

# Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations

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The social organization of most mammals is characterized by female philopatry and male dispersal. Such sex-biased dispersal can cause the genetic structure of populations to differ between the maternally inherited mitochondrial DNA (mtDNA) and the bi-parental nuclear genome. Here we report on the global genetic structure of oceanic populations of the sperm whale, one of the most widely distributed mammalian species. Groups of females and juveniles are mainly found at low latitudes, while males reach polar waters, returning to tropical and subtropical waters to breed. In comparisons between oceans, we did not find significant heterogeneity in allele frequencies of microsatellite loci (exact test;  $p = 0.23$ ). Estimates of  $G_{ST} = 0.001$  and  $R_{ST} = 0.005$  also indicated negligible if any nuclear DNA differentiation. We have previously reported significant differentiation between oceans in mtDNA sequences. These contrasting patterns suggest that interoceanic movements have been more prevalent among males than among females, consistent with observations of females being the philopatric sex and having a more limited latitudinal distribution than males. Consequently, the typical mammalian dispersal pattern may have operated on a global scale in sperm whales.

**Keywords:** sperm whale; mtDNA; microsatellites; population structure; dispersal; social organization

## 1. INTRODUCTION

Social organization can be an important determinant of the genetic structure of populations and, hence, of the potential for genetic differentiation and evolution of local adaptations. Among mammals, the predominating social organization is female philopatry and male dispersal (Greenwood 1980). Such gender differences in dispersal can influence the genetic structure of populations, particularly when the haploid and maternally inherited mitochondrial DNA (mtDNA) is compared with the bi-parental nuclear genome (Avice 1994). For example, pronounced significant differentiation in mtDNA but not in nuclear markers has been found in populations of macaques (Melnick & Hoelzer 1992) and humpback whales in the North Pacific (Palumbi & Baker 1994). In both cases, it was suggested that the observed patterns of variation might be due to limited dispersal of females but extensive dispersal of males.

The sperm whale *Physeter macrocephalus* is the largest toothed whale. It is a truly cosmopolitan species, occurring in all oceans of the world (for a review see Rice (1989)). The distribution is not continuous, but concentrations are found, for example in the traditional 'whaling grounds' (Townsend 1935) and seem to be associated with oceanographic fronts, steep bottom topography and high productivity (Gaskin 1982; Jaquet & Whitehead 1996; Jaquet *et al.* 1996). Females appear to maintain long-term

social bonds (Best 1979; Whitehead *et al.* 1991), associating in apparently matrilineally related units (Richard *et al.* 1996a; Lyrholm & Gyllensten 1998) containing approximately 13 individuals, including immatures (Whitehead *et al.* 1991). The functions of these units may include alloparental care of calves (Best 1979; Gordon 1987; Arnbom & Whitehead 1989; Whitehead *et al.* 1991; Whitehead 1996). Larger groups are formed by temporary associations between family units, which last for only a matter of days (Whitehead *et al.* 1991). Males disperse from their natal group before puberty and join other males in 'bachelor schools' (Best 1979). Males in bachelor schools decrease in sociality and increase in migration range with age; adult males reach as far as polar waters and return to tropical waters to breed (Rice 1989). In contrast, females and immatures are restricted in their movements to lower latitudes and warmer waters (above around 15 °C) (Rice 1989).

In order to investigate whether the genetic structure of populations could provide information about the dispersal patterns of male and female sperm whales on a global scale, we analysed samples collected from North Atlantic, North Pacific and Southern hemisphere oceanic populations (figure 1) with respect to allelic variation at nuclear microsatellite loci and compared the results with those from an analysis of mtDNA control region sequences (Lyrholm & Gyllensten 1998). Given that female sperm whales appear limited in their distribution to lower latitudes, they may be less likely than males to move between oceans separated by continental landmasses.

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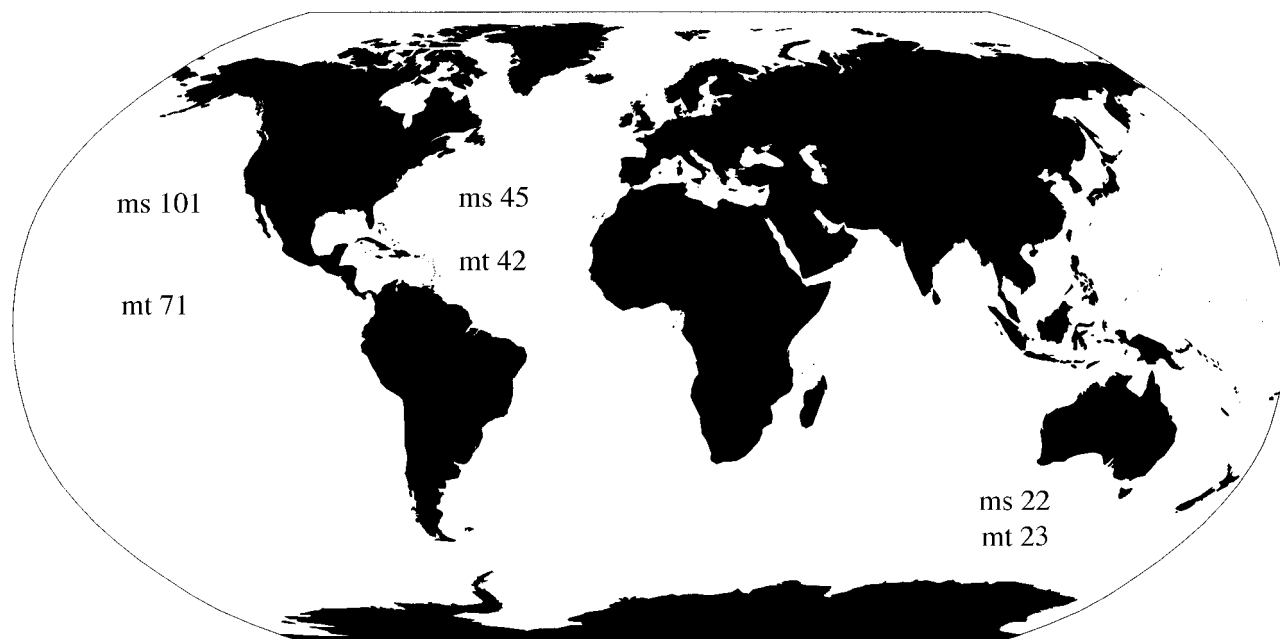


Figure 1. Number of whales represented in the interoceanic microsatellite (ms) and mitochondrial (mt) analyses.

If so, one would expect some differentiation in mtDNA between oceans, but perhaps less so in the nuclear genome.

Consistent with the hypothesis of limited female interoceanic dispersal, statistically significant differences in the frequencies of mtDNA control region sequence types were found between oceans (Lyrholm *et al.* 1996; Lyrholm & Gyllensten 1998). Here we report on the results of an analysis of nine polymorphic microsatellite loci, which may indicate whether both sexes tend to remain within oceans or whether male breeding dispersal has acted to reduce nuclear genetic differentiation on a global scale.

## 2. MATERIALS AND METHODS

### (a) *Samples*

The samples were collected using skin biopsy techniques (Lambertsen 1987), retrieval of sloughed skin (Amos *et al.* 1992) and from tissue archives. A total of 315 samples were analysed from the following areas (figure 1): North Atlantic ( $n=66$  from the Azores (29), Denmark (16), Norway (nine), Iceland (nine), Sweden (one), Florida (one) and Dominican Republic (one)), North Pacific ( $n=208$  from the Japanese coast (29), western North Pacific (35), central North Pacific (35), eastern North Pacific (60), Galápagos Islands (45) and Costa Rica (four)) and Southern hemisphere ( $n=41$  from south of Fiji (20), south-east Australia (14), southern Indian Ocean (three) and Antarctica (Indian Ocean sector) (four)).

Previous mtDNA analyses have indicated the presence of a genetic substructure from matrilineally related groups in the present material (Lyrholm & Gyllensten 1998) and initial analyses of the microsatellite data detected significant deviations from Hardy–Weinberg equilibrium in the North Pacific (exact test;  $p<0.0001$ ). Such a substructure can cause inflated statistical significance in geographical comparisons. Consequently, we used a subsample for these analyses, in which only one randomly chosen whale from each potential social

group was included, following the procedure of Lyrholm & Gyllensten (1998). This subsample consisted of 168 whales: 101 from the North Pacific (Japanese coast (21), western North Pacific (12), central North Pacific (21), eastern North Pacific (25), Galápagos Islands (21) and Costa Rica (1)), 45 from the North Atlantic (the Azores (eight) and the rest as in total material) and 22 from the Southern hemisphere (Fiji (nine), Australia (six), Indian Ocean (three) and Antarctica (four)) (figure 1).

### (b) *Laboratory procedures*

Samples were digested with proteinase K and DNA isolated using standard techniques (Sambrook *et al.* 1989).

Approximately 50 ng of genomic DNA was used in 10  $\mu$ l PCR reactions of microsatellite loci, with the following buffer conditions: 50 mM KCl, 10 mM Tris–HCl, pH 8.3, 1.5 mM MgCl<sub>2</sub>, 200  $\mu$ M of each dNTP, 0.02  $\mu$ M of each primer and 0.25 units of Taq or Taq Gold polymerases (Perkin-Elmer, Inc.). One of the primers was labelled with either of the ABI dyes HEX, 6 FAM or TET (Perkin-Elmer, Inc.).

The following microsatellite loci were analysed: EV1 and EV5 (Valsecchi & Amos, 1996), SW2, SW10, SW13, SW15 and SW19 (Richard *et al.* 1996b) and GATA28 and GATA53 (Palsbøll *et al.* 1997b). We have retained the published terminology, although it should be noted that the primers for the latter two loci were obtained from balaenopterid species and we have not confirmed the repeat structure in sperm whales.

PCR amplifications were performed on PE 9600 thermal cyclers (Perkin-Elmer, Inc.) as follows: pre-heating at 94 °C for 5 min, three cycles of 1 min 30 s at 94 °C, 30 s at the primer annealing temperature and 45 s at 72 °C, followed by 31–33 cycles of 45 s at 94 °C, 30 s at the annealing temperature and 15 s at 72 °C.

The annealing temperatures were 58 °C for the first three cycles and 55 °C for the remaining cycles (for EV1, EV5, SW10, SW15 and GATA28) or 55 °C for the first three cycles and 50 °C for the remaining cycles (for SW2, SW19 and GATA53).

Table 1. Gene diversities for the oceanic and North Pacific areas

(NA, North Atlantic; NP, North Pacific; SH, Southern hemisphere; G, Galápagos Islands; JC, Japanese coast; NPW, NPC and NPE, North Pacific western, central and eastern areas.)

locus	ocean			NP areas				
	NA	NP	SH	G	JC	NPW	NPC	NPE
EV1	0.57	0.60	0.47	0.58	0.71	0.71	0.48	0.52
EV5	0.71	0.74	0.71	0.77	0.73	0.76	0.69	0.73
GATA28	0.61	0.63	0.60	0.62	0.66	0.61	0.64	0.60
GATA53	0.81	0.80	0.82	0.75	0.82	0.82	0.79	0.77
SW2	0.57	0.49	0.67	0.44	0.46	0.47	0.45	0.58
SW10	0.86	0.86	0.85	0.87	0.84	0.87	0.90	0.82
SW13	0.83	0.84	0.85	0.85	0.85	0.83	0.82	0.83
SW15	0.70	0.64	0.65	0.57	0.63	0.75	0.66	0.58
SW19	0.88	0.91	0.91	0.86	0.88	0.92	0.91	0.91
mean	0.73	0.72	0.73	0.70	0.73	0.75	0.70	0.70

The samples were run on ABI 377 sequencing machines (Perkin-Elmer, Inc.) using scan rates of  $2400\text{ s}^{-1}$ . The ABI software Genescan Analysis and Genotyper (Perkin-Elmer, Inc.) were used to determine allele sizes. A custom software that graphically depicts allele frequency spectra was used to examine how the raw data should be categorized into allele size classes. In some cases, it was not possible to assign alleles precisely enough to a particular size, leading to the necessity to pool adjacent classes. This mainly affected the loci EV5 and GATA53. However, the statistical population analyses were performed both with and without these loci and the conclusions remained the same.

Where unknown, sex was determined using the technique of Bérubé & Palsbøll (1996).

### (c) Data analysis

Exact tests of homogeneity and of Hardy–Weinberg equilibrium were performed using version 3.1a of the software GENEPOP (Raymond & Rousset 1995). We estimated the amount of differentiation as  $G_{ST}$ , following Nei & Chesser (1983) and  $R_{ST}$  (Slatkin 1995). The latter measure, which is specific for microsatellites, assumes a stepwise mutation model of unit repeat changes (Slatkin 1995) and was only estimated for the three loci least likely to violate these assumptions (EV1, SW2 and SW13), using the software RST CALC (Goodman 1997).

## 3. RESULTS

### (a) Diversity

There was considerable allelic diversity at the sperm whale microsatellite loci, with between three and 21 alleles per locus. The least variable locus was GATA28, which was amplified with primers derived from balaenopterid whales (Palsbøll *et al.* 1997b) and only showed the same three alleles in all three oceans (Palsbøll *et al.* 1997b) reported between 11 and 17 alleles for this locus in balaenopterid whales). The gene diversity, estimated from the subsample restricted to presumably unrelated whales, ranged from 0.47 to 0.91 for the various loci in the three oceanic regions and from 0.44 to 0.92 within smaller subareas in the North Pacific (table 1).

### (b) Differentiation between oceans

The allele frequencies for each locus and ocean are given in table 2. Overall, we did not find significant heterogeneity in allele frequencies between the three oceans (table 4). Similarly,  $G_{ST}$  was estimated at 0.001 and  $R_{ST}$  at 0.005, which were not significantly different from zero (table 4). Since apparently complex mutational processes in some microsatellite loci can lead to inconsistencies in estimates of the amount of differentiation (Valsecchi *et al.* 1997), these measures should be interpreted cautiously. Nevertheless, both  $G_{ST}$  and  $R_{ST}$  indicated very low if any differentiation. In addition, alleles unique to an ocean ('private alleles') were rare.

### (c) Differentiation within the North Pacific

The allele frequencies for the sub-areas in the North Pacific are shown in table 3. Not surprisingly, given the lack of differentiation between oceans, we did not find significant heterogeneity in allele frequencies within this ocean (exact test;  $p = 0.392$ ). As in the between-ocean case, alleles unique to areas were rare. The sample material was insufficient to test for differentiation within the areas of the North Atlantic or Southern hemisphere.

### (d) Genetic structure of social groups

Since observational studies have indicated considerable stability in female–immature social group membership (Whitehead *et al.* 1991), we wanted to examine whether there was genetic heterogeneity within areas due to group structure. Based on temporal and spatial proximity of sampled whales (Lyrholm & Gyllensten 1998), we identified three potential groups in the Galápagos Islands ( $n = 4, 8$  and  $9$ ), ten in the northern North Pacific areas ( $n = 4, 4, 5, 6, 6, 7, 8, 8, 8$  and  $9$ ) and four in the Southern hemisphere ( $n = 5, 5, 4$  and  $7$ ). We only used females, since it was not possible to judge whether males shorter than *ca.* 12 m sampled at the same time as the female groups should be regarded as temporary visitors or actual members of the groups (those above this length would most likely be dispersers; Best 1979). In all cases, significant heterogeneity between groups was found within the areas (Galápagos Islands  $p = 0.01$ , North Pacific  $p = 0.007$  and Southern hemisphere  $p = 0.005$ ; all exact tests).

## 4. DISCUSSION

The lack of significant differentiation in between-ocean comparisons of microsatellite loci is in contrast to what was found in an analysis of mtDNA sequences. Lyrholm & Gyllensten (1998) reported significant heterogeneity in mtDNA haplotype frequencies between oceans and estimated that  $G_{ST} = 0.03$  (table 4). The reason we did not detect significant microsatellite allele frequency heterogeneity between oceans (and within the North Pacific) is unlikely to be insufficient power of the test, since significant heterogeneity was found between social groups within areas based on much smaller sample sizes. Taken together, our results are consistent with sex-biased dispersal, with males moving more between oceans than females, leading to less nuclear than mitochondrial differentiation on a worldwide scale.

The observed patterns of differentiation in sperm whales differ from those reported for other globally

Table 2. *Allele frequencies at microsatellite loci for three oceanic regions*

(NA, North Atlantic; NP, North Pacific; SH, Southern hemisphere. Estimated allele lengths are in bold.)

estimated allele lengths	NA	NP	SH	estimated allele lengths	NA	NP	SH
EV1				SW13 ( <i>Cont.</i> )			
<i>n</i>	84	190	42	<b>163</b>	0.190	0.170	0.143
<b>123</b>	0.631	0.605	0.714	<b>165</b>	0.083	0.072	0.048
<b>125</b>	0.060	0.042	0.048	<b>167</b>	0.155	0.124	0.095
<b>127</b>	0.012	0.005	0.000	<b>169</b>	0.048	0.103	0.071
<b>129</b>	0.000	0.005	0.000	<b>173</b>	0.012	0.021	0.024
<b>131</b>	0.024	0.026	0.000				
<b>133</b>	0.060	0.058	0.095	SW15			
<b>135</b>	0.024	0.021	0.000	<i>n</i>	39	133	25
<b>137</b>	0.024	0.037	0.048	<b>253</b>	0.051	0.000	0.000
<b>139</b>	0.167	0.174	0.095	<b>255</b>	0.051	0.045	0.000
<b>141</b>	0.000	0.021	0.000	<b>257</b>	0.026	0.023	0.040
<b>145</b>	0.000	0.005	0.000	<b>259</b>	0.359	0.286	0.400
EV5				<b>261</b>	0.410	0.519	0.440
<i>n</i>	78	194	40	<b>263</b>	0.077	0.068	0.080
<b>147</b>	0.013	0.015	0.000	<b>265</b>	0.000	0.053	0.040
<b>149</b>	0.000	0.010	0.000	<b>267</b>	0.026	0.009	0.000
<b>153*</b>	0.397	0.351	0.325				
<b>155*</b>	0.013	0.088	0.050	SW19			
<b>157*</b>	0.359	0.335	0.425	<i>n</i>	68	180	42
<b>159*</b>	0.038	0.062	0.075	<b>90</b>	0.029	0.011	0.024
<b>161</b>	0.013	0.000	0.000	<b>96</b>	0.147	0.094	0.119
<b>163*</b>	0.027	0.010	0.025	<b>98*</b>	0.000	0.006	0.000
<b>165*</b>	0.064	0.103	0.050	<b>104</b>	0.015	0.028	0.000
<b>167*</b>	0.064	0.026	0.050	<b>111</b>	0.000	0.017	0.024
<b>169*</b>	0.013	0.000	0.000	<b>113</b>	0.044	0.039	0.024
SW2				<b>115</b>	0.000	0.017	0.000
<i>n</i>	88	196	44	<b>117</b>	0.015	0.000	0.000
<b>73</b>	0.034	0.010	0.023	<b>119</b>	0.132	0.033	0.048
<b>75</b>	0.023	0.015	0.023	<b>121</b>	0.000	0.072	0.071
<b>77</b>	0.568	0.668	0.455	<b>123</b>	0.058	0.033	0.048
<b>79</b>	0.330	0.250	0.318	<b>125</b>	0.103	0.128	0.119
<b>81</b>	0.045	0.051	0.182	<b>127</b>	0.029	0.144	0.143
<b>83</b>	0.000	0.005	0.000	<b>129</b>	0.162	0.100	0.167
SW10				<b>131</b>	0.176	0.117	0.095
<i>n</i>	62	198	38	<b>133</b>	0.015	0.067	0.071
<b>137</b>	0.000	0.005	0.026	<b>135</b>	0.029	0.039	0.024
<b>141</b>	0.081	0.035	0.079	<b>137</b>	0.015	0.028	0.024
<b>143</b>	0.177	0.056	0.105	<b>139</b>	0.015	0.011	0.000
<b>145</b>	0.161	0.187	0.184	<b>141</b>	0.015	0.000	0.000
<b>147</b>	0.129	0.081	0.053	<b>146</b>	0.000	0.017	0.000
<b>149</b>	0.210	0.217	0.211				
<b>151</b>	0.097	0.167	0.184	GATA28			
<b>153</b>	0.097	0.086	0.158	<i>n</i>	88	198	44
<b>155</b>	0.032	0.066	0.000	<b>120</b>	0.386	0.318	0.295
<b>157</b>	0.000	0.081	0.000	<b>128</b>	0.477	0.480	0.545
<b>159</b>	0.016	0.015	0.000	<b>132</b>	0.136	0.202	0.159
<b>161</b>	0.000	0.005	0.000				
SW13				GATA53			
<i>n</i>	84	194	42	<i>n</i>	64	178	44
<b>134</b>	0.036	0.015	0.048	<b>257</b>	0.125	0.157	0.205
<b>149</b>	0.012	0.010	0.000	<b>261</b>	0.031	0.039	0.091
<b>155</b>	0.000	0.015	0.000	<b>265*</b>	0.172	0.096	0.091
<b>157</b>	0.036	0.098	0.167	<b>268*</b>	0.297	0.303	0.227
<b>159</b>	0.143	0.082	0.119	<b>272</b>	0.219	0.247	0.273
<b>161</b>	0.286	0.289	0.286	<b>276*</b>	0.109	0.101	0.068
				<b>279*</b>	0.047	0.056	0.045

\*Contain pooled size classes.

Table 3. Allele frequencies at microsatellite loci for areas in the North Pacific ocean

(G, Galápagos islands; JC, Japanese coast; NPW, NPC and NPE are North Pacific western, central and eastern areas, respectively. Estimated allele sizes are in bold.)

estimated allele lengths	G	JC	NPW	NPC	NPE	estimated allele lengths	G	JC	NPW	NPC	NPE
EV1						SW13 ( <i>Cont.</i> )					
<i>n</i>	40	40	22	40	46	<b>161</b>	0.275	0.250	0.333	0.333	0.260
<b>123</b>	0.625	0.475	0.500	0.700	0.673	<b>163</b>	0.125	0.125	0.166	0.166	0.239
<b>125</b>	0.025	0.050	0.136	0.025	0.021	<b>165</b>	0.150	0.125	0.041	0.023	0.021
<b>127</b>	0.000	0.000	0.045	0.000	0.000	<b>167</b>	0.100	0.175	0.125	0.095	0.130
<b>129</b>	0.025	0.000	0.000	0.000	0.000	<b>169</b>	0.050	0.075	0.166	0.142	0.108
<b>131</b>	0.025	0.075	0.000	0.000	0.021	<b>173</b>	0.050	0.000	0.041	0.000	0.021
<b>133</b>	0.025	0.050	0.045	0.075	0.086	SW15					
<b>135</b>	0.000	0.100	0.000	0.000	0.000	<i>n</i>	30	31	19	26	25
<b>137</b>	0.050	0.000	0.045	0.050	0.043	<b>255</b>	0.000	0.000	0.105	0.115	0.040
<b>139</b>	0.175	0.225	0.181	0.150	0.130	<b>257</b>	0.000	0.032	0.105	0.000	0.000
<b>141</b>	0.050	0.025	0.045	0.000	0.000	<b>259</b>	0.500	0.258	0.210	0.192	0.240
<b>145</b>	0.000	0.000	0.000	0.000	0.021	<b>261</b>	0.433	0.548	0.421	0.538	0.600
EV5						<b>263</b>	0.000	0.064	0.157	0.076	0.080
<i>n</i>	42	42	24	38	46	<b>265</b>	0.066	0.096	0.000	0.076	0.000
<b>147</b>	0.047	0.000	0.000	0.000	0.021	<b>267</b>	0.000	0.000	0.000	0.000	0.040
<b>149</b>	0.047	0.000	0.000	0.000	0.000	SW19					
<b>153*</b>	0.333	0.452	0.333	0.315	0.282	<i>n</i>	24	40	23	42	50
<b>155*</b>	0.071	0.095	0.125	0.105	0.065	<b>90</b>	0.000	0.000	0.000	0.023	0.020
<b>157*</b>	0.333	0.166	0.333	0.447	0.413	<b>96</b>	0.000	0.150	0.000	0.023	0.200
<b>159*</b>	0.071	0.071	0.041	0.078	0.043	<b>98*</b>	0.041	0.000	0.000	0.000	0.000
<b>163*</b>	0.000	0.023	0.000	0.000	0.021	<b>104</b>	0.000	0.025	0.043	0.047	0.020
<b>165*</b>	0.047	0.166	0.083	0.052	0.152	<b>111</b>	0.000	0.025	0.043	0.000	0.020
<b>167*</b>	0.047	0.023	0.083	0.000	0.000	<b>113</b>	0.041	0.000	0.086	0.071	0.020
SW2						<b>115</b>	0.041	0.050	0.000	0.000	0.000
<i>n</i>	40	42	22	42	48	<b>119</b>	0.000	0.000	0.086	0.023	0.060
<b>73</b>	0.000	0.023	0.000	0.023	0.000	<b>121</b>	0.125	0.050	0.043	0.095	0.060
<b>75</b>	0.000	0.000	0.045	0.000	0.000	<b>123</b>	0.041	0.000	0.043	0.047	0.020
<b>77</b>	0.725	0.690	0.681	0.714	0.562	<b>125</b>	0.250	0.175	0.173	0.071	0.060
<b>79</b>	0.150	0.261	0.272	0.214	0.333	<b>127</b>	0.250	0.200	0.130	0.071	0.120
<b>81</b>	0.125	0.023	0.000	0.047	0.041	<b>129</b>	0.083	0.125	0.043	0.095	0.120
<b>83</b>	0.000	0.000	0.000	0.000	0.020	<b>131</b>	0.041	0.075	0.130	0.214	0.100
SW10						<b>133</b>	0.000	0.050	0.043	0.095	0.100
<i>n</i>	40	42	24	42	48	<b>135</b>	0.041	0.050	0.086	0.023	0.020
<b>137</b>	0.000	0.000	0.000	0.023	0.000	<b>137</b>	0.000	0.000	0.043	0.047	0.040
<b>141</b>	0.050	0.047	0.041	0.023	0.020	<b>139</b>	0.041	0.000	0.000	0.023	0.000
<b>143</b>	0.025	0.071	0.083	0.119	0.000	<b>146</b>	0.000	0.025	0.000	0.023	0.020
<b>145</b>	0.200	0.214	0.166	0.119	0.208	GATA28					
<b>147</b>	0.075	0.047	0.083	0.142	0.062	<i>n</i>	42	42	24	42	46
<b>149</b>	0.125	0.261	0.291	0.142	0.291	<b>120</b>	0.261	0.333	0.250	0.404	0.304
<b>151</b>	0.175	0.190	0.083	0.142	0.208	<b>128</b>	0.523	0.404	0.541	0.404	0.543
<b>153</b>	0.150	0.023	0.083	0.071	0.104	<b>132</b>	0.214	0.261	0.208	0.190	0.152
<b>155</b>	0.100	0.071	0.041	0.071	0.041	GATA53					
<b>157</b>	0.100	0.071	0.083	0.095	0.041	<i>n</i>	30	36	24	40	46
<b>159</b>	0.000	0.000	0.000	0.047	0.020	<b>257</b>	0.133	0.166	0.166	0.150	0.152
<b>161</b>	0.000	0.000	0.041	0.000	0.000	<b>261</b>	0.000	0.083	0.083	0.025	0.021
SW13						<b>265*</b>	0.100	0.138	0.125	0.100	0.043
<i>n</i>	40	40	24	42	46	<b>268*</b>	0.166	0.305	0.333	0.325	0.369
<b>134</b>	0.025	0.000	0.000	0.023	0.021	<b>272</b>	0.433	0.166	0.125	0.250	0.239
<b>149</b>	0.000	0.025	0.041	0.000	0.000	<b>276*</b>	0.066	0.111	0.041	0.125	0.130
<b>155</b>	0.000	0.050	0.000	0.023	0.000	<b>279*</b>	0.100	0.027	0.125	0.025	0.043
<b>157</b>	0.075	0.150	0.041	0.119	0.130						
<b>159</b>	0.150	0.075	0.041	0.071	0.065						

\*Contain pooled size classes.

Table 4. *Genetic differentiation in microsatellites and mtDNA between oceans*

(Based on the restricted material containing presumably unrelated whales only.)

measure	microsatellites	mtDNA
$G_{ST}^a$	0.001	0.0300
$p^b$	0.232	0.0007

<sup>a</sup>  $G_{ST}$  was estimated following Nei & Chesser (1983).<sup>b</sup>  $p$  values are probabilities obtained in exact tests of homogeneity (Raymond & Rousset 1995).

occurring whales. Among baleen whales, minke whales (Hoelzel & Dover 1991; van Pijlen *et al.* 1995), humpback whales (Baker *et al.* 1990, 1993; Palumbi & Baker 1994; Valsecchi *et al.* 1997) and fin whales (Bérubé *et al.* 1998) all show substantially higher mtDNA diversity and strong differentiation in both mtDNA and nuclear DNA markers between and, in some cases, within oceans. In humpback whales, seasonal migrations between high-latitude feeding and low-latitude breeding grounds have been shown to involve strong fidelity to migratory destinations (Baker *et al.* 1986; Clapham *et al.* 1993). Genetic differentiation over both small and large spatial scales has been observed in some odontocetes. For example, genetic differentiation in both mtDNA and microsatellites has been reported between sympatric populations of two killer whale varieties with different diets in the north-eastern Pacific (Hoelzel *et al.* 1998a) and between parapatric nearshore and offshore populations of bottlenose dolphins in the North Atlantic (Hoelzel *et al.* 1998b).

The low sperm whale mtDNA diversity indicated a young global population structure with an age of less than *ca.* 100 000 years, perhaps even less than 25 000 years (Lyrholm *et al.* 1996; Lyrholm & Gyllensten 1998). This may reflect an expansion to the current range after the Pleistocene period glaciations, during which suitable habitats could have been restricted and ocean circulation patterns could have been different (e.g. Lehman & Keigwin 1992; Behl & Kennett 1996; McCabe & Clark 1998), perhaps affecting the availability of sperm whale prey (mainly cephalopods). The small albeit statistically highly significant mtDNA differentiation between oceans could thus be a consequence of a recent common ancestry, although it may also have been caused by gene flow.

If the global sperm whale population structure is young, an explanation for the lack of nuclear differentiation and an alternative to male-mediated gene flow could be that insufficient time has passed since the putative range expansion in order for genetic drift to act. In the absence of gene flow, the haploid mtDNA is expected to differentiate more rapidly due to drift than the nuclear genome, due to a four-fold difference in effective population size (Wilson *et al.* 1985). However, this does not appear sufficient to explain an order of magnitude difference in the amount of genetic differentiation between the mtDNA and nuclear genomes, as suggested by our data. Thus, sex-biased dispersal seems likely to have been a major factor in determining the patterns of genetic differentiation.

Females apparently disperse less than males at both the social and geographical levels. The notion of females being

philopatric to their natal groups is supported by long-term studies of identified individuals (Whitehead *et al.* 1991), although some degree of female dispersal and transfer between groups may occur (Best 1979; Richard *et al.* 1996a). Furthermore, the significant genetic heterogeneity between potential female social groups in the present study, as well as similar evidence from previous work using microsatellites and/or mtDNA (Richard *et al.* 1996a; Lyrholm & Gyllensten 1998), suggests greater relatedness within than between groups. Thus, female cooperative behaviour, such as alloparental care (Best *et al.* 1984; Gordon 1987; Whitehead 1996), may have evolved through kin selection (Hamilton 1964) and been an important factor in the evolution of sperm whale sociality.

At a geographical level, sex differences in dispersal are indicated by the latitudinal segregation of males and females (Rice 1989) and by recorded movements. Studies of known individuals conducted over several years, as well as whaling recoveries of tagged whales, have indicated some between-year fidelity to local areas in groups of females and juveniles and although extensive female movements within oceans have also been documented, they generally seem to be less than in males (Best 1979; Brown 1981; Ivashin 1981; Gordon 1987; Kasuya & Miyashita 1988; Whitehead *et al.* 1992; Dufault & Whitehead 1995). Males have been found to move considerable distances, even between the hemispheres (Ivashin 1981). Although cross-equatorial movements have also been reported for females, these have been more limited to within tropical waters in the eastern Pacific (Ivashin 1981; Dufault & Whitehead 1995). In this region and extending westwards near the equator (encompassing the traditional 'Galápagos Islands' and 'on-the-line' whaling grounds; Townsend 1935), populations of females and immatures are present year round and their relationship with populations at higher latitudes is unknown (Rice 1989). One possibility is that females here may be visited by breeding males from both hemispheres, which could provide for north-south gene flow.

If females were to move between the Atlantic and Indo-Pacific oceans, it would be most likely to occur around South Africa. Schools of females and immatures are common off the Atlantic and Indian Ocean coasts of South Africa (Best 1979), the southern point of which is at *ca.* 35° S and, thus, within the female-immature latitudinal range limits (Best 1979). This suggests the possibility of an interocean migration route, although there are as yet no reports of such movements.

Evidence that movements of females between oceans may be rare also comes from an analysis of acoustic communication, which indicated divergent repertoires between groups from different oceans (Weilgart & Whitehead 1997). There is only one record of a whale marked and recovered in different oceans, involving a movement from the south-western Indian Ocean to the south-western Atlantic (Ivashin 1981). The sex of this whale was not recorded, but the latitudinal position of marking (*ca.* 44° S) makes it likely to have been a male. It may be that males which have migrated to Antarctic feeding areas occasionally move widely across longitudes in search of abundant prey, so that upon returning north for breeding they might end up in a different ocean.

It would be of interest to gain more information about ongoing dispersal patterns in sperm whale populations, which could come from comparisons of photographically (Arnbom 1987) or genetically (Palsbøll *et al.* 1997a) identified whales and by satellite tracking (Mate *et al.* 1997).

What could be the reasons for the extreme geographical sexual segregation in sperm whales? The restriction of groups of females and immatures to low latitudes may be related to the energetic constraints imposed on females by the combination of deep diving, pregnancy and lactation. Calves need to develop diving ability before they can be weaned and the fatty spermaceti organ may be energetically expensive. Thus, calf development may be particularly demanding on female sperm whales, as indicated by a prolonged lactation period (Best *et al.* 1984). In addition, perhaps calf thermoregulatory limitations may prevent these groups from reaching high latitudes. It has also been suggested that prey species at high latitudes may occur too deeply for females and juveniles (Best 1979). Males may have been selected to disperse widely to productive high latitudes in order to avoid competition from females and to increase the rate of growth to maturation and breeding status. Thus, these factors may ultimately have contributed to the observed contrasting mitochondrial and nuclear genetic differentiation on a global scale.

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