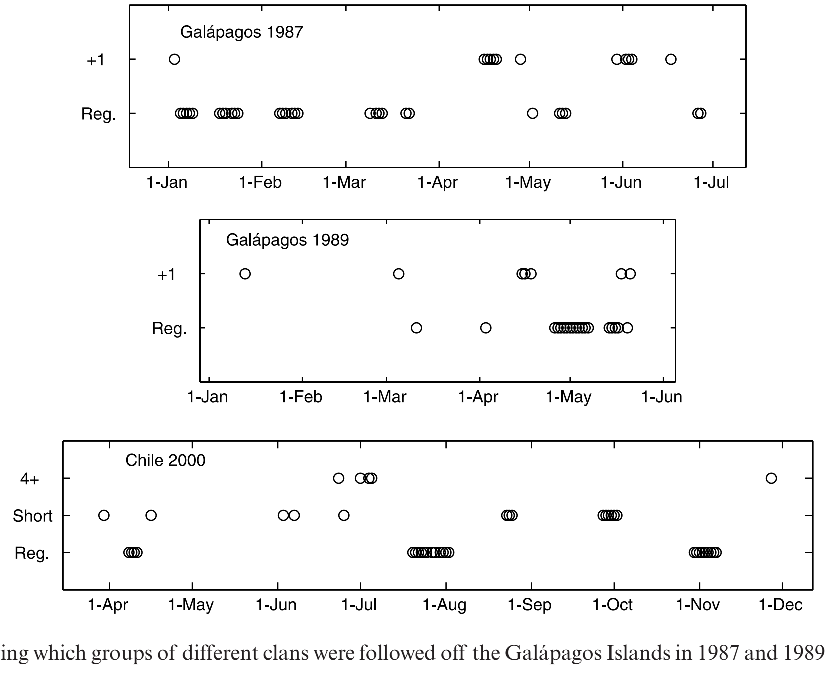

Fig. 1. Dates during which groups of different clans were followed off the Galápagos Islands in 1987 and 1989 and off northern Chile in 2000.

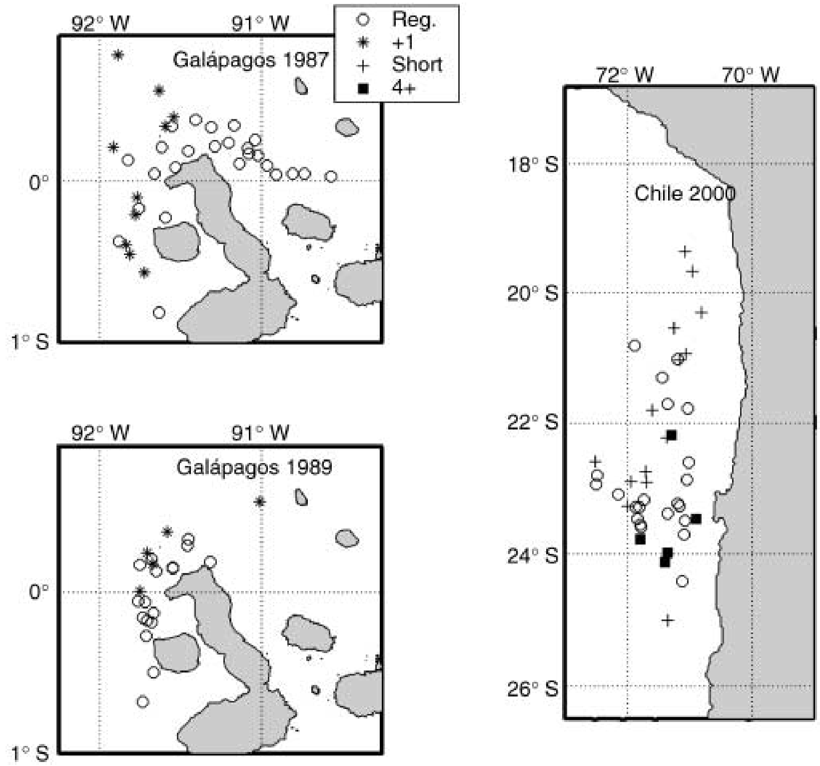

Fig. 2. Locations at midday during days spent tracking sperm whale groups which could be assigned to a clan.

feeding success of sperm whales in the area (Smith & Whitehead 1993). SSTs off Chile ranged from 15 to 21 °C, varying seasonally.

Groups of female and immature sperm whales were tracked at ranges of about 0·2–2 km visually and using directional hydrophones. A particular group was usually tracked for 1–3 days at a time. Positions came from SAT-NAV (1987, 1989) and GPS (2000) satellite navigators, and were noted at least each 3 h. During daylight (approximately 06 : 00–18 : 00), the flukes (tails) of animals were photographed for individually identifying marks as they dived or 'fluked-up' (Arnbom 1987). When the vessel was suitably placed, as each photograph was taken it was also recorded whether or not the animal defecated.

From the photographs, 440 females and immatures were identified from the Galápagos Islands study in 1987, 704 from there in 1989, and 739 off northern Chile in 2000. Sixty-four animals were identified during both Galápagos studies and two were photographed both off the Galápagos and Chile.

These photographic identifications of individuals were used to define social units for the waters off the Galápagos Islands where long-term records have been collected (see Christal, Whitehead, & Lettevall 1998 for methodology). They can also be used to link groups with nearly the same membership (e.g. Weilgart & Whitehead 1997). Except very rarely, only one group was followed on a day (Whitehead 2003), and as groups usually consist of social units from the same clan (Rendell & Whitehead 2003) it is generally possible to assign clan membership unambiguously to the sperm whales being tracked on any day. Eighty-seven days spent tracking sperm whales were then allocated to clans using the techniques described by Rendell & Whitehead (2003).

Thus for each day, the following non-movement measures were available: clan membership (called 'Regular', 'Plus-one', 'Four-plus' and 'Short' as a reference to the type of coda pattern favoured; see Rendell & Whitehead 2003); a measure of feeding success, the defecation rate (number of defecations observed divided by number of fluke-ups examined; Whitehead 1996) with an arcsine-squareroot transformation, including correction for zero values, to make the proportional data more normal (Kirk 1995). Movement was measured by the 12-h displacement between 06:00 and 18:00 positions from satellite navigators (3-h displacements were also examined, but results were similar and are not shown here). Data from clans followed on less than five days in any study were discarded.

General linear models were fitted for each study area (with *Year* omitted for Chile) using the backwards stepwise procedure, with α-to-remove = 0·15 and α-to-enter = 0·15:

$$\begin{aligned} \textit{Displacement} &= \text{Constant} + \textit{Year} + \textit{Clan} + \textit{Drate} \\ &\quad + \textit{Drate} \times \textit{Clan} + \text{Error} \\ \textit{Drate} &= \text{Constant} + \textit{Year} + \textit{Clan} + \textit{Year} \times \textit{Clan} + \text{Error} \end{aligned}$$

where *Drate* is the defecation rate (transformed when used as a dependent variable). Whether consecutive days spent tracking the same group can be considered independent was addressed by examining the autocorrelation of residuals after fitting models, and the residuals were also tested for normality using the Lilliefors test.

Table 1. Results of general linear models, examining factors affecting 12-h displacement and defecation rate (Drate). Table entries give the number of days and groups with data for the final model, the autocorrelation of residuals in the final model, the results of a Lilliefors test for normality among the residuals, the proportion of variance accounted for by the model terms, and the P-values for each of the factors in predicting the movement variables

	Galápagos		Chile	
	12-h displacement	Defecation rate	12-h displacement	Defecation rate
Days with data	29 days	37 days	26 days	28 days
Groups with data	16 groups	20 groups	20 groups	21 groups
Autocorrelation	$r = -0{\cdot}372$	$r = -0{\cdot}216$	$r = 0{\cdot}055$	$r = 0{\cdot}152$
Normality (Lilliefors)	$P = 1{\cdot}00$	$P = 0{\cdot}001$	$P = 0{\cdot}663$	$P = 0{\cdot}264$
Variance accounted for	0·402	0·579	0·395	0·249
Clan	$P = 0{\cdot}004$	$P = 0{\cdot}002$	$P = 0{\cdot}087$	$P = 0{\cdot}028$
Year	*	$P = 0{\cdot}000$	–	–
Year × Clan	–	$P = 0{\cdot}002$	–	–
Drate	$P = 0{\cdot}030$	–	$P = 0{\cdot}108$	–
Drate × Clan	*	–	$P = 0{\cdot}057$	–

– Not included in model; *removed from model by stepwise procedure.

In order to estimate the numbers of different groups used in each analysis (given in Table 1), data from any pair of days (with $N1$ and N_2 animals identified on each, and m identified on both) were assigned to the same group if $m/\min(N1,N_2) > 0{\cdot}5$. This relationship indicates that more than 50% of the animals present on one day were also present on the other.

Results

There is little sign that groups from different clans had distinctive seasonal patterns of using either study area (Fig. 1). However, in both study areas, we tended to follow groups from one particular clan over periods of one to several weeks, after which another clan would take over (Fig. 1). In all three studies there were many groups present, and usually several followed during such periods. This indicates that, at any time, groups of just one clan tend to dominate a study area numerically and that groups are broadly aggregated with other groups of their own clan over scales of a few hundred km (the approximate ranges of our studies over time periods of weeks). It also provides a warning that temporal autocorrelation could be a problem in the analyses of clan differences that follow.

Off the Galápagos Islands, and quite consistently in both 1987 and 1989, groups of the ‘Plus-one’ clan were about 10 km further from the islands than those of the ‘Regular’ clan (Fig. 2; median distances from land in 1987 and 1989: 19 km and 18 km, respectively, for the ‘Regular’ clan; 28 km and 29 km for the ‘Plus-one’ clan). Off northern Chile in 2000, the picture is less clear. However, compared with groups of the ‘Regular’ and ‘Four-plus’ clans, groups of the ‘Short’ clan were more dispersed, having the most southerly, westerly, and especially northerly locations (Fig. 2). Of the five most northerly locations recorded for the ‘Short’ clan, three were on consecutive days of the same group, so these should not be considered independent.

For both study areas there are clear differences in the movements of the different clans (Fig. 3, Table 1). Off the Galápagos Islands patterns were consistent between the 1987 and 1989 data (Fig. 3), with groups of the ‘Plus-one’ clan displacing about 30% more over 12 h than groups of the ‘Regular’ clan. Off Chile in 2000, groups of the ‘Regular’ clan were much more mobile than different groups of the same clan off the Galápagos Islands, and generally displaced more than groups of the ‘Four-plus’ clan (Fig. 3). Of the groups studied off Chile those of the ‘Short’ clan were generally most mobile, which is consistent with their wider distribution (Fig. 2).

Off the Galápagos Islands, defecation rates differed considerably between the two years, with much lower rates in the ENSO year of 1987 than in the cooler environment of 1989 (Fig. 3, Table 1). Additionally, there is a clear and statistically significant interaction between study year and clan. Groups of the ‘Plus-one’ clan had somewhat higher daily defecation rates in 1987 (median 0·018 defecations/fluke) than those of the ‘Regular’ clan (median 0·000 defecations/fluke), while groups of the ‘Regular’ clan possessing a clear advantage in 1989 (Fig. 3). The residuals from fitting this model are non-normal, mainly because of several zero defecation rates in 1987, reducing confidence in the results of model fitting (Table 1). However, the scale of the effects is very clear (Fig. 3).

It could, potentially, be argued that these differences between clans are related to demography, that groups with different sexes or ages behave differently. The groups that we tracked contained only females and immatures as members; the distinctively large mature males accompany the groups for just periods of hours at a time (Whitehead 2003), so adult sex ratio does not distinguish groups. Some groups contain first-year calves, others do not. Calves were observed with groups of all clans except the ‘Four-plus’ clan, for which we had the smallest samples (Fig. 3). A factor which coded whether

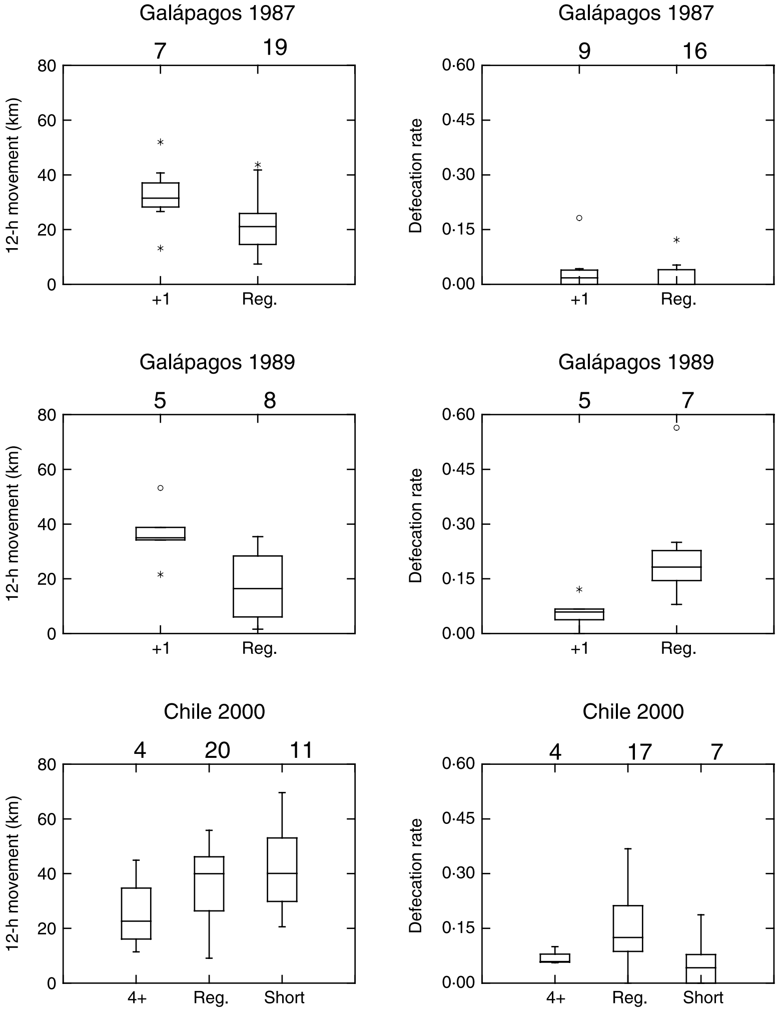

Fig. 3. Boxplots showing distribution of 12- h displacements and defecation rates for different studies and clans (sample sizes in days spent following groups of each clan are given above each plot).

a first-year calf had been observed on each day was added to the best-fit models listed in Table 1. In no case did this factor have a significant effect. Thus plausible demographic scenarios are not sufficient to explain our results.

The spatio-temporal aggregation of groups of the same clan (Fig. 1) and the practice of tracking the same group for several days raises questions of independence when days spent tracking are used as units for statistical analyses. However, a substantial number of groups are included in each analysis, and autocorrelation analyses indicated that in no case was serial dependence substantial (Table 1).

Discussion

SPATIO-TEMPORAL AGGREGATION

Sperm whale groups tend to be aggregated over scales of hundreds of km with other groups of the same clan, indicating a previously unrecognized type of socio-spatial population structure. The numerical predominance of groups of one clan in a study area at a particular time could be simply a consequence of such aggregation, but it could also result from temporary or permanent dominance among clans.

HABITAT USE AND MOVEMENT PATTERN

The two clans that we studied off the Galápagos Islands had clear and substantial differences in habitat use (Fig. 2) and movement pattern (Fig. 3), differences that were consistently maintained through quite different ecological conditions. Patterns off Chile were less clear and only available for one year, but there are also indications of clan-specific differences. A group tends to use horizontal space in a manner characteristic of its clan.

Differences between clans in both habitat use and movement measures are likely to be related to one another. Either could be primary, or both might be the consequence of some other more fundamental difference between the clans. So the ‘Plus-one’ groups could move in straighter lines (Fig. 3) and stay further from the Galápagos Islands (Fig. 2) than the ‘Regular’ groups as a result of either: ‘Plus-one’ groups preferring to move in straight lines, and so avoiding the more convoluted habitat close to the islands; or, ‘Regular’ groups preferring shallower habitats and so being found closer to the islands where they are forced to use more convoluted paths; or, the clans having different preferred food species, which have distinctive habitats and optimal harvesting methods; or some other scenario. Unfortunately we currently have insufficient data to compare diets of different clans, but this is an important research goal, as is the examination of other measures that may distinguish between clans.

The division of a population into phenotypes with different movement patterns and use of habitat is found in other animals including caribou, *Rangifer tarandus*, and Galápagos giant tortoises, *Geochelone gigantea* (Swingland *et al*. 1989; Bergman, Schaefer & Luttich 2000). However, in the case of the sperm whales the division of the population was made initially using the cultural trait of coda vocalizations, rather than morphological types, or the movement differences themselves, being used to distinguish phenotypes. Coda-usage variation is unlikely to be a functional covariate of movement pattern, habitat use or any attribute related to these, such as diet. Thus clans structure sperm whale populations along at least two independent behavioural axes–vocalizations and habitat usage–, as do 'types' in killer whales and 'tribes' in humans.

FEEDING SUCCESS AND OCEAN CLIMATE

The differences between defecation rates, especially off the Galápagos in 1989, imply that the characteristic differences among clans in movement patterns, habitat use or some other trait that we did not measure, such as diet, affect feeding success as measured through defecation rate. This might result partially from preferred food type itself directly affecting defecation rate, such that the absolute differences in defecation may not reflect absolute differences in calories ingested, but the reversal in ranking of clans by defecation rate off the Galápagos between 1987 and 1989 suggests that feeding plays a prominent part. The differences between the clans in feeding success and movement patterns fit with what we know and suspect of the general relationship between movement and feeding success in sperm whales (Whitehead 1996; Jaquet & Whitehead 1999). When feeding conditions are good, doubling back and forth over relatively small areas, as is characteristic of the 'Regular' clan, appears adaptive, while if food is highly dispersed then searching over large areas, the 'Plus-one' pattern, is probably more productive.

Our findings diverge from expectations of conventional 'optimal foraging' theory, which might have predicted that 'Regular' groups would switch to the 'Plus-one' foraging pattern during ENSO events. That this does not happen in any substantial fashion may reflect 'cultural inertia', as discussed by Estes *et al*. (2003) with reference to sea otters (*Enhydra lutris*). Like other apex predators in which intraspecific competition is the primary determinant of fitness, sperm whales probably benefit from foraging specializations, in this case at the level of the clan; but they also suffer the consequences when conditions change.

In an environment that is highly variable over longer time scales, principally because of the ENSO phenomenon, the clans seem adapted differentially to different circumstances. Climate warming seems both to increase the frequency of ENSO conditions and to make the general climate more ENSO-like (Stott *et al*. 2002). Hence, we should consider cultural diversity as an important attribute of sperm whales in facing the anthropogenically induced warming of world oceans.

IMPLICATIONS FOR GENETIC EVOLUTION

The discovery that clan membership affects the feeding success of an individual sperm whale also has implications for the genetic evolution of the species. The sperm whale has remarkably low mitochondrial DNA diversity, given that it is a very widely distributed species with a population size in the hundreds of thousands (Lyrholm, Leimar, & Gyllensten 1996). One of us has suggested that cultural evolution might have reduced mitochondrial DNA diversity in sperm whales and three other whale species with matrilineally based social systems through a process called cultural hitchhiking (Whitehead 1998). In this scenario social entities, each containing only a subset of the population's genetic diversity, compete for resources. There are cultural differences between the social entities, producing fitness differentials and resulting in asymmetric competition. Neutral genes associated with the better cultural phenotypes spread, and population genetic diversity is reduced.

For cultural hitchhiking to work there must be suitable social entities, and they must possess culturally determined fitness differences. The discovery of cultural clans in sperm whales provides a suitable social entity (Rendell & Whitehead 2003) and the work described in this paper shows that they may have fitness differences. Thus we have new support for the hypothesis that cultural hitchhiking was the driver of low mitochondrial DNA diversity in sperm whales, although the hypothesis is far from proved.

CONCLUSION AND PROSPECTS

The results of our analyses show that for South Pacific sperm whales clan membership is more than a descriptor of functionally neutral variation in a vocalization pattern (as suggested for some culturally transmitted variation in bird-song by Slater 1986). Clans have different movement patterns and, perhaps most importantly, differing feeding success in varying environmental conditions. We have thus documented a relationship between cultural trait group membership and a proxy fitness measure, showing that cultural inheritance is a far from trivial aspect of the life of a sperm whale.

Our understanding of the significance of clans would be improved greatly if there were studies of the same two, or more, clans in two, or more, study areas. With only the 'Regular' clan common to the Galápagos Islands and Chile, we cannot say whether the distinctive differences between the 'Regular' and 'Plus-one' clans found from our 1987 and 1989 Galápagos Islands studies are generally characteristic of these clans, or relate only to their use of the waters around the Galápagos Islands in these years.

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