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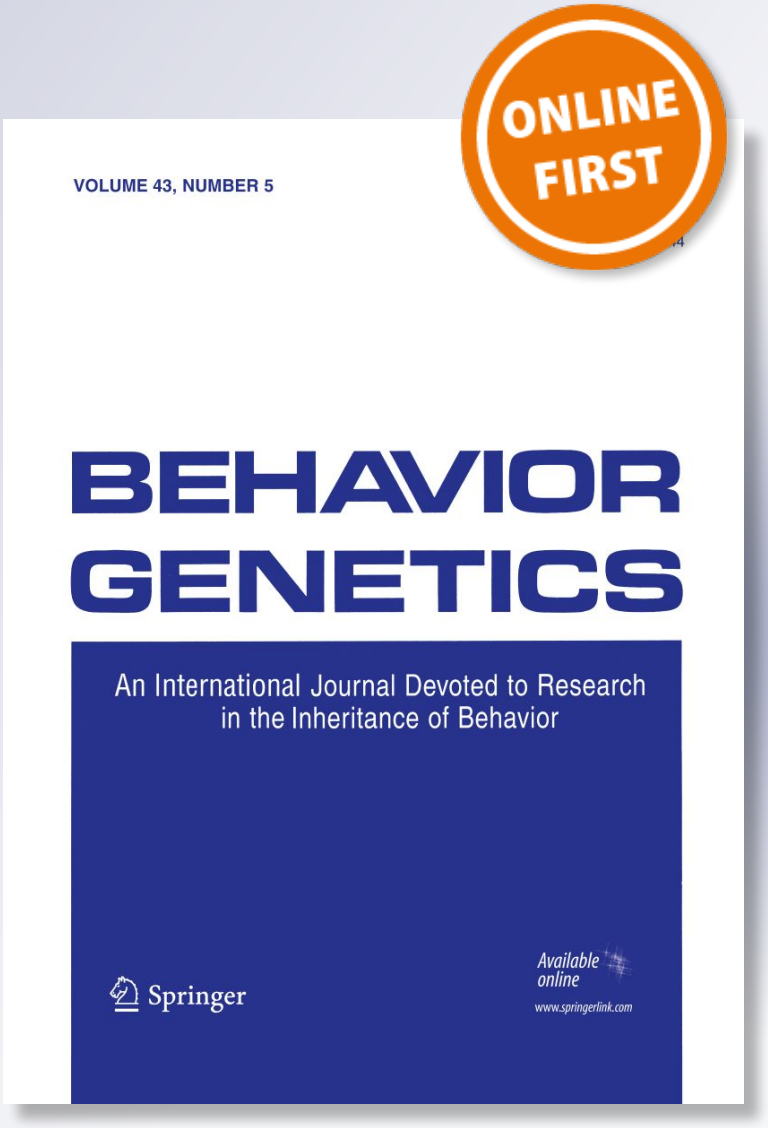

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ORIGINAL RESEARCH

Cultural Hitchhiking in the Matrilineal Whales

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Abstract Five species of whale with matrilineal social systems (daughters remain with mothers) have remarkably low levels of mitochondrial DNA diversity. Non-heritable matriline-level demography could reduce genetic diversity but the required conditions are not consistent with the natural histories of the matrilineal whales. The diversity of nuclear microsatellites is little reduced in the matrilineal whales arguing against bottlenecks. Selective sweeps of the mitochondrial genome are feasible causes but it is not clear why these only occurred in the matrilineal species. Cultural hitchhiking (cultural selection reducing diversity at neutral genetic loci transmitted in parallel to the culture) is supported in sperm whales which possess suitable matrilineal socio-cultural groups (coda clans). Killer whales are delineated into ecotypes which likely originated culturally. Culture, bottlenecks and selection, as well as their interactions, operating between- or within-ecotypes, may have reduced their mitochondrial diversity. The societies, cultures and genetics of false killer and two pilot whale species are insufficiently known to assess drivers of low mitochondrial diversity.

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Introduction

Cultural hitchhiking is a form of gene-culture coevolution in which diversity at a neutral genetic locus is reduced due to selection on culturally-inherited traits that are being transmitted in parallel with the genes (Premo 2012; Whitehead 1998). It was first proposed as an explanation for low diversities in the control regions of the mitochondrial genomes of four whale species which are matrilineal in the sense that most females remain grouped with their mothers and other close female relatives through their lives (Whitehead 1998). In essence, the relative frequency of the mitochondrial haplotypes characteristic of matrilineal groups of whales displaying more highly adaptive socially-learned traits would increase, while the relative frequency of haplotypes in matrilineal groups of whales with less adaptive socially-learned traits would decrease, leading to an overall reduction in haplotype diversity at the level of the metapopulation. Cultural hitchhiking has since been proposed as a cause for reduced genetic diversity in *Homo sapiens*—in this case low diversity of the Y-chromosome in patrilineal systems (Whitehead et al. 2002). In a related proposal, Premo and Hublin (2009) show that selection can reduce diversity at linked neutral loci in a population in which migration between relatively small groups is mediated by cultural similarity. In this scenario, unlike the original cultural hitchhiking models, cultural traits that regulate dispersal may be otherwise selectively neutral and some affected genes may have selective value. Cultural hitchhiking has also been invoked in a somewhat different form to describe the formation of small-scale population genetic structure in

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bottlenose dolphins (*Tursiops* spp.) due to culturally-transmitted foraging techniques (Kopps et al. 2014).

While computer models have shown that cultural hitchhiking has the potential to reduce the diversity of genes being transmitted in parallel with selectively important cultural traits (Whitehead 1998, 2005), the hypothesis that this actually happened in the matrilineal whales has been controversial (Amos 1999; Mesnick et al. 1999; Schlötterer 1999; Tiedemann and Milinkovitch 1999). When originally proposed in the late 1990s, there were concerns about the quality and taxonomic level of the genetic data, and as to whether cultural transmission processes and social structure in the matrilineal whales were sufficiently stable to drive cultural hitchhiking (Deecke et al. 2000; Mesnick et al. 1999; Tiedemann and Milinkovitch 1999). But, primarily, critics proposed alternative hypotheses to explain reduced mitochondrial genetic diversity in the matrilineal whales. These can be classified into three general processes:

1. Bottlenecks in the historical population trajectories of the species which reduced genetic diversity (Alexander et al. 2013; Hoelzel et al. 2002; Lyrholm et al. 1996).
2. Selection within the mitochondrial genome, and especially within the control region, thus reducing genetic diversity (Janik 2001; Mesnick et al. 1999).
3. Demography operating primarily at the level of the matrilineal group, thus reducing the effective population size, and hence the expected genetic diversity (Amos 1999; Siemann 1994; Tiedemann and Milinkovitch 1999).

While the bottleneck and selection hypotheses do not result in an expected link between low mitochondrial diversity and matrilineal social systems specifically, they are feasible processes for reducing genetic diversity in general. The third explanation is intrinsically more attractive as it links the observed matrilineal social structure of the species with low mitochondrial diversity to the hypothesized process. Exploration of the group demography hypothesis using agent-based models mapped the conditions under which stochastic non-heritable variation in group-specific reproduction or mortality could reduce genetic diversity (Whitehead 2005). These conditions, requiring either substantial group-specific variation in fitness or considerable whole-group mortality (with a consequently high species extinction rate), are too restrictive to be feasible in the case of the matrilineal whales. Thus, group-specific demography is not, by itself, a tenable explanation for the low mitochondrial diversity of the matrilineal whales, unless the demographic distinctions among groups are heritable. Matrilineally-inherited fitness differences could occur through genetic mechanisms such as mitochondrial disease (Schapira 2006), but the resulting largely negative selection would have little impact on genetic diversity. Positive matrilineal group selection is most easily achieved culturally, and this is the cultural hitchhiking scenario.

Similar models explored the conditions for cultural hitchhiking (Whitehead 2005). Genetic diversity is likely substantially reduced if: cultural groups tend to split when large, migration rate between groups is low (<~10 migrants/generation), culturally-determined fitness changes slowly within cultural groups (<~0.005%/generation), and the effects of cultural innovation within cultural groups are more significant (in their effects on fitness changes) than cultural assimilation among cultural groups. These conditions are at least feasible for the matrilineal whales (Whitehead 2005). However, as noted above, selection in the mitochondrial genome and population bottlenecks are also feasible explanations, although neither explains the link with matrilineality.

The hypothesis that selection leads to the low control region diversity was initially investigated using Tajima's D (Whitehead 1998), but this was neither a powerful test nor appropriate (Schlötterer 1999). However for one of the matrilineal species, the sperm whale (*Physeter macrocephalus*), analysis of selection on mitochondrial DNA was more definitive: nucleotide diversity was low throughout the mitochondrial genome, arguing against selection specifically within the control region (Alexander et al. 2013). However, a selective sweep on other parts of the mitochondrial genome, reducing control region diversity through genetic hitchhiking, is not ruled out (Alexander et al. 2013). In a genomic study of the mitochondrial DNA of killer whales (*Orcinus orca*), selection on the control region was not specifically tested, but no evidence for such selection is mentioned (Foote et al. 2011). A selective sweep originating elsewhere in the mitochondrial genome is a possibility and a comparison of estimates of substitution rates at different codon positions does suggest selection within the killer whale mitochondrial genome (Morin et al. 2015). There is, to our knowledge, no useful information on the presence of selection within the control region for the other matrilineal whale species.

Since the late 1990s when the concept of cultural hitchhiking was first introduced and discussed, our knowledge of the extent and importance of culture in the lives of two matrilineal whale species (the killer whale and the sperm whale) have increased considerably (Whitehead and Rendell 2015). For instance, in sperm whales, we now have a good candidate for cultural groups with both distinctive cultures and mitochondrial haplotype distributions, coda clans (Rendell et al. 2012; Rendell and Whitehead 2003). There is also evidence that reproductive rates differ between coda clans (Marcoux et al. 2007), lending more support to the cultural hitchhiking hypothesis. Over the same time period many papers have been published on cetacean genetics

(Alexander et al. 2013; Bourret et al. 2008), and a growing number using cetacean genomics (Cammen et al. 2016).

Here we use these published results on cetacean genetic diversity to assess the hypothesis that cultural hitchhiking has reduced the mitochondrial genetic diversity of the matrilineal whales. We check that the pattern of reduced mitochondrial diversity in the matrilineal whales (relative to other cetaceans) still holds with much larger data sets. And we compare nuclear and mitochondrial genetic diversity among cetacean species. If animals mate between matrilineal cultural groups, then the cultural hitchhiking hypothesis predicts that the diversity of mitochondrial DNA, which is being transmitted in parallel with selective cultural traits, should be reduced compared with the diversity of nuclear DNA for which there is no parallel transmission of culturally-selective traits (Schlötterer 1999; Whitehead 2005). In these analyses, we incorporate numerically two issues that might affect measures of genetic diversity: within-species population structure (Mesnick et al. 1999) and ascertainment bias (Schlötterer 1999).

Methods

The primary phylogeny considered here is that of the cetacean species as listed by the Society for Marine Mammalogy (Committee on Taxonomy 2016). Omitted are riverine and partially-riverine genera (*Inia, Platanista, Lipotes, Neophocoena, Sotalia*). Subspecies designations of the Cetacea were not used as these have been in considerable flux over the time period during which the molecular studies were conducted (Committee on Taxonomy 2016). Samples attributed to "*Tursiops* spp." from Shark Bay, Australia, were allocated to *Tursiops aduncus* (as recent papers on the population refer to them as *T. cf. aduncus* (e.g., Connor and Krützen 2015)). All samples from ancient DNA were omitted. Studies were designated "O" (rangewide) if covering at least 25% of the species' range, or across the extent of at least one ocean basin, and otherwise "R" (regional). Estimates for sub-populations defined on the basis of the genetic results themselves were not used.

We considered the following species matrilineal, in the sense that females are generally closely grouped with their mothers while both are alive: the killer whale, the sperm whale, the short-finned pilot whale (*Globicephala macrorhynchus*), the long-finned pilot whale (*Globicephala melas*), and the false killer whale (*Pseudorca crassidens*). While the matrilineality of the first four species has been long established (Amos et al. 1991; Ford et al. 2000; Kasuya and Marsh 1984; Whitehead 2003), false killer whales are also thought to be matrilineal (Baird et al. 2008). Although there may be other matrilineal cetacean species, there is no evidence for matrilineality for any other species whose mitochondrial diversity is considered in this paper. All the matrilineal species are from the odontoceti (toothed whale) clade. Thus, in the presentation of our results we distinguish between the odontocetes and mysticetes (baleen whales). The two clades separated (~36mya) just before the last common ancestor of the matrilineal species (~35mya) (McGowen et al. 2009).

We present the estimates of genetic diversity in the context of latitudinal range and approximate current population size for each species. Latitudinal range is the number of degrees of latitude for which the species was identified as present in the charts of Reeves et al. (2002). Approximate current census population size is from information summarized in the IUCN Red List (IUCN 2016), and is used only when it could be ascertained within about a factor of five. We used latitudinal range as a potential predictor of genetic diversity as, in contrast to census population size, it is known quite precisely for most cetacean species, and should be a good indicator of the habitat diversity used by the species, which in turn may be a factor in genetic diversity.

Diversity of mitochondrial control region DNA

A preliminary list of nucleotide diversities (average percentage of nucleotide differences per site, π) of the control region of the mitochondrial genome for cetacean species came from Table 1 of Alexander et al. (2013). These were checked and augmented by searching the Web of Science™ for each species using a search term of the form "TS=(mitochondrial OR mtDNA) AND TS=([common name] OR [Latin name])". We listed each estimate of mitochondrial nucleotide diversity from sequencing as well as the sample size, number of base pairs examined and number of haplotypes, for those estimates in which the sample size was at least 100 individuals. We excluded papers where only estimates from the least diverse regions were presented (Bérubé et al. (1998) for fin whale, *Balaenoptera physalus*), and where the estimate appears to be in error (overall estimate for dusky dolphins, *Lagenorhynchus obscurus*, off Argentina from de Castro et al. (2016), which is described as more diverse than regional estimates, but is listed as less diverse). For each species, we averaged nucleotide diversities from all eligible "O" (rangewide) and "R" (regional) data sets. Individual samples may have been included in more than one estimate.

Diversity of microsatellites

We used microsatellites to measure nuclear DNA diversity. There are challenges when comparing microsatellite diversity across species. Most importantly, there may be a positive ascertainment bias in diversity towards the species in which

Table 1 Cetacean species with latitude ranges, approximate population sizes and estimates of mitochondrial D-loop nucleotide diversity (π), and nuclear genetic (nd) diversities using microsatellites (with estimated standard errors), for both rangewide (O) and regional (R) estimates

Species	Latitude range (°)	Approx. population	π(O)	π(R)	nd(O)	SE(nd(O))	nd(R)	SE(nd(R))
Balaena mysticetus†	30	20,000	0.70	0.40			0.310	0.165
Balaenoptera acutorostrata†	82	500,000	0.76	1.00	−0.166	0.143	0.229	0.106
Balaenoptera bonaerensis†	92	760,000	1.50				1.095	0.158
Balaenoptera borealis†	139	20,000			−0.259	0.210	0.157	0.110
Balaenoptera edeni†	94		1.20	1.20				
Balaenoptera musculus†	166	17,000	1.40	1.51	0.003	0.161	0.328	0.122
Balaenoptera physalus†	166	50,000	1.13		0.202	0.146	0.484	0.114
Cephalorhynchus commersonii	28	100,000	0.40					
Cephalorhynchus eutropia	30	1000			−0.739	0.163		
Cephalorhynchus hectori	10	7400	0.74	0.44	−0.418	0.215	−0.503	0.105
Delphinapterus leucas	39	250,000	0.76	0.41	−0.082	0.224	0.174	0.131
Delphinus delphis	114	4,000,000		1.65	0.523	0.208	0.434	0.096
Eschrichtius robustus†	52	18,000	1.67		−0.186	0.242		
Eubalaena australis†	46	10,000	2.71	1.50	−0.186	0.196	0.411	0.120
Eubalaena glacialis†	48	325	0.60					
*Globicephala macrorhynchus**	100	700,000	0.84				0.169	0.123
*Globicephala melas**	97	1,000,000	0.26	0.32	−0.357	0.231	0.000	0.094
Grampus griseus	119	350,000					0.375	0.114
Hyperoodon ampullatus	42	40,000	0.14	0.15	−0.334	0.227	−0.167	0.121
Kogia breviceps	106		2.52					
Lagenorhynchus acutus	42	200,000	0.89	0.92	0.222	0.230	0.288	0.147
Lagenorhynchus albirostris	39	150,000	0.56				−0.014	0.134
Lagenorhynchus obliquidens	42	1,200,000			0.013	0.240		
Lagenorhynchus obscurus	53		1.63	1.55				
Megaptera novaeangliae†	170	80,000	2.90	2.08	0.000	0.130	0.325	0.102
Mesoplodon bidens	50				0.006	0.262		
Orcaella heinsohni		8000					−0.349	0.138
*Orcinus orca**	167	70,000	0.50	0.24	−0.126	0.168		
Phocoena phocoena	61	800,000	1.40	0.94	−0.156	0.226	0.661	0.109
Phocoenoides dalli	34	1,300,000	1.30					
*Physeter macrocephalus**	155	360,000	0.38	0.30	−0.265	0.166	0.293	0.105
Pontoporia blainvillei	23	100,000		0.90				
*Pseudorca crassidens**	112	80,000	0.37	0.21			0.247	0.109
Sousa chinensis	72						−0.225	0.131
Stenella attenuata	82	4,000,000		1.05	0.693	0.261	0.671	0.174
Stenella coeruleoalba	113	2,500,000			0.322	0.173	0.727	0.099
Stenella frontalis	81		1.47	1.40			0.244	0.109
Stenella longirostris	80	2,000,000		1.48			0.623	0.124
Steno bredanensis	89	150,000	1.90				0.119	0.147
Tursiops aduncus	80	20,000		2.21			0.074	0.106
Tursiops australis							−0.069	0.123
Tursiops truncatus	120	600,000		1.52	0.183	0.203	0.059	0.092

* Presumed matrilineal species

† mysticete species

the microsatellite was discovered, and different microsatellites may have large differences in allele numbers (Schlötterer 1999). However, microsatellites are the most widely used nuclear genetic marker among cetacean species, and there is a somewhat unusual tendency for the same microsatellites to be employed for multiple cetacean species (Bourret et al. 2008). We use statistical methods to account for sample size differences among studies, ascertainment bias and differences in allelic richness among microsatellite loci.

A list of microsatellites used in the analysis of cetacean genetics up until 2007 is given in Tables A, B, C and D of the supplementary material of Bourret et al. (2008). These data were compiled into an Excel worksheet and then reviewed. In order to add cetacean microsatellite diversity data from 2008 to 2015, we searched the Web of Science™ using the search terms "TS=(microsatellite*) AND TS=(whale* OR dolphin* OR porpoise* or cetacean*)". Of the 249 papers resulting from the search, 83 presented species-specific number of alleles encountered at specific microsatellite loci.

Thus for each entry in our table, i, we noted the species, $s(i)$, the microsatellite, $m(i)$, the sample size, n(i) (number of animals), the number of different alleles found, $a(i)$, and whether the microsatellite was ascertained on that species or not, $b(i)$ (1 or 0, respectively). For each of the "O" and "R" datasets, we restricted the data to microsatellites used for at least 5 species, species with estimates on at least 4 microsatellites, studies with a minimum sample size of 5 individuals, and at least two alleles found for the microsatellite in question (although the results are robust to variation in these criteria; Figs S2-3). Under these criteria, 31 microsatellite loci were used for the "O" estimates, and 119 for the "R" estimates. We would expect the number of alleles found to increase with sample size. Preliminary investigations (e.g., Fig. S1) suggested that a simple asymptotic curve represented this well. We estimated the functional parameter μ by fitting the following model:

$$\frac{a(i)}{mean\{a(j)(m(j)=m(i))\&(n(j)>20)\}}=\frac{n(i)\cdot\mu}{1+n(i)\cdot\mu} \quad (1)$$

The denominator on the left is the mean number of alleles for all analyses using the microsatellite in question in which the sample size was more than 20 animals. This fitting gave μ = 0.2447 (SE=0.0600) for the "O" samples and μ = 0.1975 (SE=0.0166) for the "R" samples, suggesting sample sizes of about 5 animals (1/μ) give about half as many alleles as very large samples. Corrected numbers of alleles were then calculated for each estimate:

$$a'(i)=\frac{a(i)\cdot(1+n(i)\cdot\mu)}{n(i)\cdot\mu}$$

These corrected allele numbers were then used to produce estimates of microsatellite genetic diversity for each species using the species effect sizes from a linear mixed-effects model, including a term for ascertainment bias:

$$\log\left(a'(i)\right)\sim m(i)+s(i)+b(i)$$

In this model, microsatellite (m) is a random effect, species (s) a fixed effect, and ascertainment (b) a fixed effect. We logged the corrected number of alleles as this gave more normally distributed residuals (for "O" data: skewness 0.871 for linear data vs. −0.136 for log data, kurtosis 5.820 for linear data vs. 3.206 for log data; for "R" data: skewness 0.756 for linear data vs. −0.298 for log data, kurtosis 5.851 for linear data vs. 3.477 for log data). Ascertainment bias was positive (for "O" data: +0.193 log(alleles), P=0.104, i.e. 21.3% more alleles; for "R" data: +0.150 log(alleles), P=0.000, i.e. 16.2% more alleles).

The species effect, s, indicates proportionally how many more, or less, corrected alleles the species tends to have compared to other cetacean species at the same microsatellite locus. Estimates of s were then used as measures of nuclear diversity for the different species. s is high if a species has generally more alleles at a microsatellite locus than a general cetacean species, and is low if the species generally shows few alleles (after correcting for sample size, ascertainment, and the general diversity at each locus).

Results

The control-region mitochondrial and microsatellite diversities of the cetacean species are given in Table 1, together with their latitudinal ranges and approximate population sizes.

Diversity of mitochondrial DNA in matrilineal cetaceans

General linear models in which we predicted mitochondrial nucleotide diversity using latitudinal range, the log of the approximate population size, and matrilineality, indicated that population size had little correlation with mitochondrial diversity (Table 2), but that both latitudinal range, likely in its role as a correlate of habitat diversity, and matrilineality are important predictors. The reduced nucleotide diversity of the matrilineal species is very clearly shown for both the rangewide and regional data sets when plotted against latitudinal range, and this is clear whether the mysticetes are included or not (Fig. 1). The general linear model (Table 2) indicates that matrilineal species have rangewide mtDNA diversities approximately 29.8% of that of non-matrilineal species with similar latitudinal ranges, and that for regional estimates the ratio is 16.6%.

The diversity estimates used to produce these figures are almost all from analyses completed since the original paper

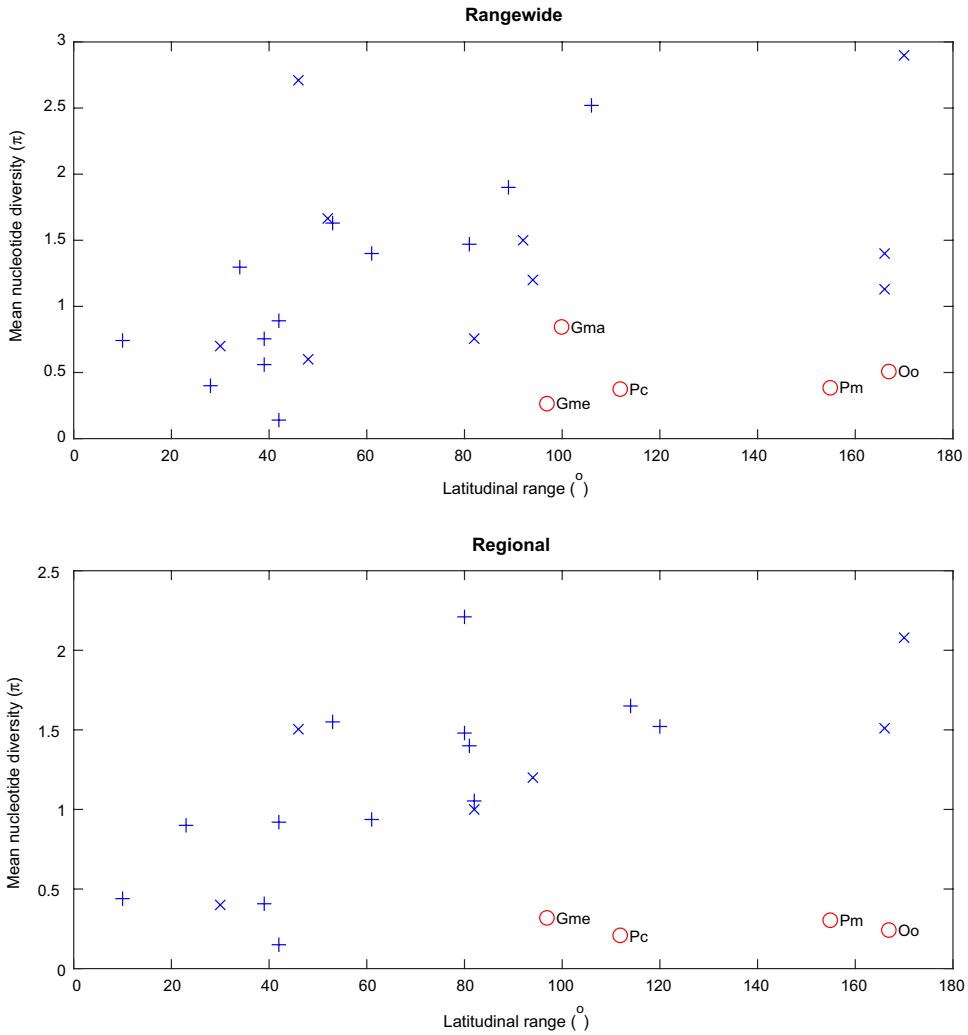

Fig. 1 Mean (across estimates for a species with $n \geq 100$) nucleotide diversity against latitudinal range of cetacean species, for rangewide estimates (*above*) and regional estimates (*below*). Non-matrilineal odontocete species are indicated by '+', mysticete species by'x', and matrilineal (all odontocete) species by 'o': 'Oo' killer whale; 'Pm' sperm whale; 'Gma' short-finned pilot whale; 'Gme' long-finned pilot whale; 'Pc' false killer whale

Table 2 Coefficients (and P values from partial F-tests) of general linear models predicting the log of the nucleotide diversity of the control region of the mitochondrial DNA using approximate population size, latitudinal range and matrilineality

Predictor	"O" (rangewide) data set	"R" (regional) data set
Population size (log)	0.040 (P = 0.587)	0.055 (P = 0.419)
Latitudinal range	0.0062 (P = 0.049)	0.008 (P = 0.010)
Matrilineality	−1.211 (P = 0.005)	−1.792 (P = 0.000)

that proposed cultural hitchhiking (Whitehead 1998); only 6 of the estimates used in the original paper had samples sizes ≥ 100 that would make them eligible for the analyses here, whereas the plots in Fig. 1 use 52 rangewide and 77 regional diversity estimates from studies with sample sizes ≥ 100. Given their latitudinal ranges, the only potential overlap between the diversity estimates for matrilineal and non-matrilineal cetaceans is in the rangewide diversity of the short-finned pilot whale of 0.84%. This is largely dependent on a relatively high diversity off southern Japan, from where 9 haplotypes were identified from 82 individuals, with 3 or fewer haplotypes being the rule for this species from all other locations (Oremus et al. 2009; Téllez et al. 2014).

Mitochondrial and nuclear diversity

If there is mating between matrilineal cultural groups, then cultural hitchhiking can reduce mitochondrial DNA diversity but should leave nuclear diversity unaffected (Alexander et al. 2013; Schlötterer 1999; Whitehead 2005). In Fig. 2 we plot nuclear diversity (inferred from microsatellite studies) against approximate population size and latitudinal range for cetacean species. For the regional data set, there is no sign that microsatellite diversity is lower than expected given population size in the matrilineal whales. In the rangewide data set, it is perhaps slightly lower than

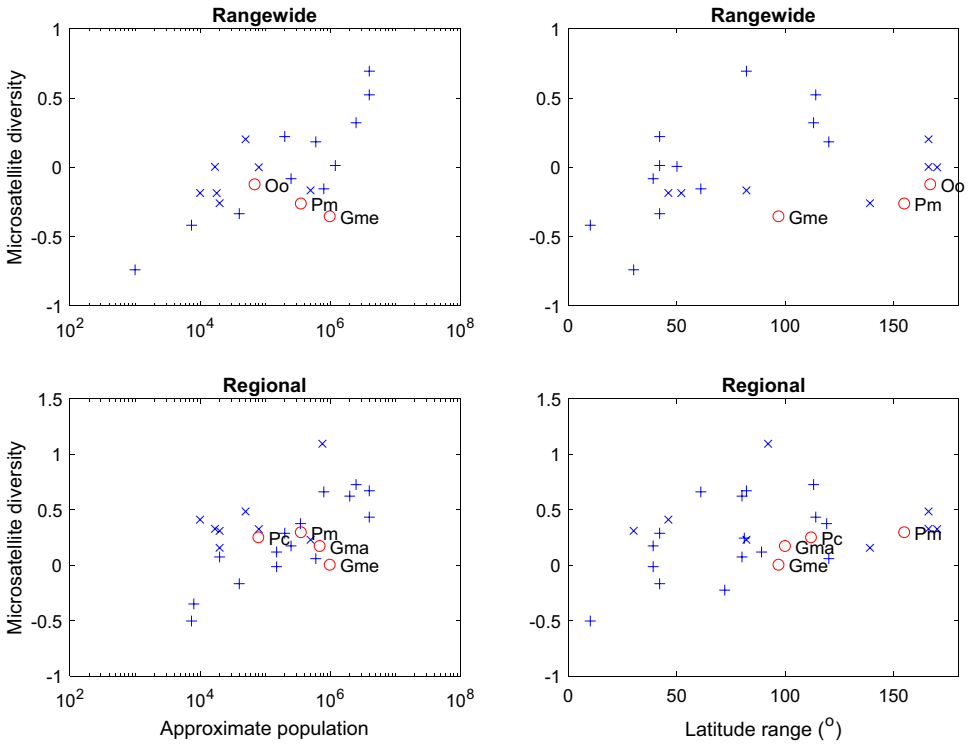

Fig. 2 Estimated nuclear diversity from microsatellites diversity against latitudinal range and approximate census population size of cetacean species, for rangewide estimates (above) and regional estimates (below). Non-matrilineal odontocete species are indicated by '+', mysticete species by'x', and matrilineal (all odontocete) species by 'o': 'Oo' killer whale; 'Pm' sperm whale; 'Gma' short-finned pilot whale; 'Gme' long-finned pilot whale; 'Pc' false killer whale

expected given population size, but nowhere near the reduction found for mitochondrial DNA (Fig. 1). These patterns hold whether the mysticete species are excluded or not.

Discussion

Our summary of recent genetic data shows the remarkably low mitochondrial DNA diversity of the matrilineal cetaceans given their latitudinal ranges, an indicator of habitat diversity, (Fig. 1). What is the status of cultural hitchhiking as an explanation for these low mitochondrial diversities in the different species of matrilineal cetacean?

Sperm whale

The sperm whale, despite its very wide range (almost all the deeper waters of the world's oceans that are not covered by ice) and a reasonably large population size [~360,000 today vs. ~1,100,000 before whaling (Whitehead 2002)], has one of the lowest mtDNA diversities of any species of Cetacea (Fig. 1, Alexander et al. 2013). Females within matrilineal units do not, to any extent, reproduce or die together, essentially ruling out non-heritable demographics of matrilines as a driver of low mtDNA diversity (Whitehead 2005). While selection within the sperm whale's control region is not supported (Alexander et al. 2013), a selective sweep elsewhere in the mitochondrial genome is still a possible driver of low diversity. Alexander et al. (2013) discuss the possibility that deep diving, a characteristic of the sperm whale, might impose particular selective pressures on the mitochondrial genome. However Cuvier's beaked whale (*Ziphius cavirostris*), the deepest known diver among cetaceans (Schorr et al. 2014), has mtDNA diversity ($\pi = 1.27\%$[1]) over three times larger than that of the sperm whale (Dalebout et al. 2005).

For sperm whales, the most feasible cultural groups, and the targets of selection in the cultural hitchhiking hypothesis, are coda clans (Rendell and Whitehead 2003). These have distinct mtDNA haplotype distributions, indicating little female dispersion, can be sympatric, contain hundreds to tens of thousands of members, and show consistent differences in behavior (Cantor and Whitehead 2015; Gero et al. 2016; Rendell et al. 2012; Rendell and Whitehead 2003; Whitehead and Rendell 2004). They also differ in indicators of reproductive success (Marcoux et al. 2007).

There is little differentiation in sperm whale nuclear genes at almost any geographical scale (Alexander et al. 2016), and a preliminary analysis suggests virtually no nuclear DNA differentiation between coda clans (Whitehead 2003). Thus it seems that male sperm whales often mate outside their natal clan. In this situation, nuclear DNA would be reduced if there had been a population bottleneck,

[1] This estimate is not included in Table 1, as $n = 87$, below the $n \geq 100$ threshold for Table 1.

but not if the species' low mtDNA diversity resulted from cultural hitchhiking or a selective sweep. That sperm whales do not show clearly reduced nuclear DNA diversity in microsatellites relative to population size (Table 1; Fig. 2) argues against a population bottleneck.

In summary, current evidence supports cultural hitchhiking as the most plausible cause of low diversity in the mtDNA of sperm whales.

Killer whale

The killer whale has a very wide distribution—the widest of all mammals outside modern humans—and very low mtDNA diversity (Table 1, Moura et al. 2014). Nuclear diversity is about what might be expected given their population size (Fig. 2) and killer whale life history characteristics are not consistent with the conditions under which purely demographic models of matrilineal populations can reduce diversity (Whitehead 2005). In these respects the killer whale is similar to the sperm whale.

However, when we consider population structure, the contrasts between the species are profound. Killer whale populations are structured into ecotypes, which differ considerably in behavior and diet, and more subtly in morphology and genetics (Foote et al. 2016; Riesch et al. 2012). There have been suggestions that the killer whale ecotypes are separate species (Morin et al. 2010). However this proposal has not been implemented. Mature male sperm whales have distributions and social relationships that are distinct from those of females, forsaking their natal habitat and natal coda clan at maturity, which leads to widespread diffusion of nuclear genes (Whitehead 2003). In contrast, male killer whales remain, and mate, within the same ecotypes as their female relatives (Morin et al. 2015). Ecotypes are believed to have formed as matrilineal groups developed culturally-transmitted foraging specializations, with the ecotypes subsequently delimiting mating opportunities (Riesch et al. 2012).

The division of the world's killer whale population into ecotypes sets up a number of potential mechanisms that might reduce genetic diversity. Ecotypes themselves, particularly the more specialized ones, are vulnerable to extirpation, due to small population sizes and reliance on a narrow range of resources that may crash for extrinsic reasons or be overexploited by the killer whales themselves (Whitehead and Rendell 2015). Thus, mechanisms that reduce genetic diversity within ecotypes may, in the long term, reduce overall species diversity. Processes acting either among or within ecotypes that could reduce genetic diversity in killer whales, include:

1. Fundamentally, a subdivided population tends to have lower diversity than a panmictic population of the same size (Whitlock and Barton 1997). But in the killer whale case this subdivision is due to a culturally-mediated aversion to mating between ecotypes, rather than geographical or ecological barriers. Thus the situation has much in common with the models of Premo and Hublin (2009) in which culturally-mediated dispersal patterns among humans sets up conditions in which selection reduces genetic diversity. Whitlock and Barton (1997) show that if there is frequent local extirpation of subpopulations, effective population size, and so genetic diversity, can be greatly reduced. As noted above, the specialized life styles of the killer whale ecotypes may make them particularly vulnerable to extirpation, promoting this path to reduced genetic diversity.
2. Cultural hitchhiking of ecotypes. In this scenario the ecotypes are subjected to selection based on their culturally-transmitted typical behavior, as hypothesized for sperm whale coda clans, and proposed by the original models of cultural hitchhiking (Whitehead 1998, 2005). However, one part of the cultural hitchhiking scenario, competition between cultural groups, is problematic if ecotypes are the cultural groups. While derivative specialized ecotypes might outcompete more generalized sympatric ecotypes, it is less easy to see how specialized ecotypes using very different resources could compete with one another. Baird et al. (1992) discuss indirect trophic effects of one ecotype on another (e.g., ecotype 1 eats seals, and the seals, together with ecotype 2, eat salmon), but these will rarely result in strong competition. Thus, this explanation for low diversity in killer whales seems incomplete.
3. Cultural hitchhiking within ecotypes. In this scenario, within-ecotype structures, such as the communities of the "resident" salmon-eating ecotype of the North Pacific, are the subject of cultural hitchhiking, reducing diversity within ecotypes. Communities of "resident" killer whales have similar overall foraging methods but important differences in other forms of behavior which are likely culturally-transmitted (Barrett-Lennard 2011; Ford et al. 2000; Whitehead and Rendell 2015), although we do not know whether these differences in behavior translate into fitness differentials. While communities are largely allopatric, there is some overlap that might provide a forum for competition.
4. Bottlenecks within ecotypes. The proposed origin of ecotypes, culturally-mediated specialization, as well as population genetic analyses, both indicate that population sizes of ecotypes soon after founding were likely small, setting up bottlenecks in each new ecotype (Foote et al. 2016).

5. Selection within ecotypes. There is evidence for selection of functional genes within ecotypes, based upon their differences in typical culturally-transmitted behavior, including genes related to diet and habitat use (Foote et al. 2016). This evidence for gene-culture coevolution relates to nuclear genes but there are indications that mitochondrial genes may also have differential selection coefficients in different ecotypes (Foote et al. 2011). This scenario mirrors a suggestion of Premo and Hublin (2009) for the reduction of gene diversity through selection of functional genes in human populations that are structured by culturally-mediated dispersal.

As mating almost always occurs within ecotypes (Foote et al. 2016), most of these processes would be expected to reduce nuclear as well as mitochondrial genetic diversity. Possible exceptions are process 3, cultural hitchhiking within ecotypes, if mating sometimes occurs between the cultural groups, and process 5, if there is selection on the mitochondrial genome. Additionally, due to the quadrupling of effective population size, and high mutation rate of microsatellites, bottlenecks and cultural hitchhiking would have less impact on nuclear diversity than mitochondrial diversity. These factors, together with a small amount of male-mediated gene flow between ecotypes (Hoelzel et al. 2007), may explain our finding that, at least for microsatellites, killer whale nuclear diversity is not much less than expected for a cetacean species of its population size (Fig. 2).

In summary, the genetics of global killer whale populations are complex and highly structured by a culturally-mediated division into ecotypes. In this situation, a number of processes can reduce genetic diversity. These range from culture setting up the ecotypes in the first place and then more standard population-genetic processes such as bottlenecks taking over, to processes such as cultural hitchhiking and gene-culture coevolution within ecotypes, in which cultural differences in behavior are driving the reduction in genetic diversity more directly.

Pilot and false-killer whales

The two species of pilot whale as well as false killer whales have low mtDNA diversity (Fig. 1). However, we have much less information on the social structure, population structure, and genomics of these species. There is support for matrilineality in each of these species (Amos et al. 1993; Baird et al. 2008; Kasuya and Marsh 1984), but evidence for how this matrilineality operates is quite sparse and circumstantial. For long-finned pilot whales, there seem to be differences in social structure between locations (Amos et al. 1993; De Stephanis et al. 2008; Ottensmeyer and Whitehead 2003), and for short-finned pilot whales there are large differences in genetic diversity in different ocean areas (Oremus et al. 2009). While genetic data suggest a lack of male dispersal in long-finned pilot whales (Amos et al. 1993), and thus similarities with killer whales, other predictions based upon long-finned pilot whales having similar social structures to killer whales, or sperm whales, have not born out (e.g., Augusto et al. 2016). There is even less information for false killer whales. Thus in these species cultural hitchhiking, as well as the alternative explanations for low mtDNA diversity, remain conjecture. However, these species do constitute a substantial part of the dramatic pattern of reduced mitochondrial diversity in the cetacean species with matrilineal social systems.

Other species

Cultural hitchhiking requires a quite unusual combination of characteristics: kinship-based groups with stable differentiated cultures and little gene flow between them, but which nevertheless compete for resources in a manner such that success is culturally-dependent (Whitehead 2005). Cultural hitchhiking works most simply with sympatric groups, and requires a much larger cultural impact on fitness when groups only compete with territorial neighbors (Whitehead et al. 2002; Whitehead 2005). The fluidity of the ocean environment enhances group sympatry and thus the potential for cultural hitchhiking. Hence we suspect that the best candidates for cultural hitchhiking outside the five species considered in this paper are other cetaceans, perhaps especially among the lesser-known Globicephalinae (e.g., melon-headed whale, *Peponocephala electra*, and pygmy killer whale, *Feresa attenuata*) that are phylogenetically related to killer, false killer and pilot whales, and may have somewhat similar social systems. Humans have suitable groups with powerful cultures, but as these are predominantly patrilineal, cultural hitchhiking is primarily a candidate explanation for low Y-chromosome gene diversity (Whitehead et al. 2002).

Conclusion

The overall patterns of genetic diversity found in our study of cetaceans mirror those found across a much wider range of taxa: variation at nuclear markers tracks well with estimates of population size whereas estimates of mitochondrial diversity do not (e.g., Bazin et al. 2006). However, on top of this general pattern, we found that among the species with matrilineal social systems mitochondrial diversity was markedly lower than expectations. The two most plausible hypotheses for this reduced mitochondrial diversity, without a corresponding reduced variability of nuclear

DNA, are: (a) cultural hitchhiking, and (b) selective sweeps of the mitochondrial DNA. Differentiating between these hypotheses is difficult, because they result in the same expectations regarding relative patterns of mitochondrial and nuclear diversity. However, the cultural hitchhiking hypothesis is more parsimonious with the data, because this hypothesis specifically predicts that the matrilineal species should stand out as outliers in the analyses (as they do when plotted against latitudinal range), whereas the mitochondrial selective sweep hypothesis makes no such predictions regarding which species may show this pattern. Thus, these analyses suggest that cultural hitchhiking is a major factor influencing mitochondrial diversity in matrilineal species.

In summary, recent genetic studies emphasize a remarkable reduction in mtDNA diversity in the five cetacean species having known, or suspected, matrilineal social systems. These species do not have noticeably reduced nuclear diversity, as indicated by microsatellites. Cultural hitchhiking, in which selective cultural traits are transmitted in parallel (matrilineally) to genes, is a potential explanation for the reduced mitochondrial diversity in these matrilineal species. In sperm whales, a suitable candidate for the selected cultural groups has been identified—the coda clan—, and other data support cultural hitchhiking as the process behind low mtDNA diversity. Killer whales are segregated into distinct ecotypes, which likely originated culturally. This leads to a number of candidate processes operating among or within ecotypes, and including cultural hitchhiking, selection and bottlenecks that could have played a role in reducing genetic diversity. Much less is known of the other three presumed matrilineal species, and cultural hitchhiking is just one of several processes that might have had a role in their low mtDNA diversities. Further studies of the genetics and genomics of these species, as well as continued research into their social structures and cultures, will improve our ability to assess the role of cultural hitchhiking in structuring cetacean population genetics.

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Compliance with Ethical Standards

Conflict of interest Hal Whitehead, Felicia Vachon and Timothy R. Frasier declare that they have no conflict of interest.

Human and Animal Studies The study involved no direct research on humans or other animals.

Informed consent There was no research on humans in this study.

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