Behav Genet
DOI 10.1007/s10519-011-9513-y

ORIGINAL RESEARCH

Can Genetic Differences Explain Vocal Dialect Variation in Sperm Whales, *Physeter macrocephalus*?

Luke Rendell · Sarah L. Mesnick · Merel L. Dalebout · Jessica Burtenshaw · Hal Whitehead

Received: 7 January 2011 / Accepted: 13 October 2011

Abstract Sperm whale social groups can be assigned to vocal clans based on their production of codas, short stereotyped patterns of clicks. It is currently unclear whether genetic variation could account for these behavioural differences. We studied mitochondrial DNA (mtDNA) variation among sympatric vocal clans in the Pacific Ocean, using sequences extracted from sloughed skin samples. We sampled 194 individuals from 30 social groups belonging to one of three vocal clans. As in previous studies of sperm whales, mtDNA control region diversity was low ($\pi = 0.003$), with just 14 haplotypes present in our sample. Both hierarchical AMOVAs and partial Mantel tests showed that vocal clan was a more important factor in matrilineal population genetic structure than geography, even though our sampling spanned thousands of kilometres. The variance component attributed to vocal dialects (7.7%) was an order of magnitude higher than those previously reported in birds, while the variance component attributed to geographic area was negligible. Despite this, the two most common haplotypes were present in significant quantities in each clan, meaning that variation in the control region cannot account for behavioural variation between clans, and instead parallels the situation in humans where parent-offspring transmission of language variation has resulted in correlations with neutral genes. Our results also raise questions for the management of sperm whale populations, which has traditionally been based on dividing populations into geographic 'stocks', suggesting that culturally-defined vocal clans may be more appropriate management units.

Keywords Sperm whale · Vocal dialect · Cultural transmission · Genetic population structure

Edited by Stephen Maxson.

L. Rendell (✉)
Centre for Social Learning and Cognitive Evolution,
School of Biology, University of St Andrews,
St Andrews, Fife KY16 8LB, UK
e-mail: ler4@st-andrews.ac.uk

S. L. Mesnick · J. Burtenshaw
Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508, USA

S. L. Mesnick · J. Burtenshaw
Center for Marine Biodiversity and Conservation,
Scripps Institution of Oceanography University of California,
San Diego, La Jolla, CA 92093-0202, USA

M. L. Dalebout · H. Whitehead
Department of Biology, Dalhousie University, Halifax,
NS B3H 4J1, Canada

Present Address:
M. L. Dalebout
School of Biological, Earth and Environmental Sciences,
University of New South Wales, Sydney, NSW 2052, Australia

Introduction

The relationship between cultural and genetic transmission and the evolutionary consequences thereof are poorly understood in nature, despite much theoretical attention (e.g. Boyd and Richerson 1985; Lachlan and Slater 1999; Laland 1992). Outside humans, the relationship between genetic inheritance and the cultural transmission of dialect in animals capable of vocal learning has been a particular focus of study in birds (Baker and Cunningham 1985; Catchpole and Slater 1995), motivated not least by the posited relationship between song learning and speciation (e.g. Grant and Grant 1996). There has been little study of

Published online: 21 October 2011

these questions in cetaceans, another group noted for vocal learning abilities (Janik and Slater 1997) and other forms of cultural transmission (Rendell and Whitehead 2001). In this study we investigated the relationship between mitochondrial DNA (mtDNA) variation and vocal dialects in sperm whales, *Physeter macrocephalus*.

In birds, studies focussed on the genetic relationships between sets of individuals with different dialects have produced varied results (Baker 1982; Baker and Cunningham 1985; Soha et al. 2004). In songbirds, some have found little correlation between genetic population structure and dialect variation. For example, Lougheed et al. (1993) sampled 42 breeding male rufous-collared sparrows, *Zonotrichia capensis*, and found little evidence that cultural transmission of song variants affects dispersal or mating patterns. Similarly, in the white-crowned sparrow, *Z. leucophrys pugetensis*, Soha et al. (2004) found that patterns of microsatellite variation showed little relation to dialect variation once geographic distance had been controlled for. However, other studies have found that dialects do explain significant, if small, amounts of genetic variation. In the mountain subspecies of the white-crowned sparrow (*Z. l. oriantha*), MacDougall-Shackleton and MacDougall-Shackleton (2001) estimated that dialects accounted for 0.79% of observed genetic variance, versus a 0.51% geographic variance component. Outside the songbirds, Wright and Wilkinson (2001) sampled the mtDNA of similar numbers of amazon parrots (*Amazona auropalliata*) on either side of a dialect boundary, and found no evidence that haplotypes segregated by dialect. They concluded that (a) there were high levels of gene flow across dialect boundaries, and (b) individuals change dialects when they migrate by learning the most common dialect in the population they enter—a phenomenon termed conformist oblique cultural transmission (Boyd and Richerson 1985). As Wright and Wilkinson (2001) highlight, this pattern contrasts with humans, where the correlations between neutral genes and language groups suggest that vertical (parent to offspring) transmission is more important (c.f. Cavalli-Sforza 1997). Overall, the emerging picture in birds is that geography accounts for equal or greater amounts of genetic variance than vocal dialect variation.

In cetaceans the relationship between genetic variation and any kind of behavioural variation has only received recent attention, but the few existing studies show distinctly different patterns to those in birds. There are strong relationships between the cultural transmission of vocal patterns (Ford 1991; Yurk et al. 2002) and mating patterns in the killer whale *Orcinus orca*. In the Northeast Pacific northern "resident" population males mate largely outside their vocal clan (Barrett-Lennard 2000), while in the southern "resident" population mating appears to occur exclusively within clan (Ford et al. 2011). Among the bottlenose dolphins, *Tursiops* spp., of Shark Bay, Australia, apparent tool use by females is restricted to carriers of a single mitochondrial haplotype identified by non-coding DNA, but unrelated to variation in functional coding mtDNA (Bacher et al. 2010; Krützen et al. 2005). In humpback whales, *Megaptera novaeangliae*, matrilineal social transmission of migration routes is a major factor in population structure (Baker et al. 1990; Palsbøll et al. 1995). Vertical cultural transmission thus appears to be important in cetaceans, but there has been very little study of the relationship between genetic variation and vocal dialects.

Sperm whales provide an opportunity to study this relationship. Female and immature sperm whales live in long-term bond groups called social units, which are partially matrilineal but may contain two or more unrelated matrilines (Christal et al. 1998; Lyrholm and Gyllensten 1998; Mesnick 2001). At sea, these units are usually encountered in temporary association with other units, forming what have been termed social groups (Christal et al. 1998). Males disperse from the natal unit at some point between 3 and 15 years of age (Whitehead 2003). Little is known about their subsequent movements, but there is genetic evidence, in the form of contrasting mtDNA and nuclear DNA population structure, that males switch ocean basins much more than females, with the nuclear DNA showing little between-ocean differentiation (Lyrholm et al. 1999). There is relatively high mtDNA haplotype differentiation among female groups-G_{ST} between groups within oceans was an estimated order of magnitude higher (0.4 vs 0.04) than that between oceans (Lyrholm and Gyllensten 1998). In contrast, within-ocean geographic structure in mtDNA independent of group structure appears to be either non-existent or low, based on very low levels of genetic differentiation (Lyrholm and Gyllensten 1998; Mesnick et al. 2011).

Sperm whales in social groups regularly emit short patterns of clicks termed 'codas' (Watkins and Schevill 1977) in social contexts. Whitehead et al. (1998) showed that coda repertoire similarity, quantified by measuring the time intervals between clicks in codas, and mtDNA haplotype similarity were correlated across 6 such largely matrilineal social groups, and suggested that coda repertoire was transmitted in parallel to mtDNA by vertical cultural transmission within largely matrilineal groups. Subsequently, Rendell and Whitehead (2003a) showed that the coda repertoires of 18 social units around the Galápagos Islands and 61 groups from the wider South Pacific clustered into five dialect groups, based on the usage of different coda patterns (for example, the 'regular' clan made codas containing regularly spaced clicks, while the '4+' clan made codas that started with 4 regular clicks followed by a variety of other patterns). They also found that groups with different dialects were spatially (and

sometimes temporally) sympatric. These dialect groups, termed 'vocal clans', are most likely the result of cultural transmission, although it is not known for certain that coda dialects are learned. It appears that social units form groups primarily with other units of the same vocal clan (Rendell and Whitehead 2003a). These clans have subsequently been shown to vary in movement patterns and foraging success (Whitehead and Rendell 2004) as well as reproductive success (Marcoux et al. 2007).

The correlations found by Whitehead et al. (1998) raise the question of whether genetic variation, rather than social learning, could account for the behavioural differences between clans. This question has been raised for other examples of purported social learning in the wild (Laland and Janik 2006), and a very similar analysis to the one we present here recently showed that behavioural variation among chimpanzee populations was indeed correlated with mtDNA variation (Langergraber et al. 2010), although this is still far from establishing a causal link of the kind suggested by Laland and Janik (2006). Here, we analyse the mtDNA control region in samples from 30 sperm whale groups from which we also had recordings of codas. As this region is non-coding, it is unlikely in the extreme that it directly controls coda repertoire, but we wanted to test whether the mtDNA inheritance pattern correlates with the pattern of coda repertoires, because suggestions have been made in the literature that such correlations could indicate a genetic basis for behavioural variation that would otherwise be considered cultural (Laland and Janik 2006; Langergraber et al. 2010). As the control region is hypervariable, it is particularly appropriate for assaying genetic variation within populations (Duchene et al. 2011; Moritz 1994). If maternally inherited genetic variation were largely driving vocal variation, we would expect (a) very little sharing of haplotypes between clans, and (b) correlations between mtDNA variation and vocal clan membership which (c) are consistent whether one examines haplotype frequencies or sequence divergence across clans, since we would expect dialects and genetic markers to have had similar histories of descent with modification.

Materials and methods

Acoustic and genetic data

We collected individual identification photographs, sloughed skin samples and acoustic recordings from sperm whale social groups using small vessels and established protocols (Amos et al. 1992; Arnbom 1987; Rendell and Whitehead 2003a, b; Whitehead et al. 1990). Fieldwork took place in the South Pacific during several studies between 1991 and 2000. Single days of data collection were assigned to the same group if $n_{ab} > 0.25 \min\{n_a, n_b\}$ where n_{ab} is the number of individuals photographed on both dates, n_a the number photographed on the first day and n_b the number photographed on the second day (as in Weilgart and Whitehead 1997). Acoustic recordings of codas were assigned to the group being followed on the day the recording was made (it was impossible to assign codas to individuals), and only groups with at least 25 codas were retained in the analysis (see Rendell and Whitehead 2003a, b). Groups were assigned to vocal clans according to which branch they appeared on in a dendrogram of vocal repertoire similarities (see Rendell and Whitehead 2003a). DNA from skin samples collected from Chilean waters in 2000 was sequenced for this study as described below, while haplotype data for groups sampled prior to 2000 in the wider South Pacific were obtained from published sequences (Dillon 1996; Dillon et al. 2002). We only used samples that had been unambiguously linked to photographically identified individuals, to avoid replication. Once skin samples were assigned to groups and groups assigned to clans, only those groups for which genetic and acoustic data were available were carried forward for analysis.

mtDNA extraction

For samples from 2000, we used Qiagen DNeasy kits to extract DNA from the sloughed skin samples. We then amplified and sequenced the first 399 base pairs of hypervariable region I of the mtDNA control region using primers Pmac D 5′CCTGAGAATTGCAACTAGAGG3′ (designed at the Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA) which anneals to a conserved section within the control region and TRO (5′CCTCCCTAAGACTCAAGGAAG3′) which anneals to the tRNA proline gene. The PCR master mix contained 2 mM $MgCl_2$, 10 mM Tris–HCl (pH 8.3), 50 mM KCl, 150 μM of each dNTP, 1.25 units Taq DNA polymerase, 0.3 μM of each primer, and Milli-Q water to 49 μl and 1.0 μl of DNA. PCR was performed with an initial denaturation at 90°C for 2 min followed by 35 cycles of (94°C for 0:10, 48°C for 0:10, and 72°C for 0:10) and a final extension at 72°C for 5 min. Aliquots of each sample were electrophoresed on a 2% (w/v) agarose gel, stained with ethidium bromide, and visualized with an UV transilluminator. PCR products were cleaned with Qiagen's QIAquick™ PCR purification kit, slightly modified from the manufacturer's protocol. Both heavy and light strands were cycle-sequenced using PRISM Big Dye™ Terminator Cycle Sequencing Kits (Applied Biosystems Inc.) according to the manufacturer's protocol. Sequences were run on an ABI 3100 automated sequencer and opposing strands were aligned and edited simultaneously using

SeqEd v. 1.0.3 software. Any samples found to belong to rare haplotypes were re-extracted and re-sequenced to confirm their haplotype identity. Details of DNA extraction and sequencing for pre-2000 samples are already published (Dillon and Wright 1993; Dillon 1996). We then produced a parsimony network of the resultant haplotypes using TCS v1.21 set with 95% probability of parsimony (Clement et al. 2000).

Statistical analysis

We examined two putative population divisions using hierarchical analyses of molecular variance or AMOVAs, analogous to nested ANOVAs, using the Arlequin (v3.5) software package (Excoffier et al. 1992). In the first putative partition, groups were divided into vocal clans based on the similarity of their recorded repertoire, and in the second, groups were divided according to where they were sampled (Fig. 1). The AMOVA structure allows independent estimates of the proportion of genetic variance explained within groups, between groups within clans or areas, and between clans. This is most appropriate for the present study since we know that there is strong group level mtDNA structuring due to partial natal philopatry (Lyrholm and Gyllensten 1998; Mesnick 2001). We ran AMOVA analyses using both F_{ST} based on haplotype distribution (i.e. all non-identical haplotypes are assigned a distance of 1), and Φ_{ST}, which takes into account the amount of sequence divergence between haplotypes (Excoffier et al. 1992). We carried out the Φ_{ST} analysis twice with different methods of computing the genetic distances, firstly using the standard pairwise difference method of Arlequin, and secondly using the substitution model of Tamura and Nei (1993), as the latter was selected by both Akaike's Information Criterion and the Bayesian Information Criterion to be the best fitting model, of those

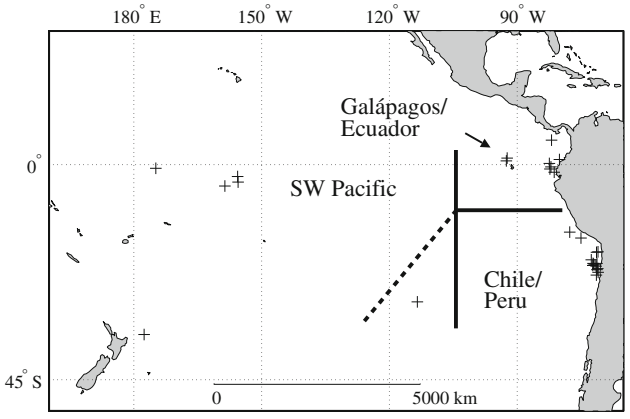

Fig. 1 Map showing locations of sampled groups and geographic partitioning. *Dashed line* shows an alternative feasible partition between SW Pacific and Chile/Peru to which all results were robust

available in Arlequin, to our data. We used the software jModelTest for this model selection (Posada 2009). The null distributions of pairwise F_{ST} or Φ_{ST} values under the hypothesis of panmixia were obtained by 10,000 permutations of the original data set in Arlequin (Schneider et al. 1999).

We looked for correlations between genetic, vocal and geographic distance matrices using Mantel and partial Mantel tests (Smouse et al. 1986) as in previous studies (MacDougall-Shackleton and MacDougall-Shackleton 2001; Soha et al. 2004; Whitehead et al. 1998; Wright and Wilkinson 2001). These tests compute correlations between two matrices, or in the case of the partial test, the correlations between the residuals of two matrices that have been regressed on a third, thereby controlling for effects due to the third matrix (Smouse et al. 1986). For these tests, we calculated the genetic distance between groups in three different ways. Firstly, we used the same measure as Whitehead et al. (1998), who defined the distance between groups X and Y as

$$d_{\{X,Y\}} = 1 - \frac{\sum_1^i X_i Y_i}{\sum_1^i X_i \sum_1^i Y_i}$$

where X_i and Y_i are the number of individuals in groups X and Y carrying haplotype i; this metric represents the probability that two individuals chosen randomly one from each group will share the same haplotype. Secondly, we calculated Jost's D between groups (Chao et al. 2008; Gerlach et al. 2010; Jost 2008). Finally, as both these measures rely only on haplotype frequency, we also used a sequence divergence measure, calculated as above using the Tamura and Nei (1993) model and the software MEGA (Posada 2009). Here, the distance measure was the average pairwise sequence divergence between the two groups. Vocal similarities were calculated using an averaged multivariate distance metric (see Rendell and Whitehead 2003a, b). We calculated the similarity between coda sets A and B as

$$s_{\{A,B\}} = \frac{\sum_{i=1}^{n_A} \sum_{j=1 | l_j = l_i}^{n_B} \frac{0.01}{0.01 + d_{ij}}}{n_A . n_B}$$

where 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 standardised inter-click-intervals of the codas x_i and x_j ($\|x_i - x_j\|_\infty$). This measure represents the average similarity between codas with the same number of clicks in the two repertoires. Geographic distances were simply the great-circle distances between the midday fixes on the first day of encounter with each group. We used Matlab v7 for the calculation of distance metrics and the Mantel tests.

Results

The final data set contained sequences from 194 individuals from 30 groups: 72 individuals from 13 social groups sampled in 2000 and 122 individuals from 17 social groups sampled prior to 2000. Sixteen groups were sampled off Chile/Peru, 8 off Galapagos/Ecuador, and 6 in the wider SW Pacific (Fig. 1). Of these groups, 8 were assigned to the 'Regular' clan, 13 to the 'Short' clan (that typically produce codas with 4 or fewer clicks), and 9 to the '4+' clan (Table 1).

There were 14 haplotypes present in the sample, defined by 15 polymorphic sites over the 399 bp region sequenced (Table 2), including one not previously found (#z). As in previous studies (Dillon 1996; Lyrholm and Gyllensten 1998), the haplotypes were distinguished only by transition substitutions, mostly of a single base pair, and there no transversions were observed. Nucleotide diversity was low ($\pi = 0.003$), but close to that found in previous studies of this species (Engelhaupt et al. 2009; Lyrholm and Gyllensten 1998; Mesnick et al. 2011). The maximum distance between haplotypes was 8 transitions (haplotype #f–#o), a maximum divergence of 2%. There were large heterogeneities in the frequencies of the different haplotypes—the three most common, #a, #b and #c, accounted for 82% of the sampled individuals, while none of the others accounted for more than 3% of the sample, again in line with existing studies (Engelhaupt et al. 2009; Lyrholm and Gyllensten 1998; Mesnick et al. 2011). Seven of these rarer haplotypes were unique to a single vocal clan (#j, #n, #h and #z were unique to the regular clan, #f and #o to the short clan and #e to the '4+' clan; Table 1). The haplotype network showed a star-shaped genealogy with the three common haplotypes lying centrally (Fig. 2), a pattern thought typical of relatively recent expansion from reduced diversity (Slatkin and Hudson 1991).

The hierarchical AMOVAs using F_{ST} (i.e. haplotype frequencies only) estimated the proportion of variation explained by grouping the data into vocal clans at 7.7% ($P = 0.055$; Table 3). This contrasts with the estimate for geographic partitioning, which was indistinguishable from zero ($P = 0.681$; Table 3). AMOVAs using sequence divergence data (Φ_{ST}) produced identical results with respect to area (Table 4), but estimated a much reduced proportion of variation explained by vocal clans (1.6%, $P = 0.286$). Using the Tamura and Nei (1993) substitution model produced virtually identical results (Dialect, among clans: 1.1%, $P = 0.30$; geography, among areas: −2.6%, $P = 0.638$). In all analyses there were large (31–40%) and significant variance component estimates for variation among groups within vocal clans and within areas.

We noted that our distribution of sample sizes from each group was both bimodal and discontinuous, with 5 groups each contributing 17 or more samples and the rest contributing 7 or less. This prompted us to test how the data from these better sampled groups were influencing the results above. We did this by running 1,000 further AMOVA analyses in which each of the larger groups was replaced by a group of 3 individuals sampled at random with replacement from that large group. We sub-sampled 3 individuals because the mean sample size of those groups represented by 7 or less individuals was 3.14. For the F_{ST} analysis, of these sub-sampled AMOVAs, 90% gave a smaller proportion of variance explained by clan than that estimated from the full dataset, but 95% gave a P value less than that estimated from the full dataset, while for the geographic analysis, 100% of the sub-sampled AMOVAs estimated a higher portion of variance explained and lower associated P values compared with the full dataset (Fig. 3). Using Φ_{ST}, the results were very similar for the geographic analysis—100% of the sub-sampled AMOVAs estimated a higher portion of variance explained and lower associated P values—but the clan analysis showed little shift in estimates when larger groups were sub-sampled, with the values estimated for the full dataset falling at the 75 and 25th percentile for variance estimates and associated P values respectively.

The Mantel tests showed a similar, but clearer, pattern compared to the AMOVAs. Genetic similarity based on the Whitehead et al. (1998) measure was positively (matrix correlation = 0.17) and significantly ($P = 0.003$) correlated with vocal similarity, but showed no detectable relation to geographic distance (matrix correlation = −0.07, $P = 0.220$). Similarly, genetic differentiation as measured by Jost's D was negatively (matrix correlation = −0.14) and significantly ($P = 0.014$) correlated with vocal similarity, but again showed little relation to geographic distance (matrix correlation = −0.03, $P = 0.394$). In contrast, averaged pairwise sequence divergence was not significantly related to either vocal similarity (matrix correlation = −0.03, $P = 0.376$) or geographic distance (matrix correlation = 0.10, $P = 0.240$). In the partial Mantel tests the results were unaffected by the addition of extra factors (genetic vs. vocal|geographic distance: matrix correlations = 0.17, $P = 0.009$; −0.14, $P = 0.029$; −0.03, $P = 0.378$, for Whitehead et al., Jost's D, and sequence divergence measures respectively; genetic vs. geographic distance|vocal: matrix correlation = −0.06, $P = 0.230$; −0.03, $P = 0.406$; 0.10, $P = 0.227$, again for the three genetic measures respectively). Although the validity of P values from partial Mantel tests have been questioned (Raufaste and Rousset 2001), here the estimated effect sizes (i.e. the matrix correlations) are virtually identical for the regular and partial Mantel tests, indicating robustness to these issues.

Table 1 Groups, samples and haplotypes by vocal clan and geographic area (A) Data by clan (B) Data by geographic area

A	Group		Haplotype code													
Clan	Code	*n*	#a	#b	#c	#e	#g	#i	#j	#d	#o	#n	#f	#m	#h	#z
Regular	C3	4	1	0	2	0	0	0	0	0	0	0	0	0	0	1
	C5	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
	C23	5	0	1	2	0	0	0	2	0	0	0	0	0	0	0
	C24	4	2	1	0	0	0	1	0	0	0	0	0	0	0	0
	C29	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0
	C44	24	19	5	0	0	0	0	0	0	0	0	0	0	0	0
	M39	21	9	0	4	0	1	0	0	0	0	3	0	4	0	0
	M21	18	17	0	0	0	0	0	0	0	0	0	0	0	1	0
	TOTAL	80	48	8	9	0	1	1	4	0	0	3	0	4	1	1
Short	C34	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0
	C40	17	7	8	2	0	0	0	0	0	0	0	0	0	0	0
	C41	5	2	2	0	0	0	0	0	0	1	0	0	0	0	0
	M37	18	3	13	1	0	0	0	0	0	0	0	1	0	0	0
	M38	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0
	M40	20	1	2	17	0	0	0	0	0	0	0	0	0	0	0
	M42	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0
	M43	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0
	M44	4	1	0	2	0	0	0	0	0	1	0	0	0	0	0
	M46	4	2	0	1	0	0	0	0	0	0	0	0	1	0	0
	M48	6	1	2	0	0	2	0	0	1	0	0	0	0	0	0
	M55	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	M62	5	2	0	0	0	0	0	0	3	0	0	0	0	0	0
	TOTAL	91	28	27	26	0	2	0	0	4	2	0	1	1	0	0
4+	C18	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0
	C19	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0
	C20	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	C47	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	M36	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	M45	6	0	0	0	0	1	5	0	0	0	0	0	0	0	0
	M49	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	M52	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	M53	7	1	6	0	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	23	2	11	0	3	1	5	0	1	0	0	0	0	0	0
Grand total		194	78	46	35	3	4	6	4	5	2	3	1	5	1	1
B	Group		Haplotype code													
Area	Code	*n*	#a	#b	#c	#e	#g	#i	#j	#d	#o	#n	#f	#m	#h	#z
Chile/Peru	C3	4	1	0	2	0	0	0	0	0	0	0	0	0	0	1
	C5	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0
	C23	5	0	1	2	0	0	0	2	0	0	0	0	0	0	0
	C24	4	2	1	0	0	0	1	0	0	0	0	0	0	0	0
	C29	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0
	C44	24	19	5	0	0	0	0	0	0	0	0	0	0	0	0
	C34	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0
	C40	17	7	8	2	0	0	0	0	0	0	0	0	0	0	0
	C41	5	2	2	0	0	0	0	0	0	1	0	0	0	0	0
	C18	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0

Table 1 continued

B	Group		Haplotype code													
Area	Code	*n*	#a	#b	#c	#e	#g	#i	#j	#d	#o	#n	#f	#m	#h	#z
	C19	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0
	C20	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	C47	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	M52	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
	M53	7	1	6	0	0	0	0	0	0	0	0	0	0	0	0
	M55	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	81	34	28	8	3	0	1	4	1	1	0	0	0	0	1
Gal/Ecuador	M39	21	9	0	4	0	1	0	0	0	0	3	0	4	0	0
	M21	18	17	0	0	0	0	0	0	0	0	0	0	0	1	0
	M37	18	3	13	1	0	0	0	0	0	0	0	1	0	0	0
	M38	3	3	0	0	0	0	0	0	0	0	0	0	0	0	0
	M40	20	1	2	17	0	0	0	0	0	0	0	0	0	0	0
	M42	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0
	M62	5	2	0	0	0	0	0	0	3	0	0	0	0	0	0
	M36	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	88	36	15	24	0	1	0	0	3	0	3	1	4	1	0
SW Pacific	M43	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0
	M44	4	1	0	2	0	0	0	0	0	1	0	0	0	0	0
	M46	4	2	0	1	0	0	0	0	0	0	0	0	1	0	0
	M48	6	1	2	0	0	2	0	0	1	0	0	0	0	0	0
	M45	6	0	0	0	0	1	5	0	0	0	0	0	0	0	0
	M49	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	TOTAL	25	8	3	3	0	3	5	0	1	1	0	0	1	0	0
GRAND TOTAL		194	78	46	35	3	4	6	4	5	2	3	1	5	1	1

Discussion

Our results show that there is no simple relationship between maternal genes and coda dialect. The Mantel tests showed that between-group differences in haplotype frequencies are more strongly correlated with similarity of dialect between groups than their geographic proximity. The AMOVA analyses of F_{ST} also suggest that vocal clan membership explains more variation in sperm whale mtDNA haplotype distributions than does geographical area. While the statistical significance of the clan effect is difficult to interpret, as it is not over the threshold for significance, the contrast in variance attributed to clan versus geographic area is clear. These findings contrast with the typical mammalian pattern of geographic variation (e.g. Chepko-Sade and Halpin 1987; Greenwood 1980), and support previous findings of non-geographic population structure in sperm whale social groups (Whitehead et al. 1998). They also contrast with studies on bird dialects that show geographic structuring at least as strong as that resulting from segregation by dialect groups (Lougheed et al. 1993; Soha et al. 2004; Wright and Wilkinson 2001). Our results are similar to those found in killer whales (*O. orca*), which show relatively weak geographic structuring as well as low global mtDNA diversity (Hoelzel et al. 2002). In killer whales there is also deep divergence between often sympatric ecotypes (Morin et al. 2010), but there does not appear to be a sperm whale equivalent to killer whale ecotypes.

These results were not however reproduced in the AMOVAs that included sequence divergence using Φ_{ST}, nor the Mantel tests based on sequence divergence. In this case, vocal clan membership accounted for much less variation than in the F_{ST} analyses, and neither it nor geographic area even approached statistical significance. We wanted to know whether genetic variation could account for behavioural variation between clans. Referring to the expectations we laid out in the introduction, we have shown that mtDNA haplotypes are shared extensively among clans, which is inconsistent with a largely genetic casual basis for vocal variation, but is consistent with photo-identification studies showing females occasionally

Table 2 Segregating sites in the 399 bp 5′ mtDNA control region sequence. Alphabetic haplotype codes used in the present study are linked to numerical codes used by Lyrholm and Gyllensten (1998) where possible; Genbank accession codes are also shown for each sequence

This study	Genbank accession code	Sequence position														
		58	62	150	184	200	211	260	273	286	287	288	308	319	324	350
#a (1)	DQ512921	T	C	C	T	T	C	A	C	A	A	A	A	G	C	C
#b (3)	DQ512922		T													
#c (2)	DQ512923		T									G				
#d (13)	DQ512924					C	T									
#e (5)	DQ512925	C														
#f	DQ512926	C		T					T							
#g	DQ512927	C														T
#h (10)	DQ512928								T		G					
#i	DQ512929														T	
#j (7)	DQ512930											G				
#m (11)	DQ512933		T							G						
#n (8)	DQ512934		T											A		
#o (9)	DQ512935		T		C			G						A	T	
#z	DQ512946		T									G	G			

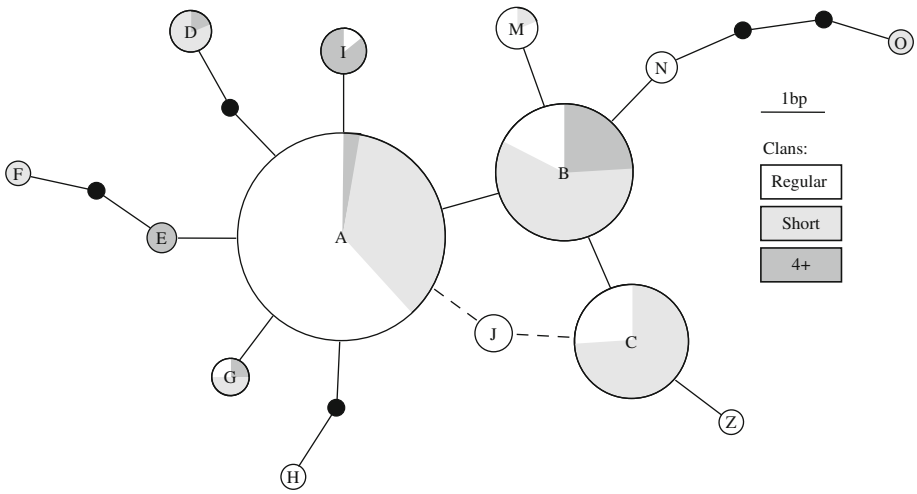

Fig. 2 Parsimony network of the haplotypes in this study. Node size is proportional to haplotype frequency, unlabelled nodes show intermediate 'missing' haplotypes, and dashed lines indicate ambiguous connections. Note that there are other known sequences from this species and this region, some of which are marked as 'missing' here (Mesnick, unpublished data)

Table 3 Results of hierarchical AMOVAs using F_{ST}

Test	Source of variance	d.f.	Percentage variance	*P*
	Among clans	2	7.67	0.055 ± 0.001
Dialect	Among groups, within clans	27	31.48	<0.00001
	Within Groups	164	60.85	<0.00001
	Among areas	2	−2.84	0.681 ± 0.002
Geography	Among groups, within areas	27	39.64	<0.00001
	Within groups	164	63.19	<0.00001

switching social units and more rarely, clans (Christal et al. 1998; Rendell and Whitehead 2003a). We did find a correlation between vocal and genetic similarities between groups, but the variance component associated with vocal clan membership was swamped by the components attributed to variation between and within groups-depending on the analysis, between 92 and 98% of the genetic variation we observed occurred within clans—and the statistical

Table 4 Results of hierarchical AMOVAs using Φ_{ST} (pairwise difference model)

Test	Source of variance	d.f.	Percentage variance	*P*
	Among clans	2	1.64	0.286 ± 0.004
Dialect	Among groups, within clans	27	35.26	<0.00001
	Within groups	164	63.10	<0.00001
	Among areas	2	−3.78	0.643 ± 0.004
Geography	Among groups, within areas	27	39.47	<0.00001
	Within groups	164	64.32	<0.00001

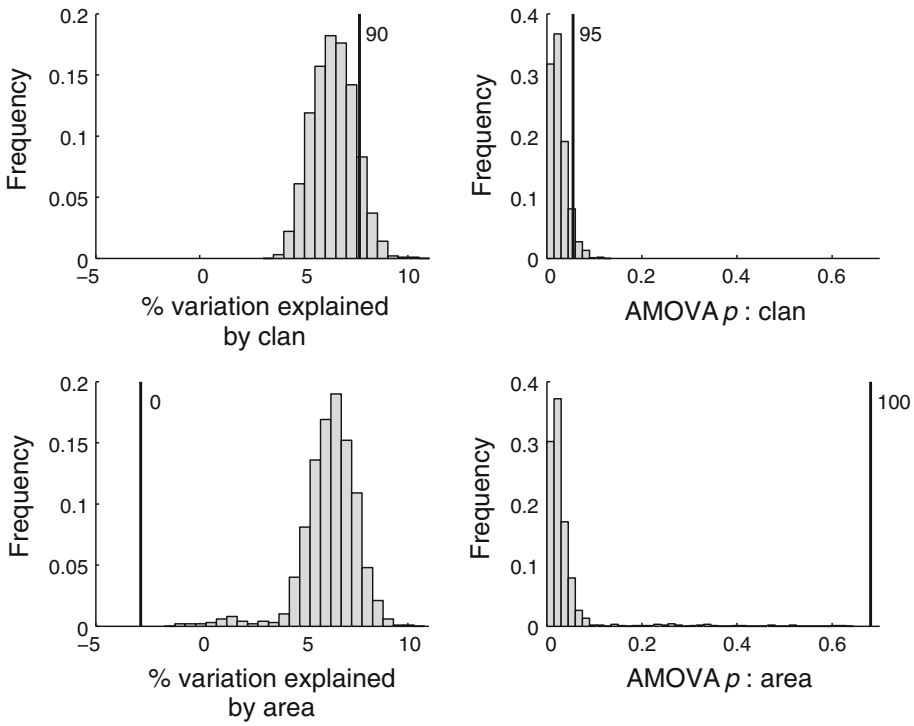

Fig. 3 Results of F_{ST} AMOVAs using sub-sampled larger groups. *Bars* show distribution of variance component estimates and *P* values from 1,000 sub-sampled analyses, *black lines* show the values obtained from the full dataset with the numbers indicating which percentile of the sub-sampled distribution the values represent

significance of variation between clans was marginal. Furthermore, analyses of sequence divergence were not consistent with analyses of haplotype frequencies—we saw no indication at all of the relationship between sequence divergence and vocal clan membership we would expect if both resulted from the same path of descent and modification. The broad picture of our results is therefore not consistent with a link between variation in the control region and dialect variation. It is however consistent with the hypothesis of generally vertical maternal cultural transmission, oblique (i.e. non-parental) transmission within matrilineal social units, and horizontal/oblique transmission when females occasionally switch clans. Correlations with haplotype frequencies build up under this scenario because of the generally parallel vertical transmission of dialect and haplotype.

Conceivably, dialect variation could be influenced by biparentally-inherited genes provided males mated exclusively or primarily within their own clan. Since we know that males disperse from their natal groups, and drive the exchange of nuclear DNA between oceans (Lyrholm et al. 1999), this would appear highly unlikely. However, we did not examine nuclear DNA here, so we still cannot answer the important question of whether males mate within clans or between clans. While we know that male dispersal is a likely driver of contrasting mitochondrial and nuclear genetic population structure on a global scale (Lyrholm et al. 1999), there is some evidence that males return to their natal populations to mate (Mesnick et al. 2011), and there is some weak behavioural evidence that males may prefer to associate with a single clan (Rendell et al. 2005). Therefore, comparing nuclear DNA across vocal clans is an important future research topic. Similarly, once mitogenomic data become available, they will also give a more complete picture (Duchene et al. 2011; Knaus et al. 2011), although other mtDNA regions commonly used to infer phylogenetic relationships such as cytochrome B have been shown to be invariant in sperm whales (Mesnick et al., unpublished data).

The effect of sub-sampling the 6 better sampled groups was different for analyses of clan membership and of geographic area—for the clan analyses, the distribution of the sub-sampled results comfortably included the values obtained from the full dataset, but for the area analysis they did not, with the full dataset results falling well outside the distribution of sub-sampled results (Fig. 3). The result that geographic area explained little variation depends on the groups with the larger sample sizes, whereas the larger amount of variation attributed to clans changed relatively little with sub-sampling. As the sub-sampling procedure generally results in rarer halotypes being lost from the better-sampled groups, it seems that some rarer haplotypes in the large groups (e.g., #g and #m in group M39) are important indicators of rare but important movements between areas, whereas the results for clan do not change when those rare haplotypes are excluded.

The haplotype frequency distribution we observed parallels previous studies: the haplotypes #a, #b and #c are the same as Lyrholm and Gyllensten (1998) haplotypes 1, 3 and 2 respectively. At least one of these haplotypes is common (frequency > 0.25) in all the ocean basins sampled by Lyrholm and Gyllensten (1998). These haplotypes have clearly come to dominate the population through past demographic events. Possible mechanisms include being carried through bottlenecks and founding subsequent population expansion (Lyrholm and Gyllensten 1998), relative spread by selective sweeps such as in cultural hitchhiking (Whitehead 1998), or other demographic effects (Tiedemann and Milinkovitch 1999). This is similar to the pattern observed in killer whales, which also have a haplotype distribution consistent both with population expansion, either globally or within regions, and cultural hitchhiking (Hoelzel et al. 2002; Morin et al. 2010). While our data are limited in their ability to distinguish between different hypotheses regarding historical evolutionary processes in sperm whales, they can serve as benchmarks against which models of those processes (e.g. Whitehead 2005) could be tested.

Our finding that genetic variation has little relationship with geography compared with dialects has important implications for understanding how sperm whale populations may be structured and potentially for how they should be managed with respect to goals such as retaining genetic diversity. Sperm whale management has traditionally been based on the concept of geographically segregated within-ocean stocks (Donovan 1991). As knowledge of sperm whale social structure and movements has grown, some have suggested that this approach is misguided (Dufault et al. 1999; Whitehead 2003). Our results support this view. Vocal clans do not meet the reciprocal monophyly condition some require to designate 'evolutionarily significant units' (Moritz 1994), but they are nevertheless likely to be unique repositories of complexes of genetic (half of the haplotypes in this study were unique to a single clan) and behavioural (Rendell and Whitehead 2003a; Whitehead and Rendell 2004) diversity. The challenging issue is to understand how our increasing knowledge of the structural complexities of sperm whale populations, particularly as related to cultural transmission, should be incorporated into management and conservation (Ryan 2006; Whitehead et al. 2004).

Acknowledgments The National Geographic Society and the Natural Sciences and Engineering Research Council of Canada provided funding for fieldwork. L.R. was supported by a NERC Postdoctoral Fellowship and M.L.D. was supported by a Killam Memorial Postdoctoral Fellowship and a Vice-Chancellor's Postdoctoral Fellowship (UNSW). Mary Dillon and Jenny Christal kindly shared the results of their genetic and photographic analyses respectively. Mike Ritchie, Jeff Graves, Kelly Stewart and Valentina Islas provided analytical advice and support. We thank Jeff Graves, Karen Martien, Kelly Stewart and two anonymous reviewers for comments that improved the manuscript.

References

Amos W, Whitehead H, Ferrari MJ, Glockner-Ferrari DA, Payne R, Gordon J (1992) Restrictable DNA from sloughed cetacean skin; its potential for use in population analysis. Mar Mammal Sci 8:275–283

Arnbom T (1987) Individual identification of sperm whales. Rep Int Whal Commn 37:201–204

Bacher K, Allen S, Lindholm A, Bejder L, Krützen M (2010) Genes or culture: are mitochondrial genes associated with tool use in bottlenose dolphins (*Tursiops* sp.). Behav Genet 40(5):706–714. doi:10.1007/s10519-010-9375-8

Baker MC (1982) Vocal dialect recognition and population genetic consequences. Am Zool 22:561–569

Baker MC, Cunningham MA (1985) The biology of bird-song dialects. Behav Brain Sci 8:85–133

Baker CS, Palumbi SR, Lambertsen RH, Weinrich MT, Calambokidis J, O'Brien SJ (1990) Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. Nature 344:238–240

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

Boyd R, Richerson PJ (1985) Culture and the evolutionary process. University of Chicago Press, Chicago

Catchpole CK, Slater PJB (1995) Bird song: biological themes and variations. Cambridge University Press, Cambridge

Cavalli-Sforza LL (1997) Genes, peoples and languages. Proc Natl Acad Sci USA 94:7719–7724

Chao A, Jost L, Chiang SC, Jiang YH, Chazdon RL (2008) A two-Stage probabilistic approach to multiple-community similarity indices. Biometrics 64(4):1178–1186. doi:10.1111/j.1541-0420.2008.01010.x

Chepko-Sade DB, Halpin ZT (eds) (1987) Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago

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

Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. Mol Ecol 9(10):1657–1660. doi:10.1046/j.1365-294x.2000.01020

Dillon MC (1996) Genetic structure of sperm whale populations assessed by mitochondrial DNA sequence variation. PhD Thesis, Dalhousie University, Halifax

Dillon MC, Wright JM (1993) Nucleotide sequence of the D-loop region of the sperm whale (*Physeter macrocephalus*) mitochondrial genome. Mol Biol Evol 10(2):296–305

Dillon MC, Richard KR, Whitehead H, Wright JM (2002) Social and population genetic structure of sperm whales assessed by molecular genetic analyses. In: Pfeiffer C (ed) Molecular and cell biology of marine mammals. Krieger, Malabar, pp 43–52

Donovan GP (1991) A review of IWC stock boundaries. Rep Int Whal Comm 13:39–68

Duchene S, Archer FI, Vilstrup J, Caballero S, Morin PA (2011) Mitogenome phylogenetics: the impact of using single regions and partitioning schemes on topology, substitution rate and divergence time estimation. PLoS One

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 Manage 1(1):1–10

Engelhaupt D, Rus Hoelzel A, Nicholson C, Frantzis A, Mesnick S, Gero S, Whitehead H, Rendell L, Miller P, De Stefanis R, Cañadas A, Airoldi S, Mignucci-Giannoni AA (2009) Female philopatry in coastal basins and male dispersion across the North Atlantic in a highly mobile marine species, the sperm whale (*Physeter macrocephalus*). Mol Ecol 18(20):4193–4205. doi:10.1111/j.1365-294X.2009.04355.x

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491

Ford JKB (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can J Zool 69:1454–1483

Ford MJ, Hanson MB, Hempelmann JA, Ayres KL, Emmons CK, Schorr GS, Baird RW, Balcomb KC, Wasser SK, Parsons KM, Balcomb-Bartok K (2011) Inferred paternity and male reproductive success in a killer whale (*Orcinus orca*) population. J Hered. doi:10.1093/jhered/esr067

Gerlach G, Jueterbock A, Kraemer P, Deppermann J, Harmand P (2010) Calculations of population differentiation based on GST and D: forget GST but not all of statistics! Mol Ecol 19(18):3845–3852. doi:10.1111/j.1365-294X.2010.04784.x

Grant BR, Grant PR (1996) Cultural inheritance of song and its role in the evolution of Darwin's finches. Evolution 50:2471–2487

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28(4):1140–1162

Hoelzel AR, Natoli A, Dahlheim M, Olavarria C, Baird RW, Black N (2002) Low worldwide genetic diversity in the killer whale (*Orcinus orca*): implications for demographic history. Proc Roy Soc Lond B 269:1467–1473. doi:10.1098/rspb.2002.2033

Janik VM, Slater PJB (1997) Vocal learning in mammals. Adv Study Behav 26:59–99

Jost L (2008) GST and its relatives do not measure differentiation. Mol Ecol 17(18):4015–4026. doi:10.1111/j.1365-294X.2008.03887.x

Knaus B, Cronn R, Liston A, Pilgrim K, Schwartz M (2011) Mitochondrial genome sequences illuminate maternal lineages of conservation concern in a rare carnivore. BMC Ecology 11(1):10

Krützen M, Mann J, Heithaus MR, Connor RC, Bejder L, Sherwin WB (2005) Cultural transmission of tool use in bottlenose dolphins. PNAS 102(25):8939–8943. doi:10.1073/pnas.0500232102

Lachlan RF, Slater PJB (1999) The maintenance of vocal learning by gene-culture interaction: the cultural trap hypothesis. Proc Roy Soc Lond B 266:701–706. doi:10.1098/rspb.1999.0692

Laland KN (1992) A theoretical investigation of the role of social transmission in evolution. Ethol Sociobiol 13:87–113

Laland KN, Janik VM (2006) The animal cultures debate. Trends Ecol Evol 21:542–547. doi:10.1016/j.tree.2006.06.005

Langergraber KE, Boesch C, Inoue E, Inoue-Murayama M, Mitani JC, Nishida T, Pusey A, Reynolds V, Schubert G, Wrangham RW, Wroblewski E, Vigilant L (2010) Genetic and 'cultural' similarity in wild chimpanzees. Proc Roy Soc Lond B 278:408–416. doi:10.1098/rspb.2010.1112

Lougheed SC, Handford P, Baker AJ (1993) Mitochondrial DNA hyper diversity and vocal dialects in a subspecies transition of the rufous-collared sparrow. Condor 95:889–895

Lyrholm T, Gyllensten U (1998) Global matrilineal population structure in sperm whales as indicated by mitochondrial DNA sequences. Proc Roy Soc Lond B 265:1679–1684. doi:10.1098/rspb.1998.0488

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 Roy Soc Lond B 266:347–354. doi:10.1098/rspb.1999.0644

MacDougall-Shackleton EA, MacDougall-Shackleton SA (2001) Cultural and genetic evolution in mountain white-crowned sparrows: song dialects are associated with population structure. Evolution 55(12):2568–2575. doi:10.1111/j.0014-3820.2001.tb00769.x

Marcoux M, Rendell L, Whitehead H (2007) Indications of fitness differences among vocal clans of sperm whales. Behav Ecol Sociobiol 61(7):1093–1098. doi:10.1007/s00265-006-0342-6

Mesnick SL (2001) Genetic relatedness in sperm whales: evidence and cultural implications. Behav Brain Sci 24(2):346–347

Mesnick SL, Taylor BL, Archer FI, Martien KK, Treviño SE, Hancock-Hanser BL, Medina SCM, Pease VL, Robertson KM, Straley JM, Baird RW, Calambokidis J, Schorr GS, Wade P, Burkanov V, Lunsford CR, Rendell L, Morin PA (2011) Sperm whale population structure in the eastern and central north pacific inferred by the use of single nucleotide polymorphisms (SNPs), microsatellites and mitochondrial DNA. Mol Ecol Res 11:278–298. doi:10.1111/j.1755-0998.2010.02973.x

Morin PA, Archer FI, Foote AD, Vilstrup J, Allen EE, Wade P, Durban J, Parsons K, Pitman R, Li L, Bouffard P, Abel Nielsen SC, Rasmussen M, Willerslev E, Gilbert MTP, Harkins T (2010) Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. Genome Res 20(7):908–916. doi:10.1101/gr.102954.109

Moritz C (1994) Defining 'evolutionarily significant units' for conservation. Trends Ecol Evol 9:373–375

Palsbøll PJ, Clapham PJ, Matilla DK, Larsen F, Sears R, Siegismund HR, Sigurjønsson J, Vasquez O, Arctander P (1995) Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behaviour on population structure. Mar Ecol Prog Ser 116:1–10

Posada D (2009) Selection of models of DNA evolution with JModelTest. In: Posada D (ed) Bioinformatic analysis of DNA sequences. Humana Press, New York, pp 93–112

Raufaste N, Rousset F (2001) Are partial mantel tests adequate. Evolution 55(8):1703–1705. doi:10.1111/j.0014-3820.2001.tb00689.x

Rendell LE, Whitehead H (2001) Culture in whales and dolphins. Behav Brain Sci 24(2):309–382

Rendell LE, Whitehead H (2003a) Vocal clans in sperm whales (*Physeter macrocephalus*). Proc Roy Soc Lond B 270:225–231. doi:10.1098/rspb.2002.2239

Rendell LE, Whitehead H (2003b) Comparing repertoires of sperm whales: a multiple methods approach. Bioacoustics 14(1):61–81

Rendell L, Whitehead H, Coakes A (2005) Do breeding male sperm whales show preferences among vocal clans of females? Mar Mammal Sci 21(2):317–322. doi:10.1111/j.1748-7692.2005.tb01231.x

Ryan SJ (2006) Diversity: the role of culture in conservation planning for small or endangered populations. Conserv Biol 20(4): 1321–1324. doi:10.1111/j.1523-1739.2006.00347.x

Schneider S, Roessli D, Excoffier L (1999) Estimation of past demographic parameters from the distribution of pair-wise differences when the mutation rates vary among sites: application to human mitochondrial DNA. Genetics 152:1079–1089

Slatkin M, Hudson RR (1991) Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. Genetics 129:555–562

Smouse PE, Long JC, Sokal RR (1986) Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Syst Zool 35:627–632

Soha JA, Nelson DA, Parker PP (2004) Genetic analysis of song dialect populations in Puget Sound white-crowned sparrows. Behav Ecol 15(4):636–646. doi:10.1093/beheco/arh055

Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol Biol Evol 10(3):512–526

Tiedemann R, Milinkovitch MC (1999) Culture and genetic evolution in whales. Science 284:2055a

Watkins WA, Schevill WE (1977) Sperm whale codas. J Acoust 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 (1998) Cultural selection and genetic diversity in matrilineal whales. Science 282:1708–1711. doi:10.1126/science.282.5394.1708

Whitehead H (2003) Sperm whales: social evolution in the ocean. University of Chicago Press, Chicago

Whitehead H (2005) Genetic diversity in the matrilineal whales: models of cultural hitchhiking and group-specific non-heritable demographic variation. Mar Mammal Sci 21:58–79. doi:10.1111/j.1748-7692.2005.tb01208.x

Whitehead H, Rendell L (2004) Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. J Anim Ecol 73(1):190–196. doi:10.1111/j.1365-2656.2004.00798.x

Whitehead H, Gordon J, Mathews EA, Richard KR (1990) Obtaining skin samples from living sperm whales. Mar Mammal Sci 6: 316–326

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. doi:10.1046/j.1365-2656.1998.00187.x

Whitehead H, Rendell L, Osborne RW, Würsig B (2004) Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. Biol Conserv 120:427–437. doi:10.1016/j.biocon.2004.03.017

Wright TF, Wilkinson GS (2001) Population genetic structure and vocal dialects in an amazon parrot. Proc Roy Soc Lond B 268:609–616. doi:10.1098/rspb.2000.1403

Yurk H, Barrett-Lennard L, Ford JKB, Matkin CO (2002) Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. Anim Behav 63:1103–1119. doi:10.1006/anbe.2002.3012