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Hierarchical structure of mitochondrial DNA gene flow among humpback whales *Megaptera novaeangliae*, world-wide

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Abstract

The genetic structure of humpback whale populations and subpopulation divisions is described by restriction fragment length analysis of the mitochondrial (mt) DNA from samples of 230 whales collected by biopsy darting in 11 seasonal habitats representing six subpopulations, or 'stocks', world-wide. The hierarchical structure of mtDNA haplotype diversity among population subdivisions is described using the analysis of molecular variance (AMOVA) procedure, the analysis of gene identity, and the genealogical relationship of haplotypes as constructed by parsimony analysis and distance clustering. These analyses revealed: (i) significant partitioning of world-wide genetic variation among oceanic populations, among subpopulations or 'stocks' within oceanic populations and among seasonal habitats within stocks; (ii) fixed categorical segregation of haplotypes on the south-eastern Alaska and central California feeding grounds of the North Pacific; (iii) support for the division of the North Pacific population into a central stock which feeds in Alaska and winters in Hawaii, and an eastern or 'American' stock which feeds along the coast of California and winters near Mexico; (iv) evidence of genetic heterogeneity within the Gulf of Maine feeding grounds and among the sampled feeding and breeding grounds of the western North Atlantic; and (v) support for the historical division between the Group IV (Western Australia) and Group V (eastern Australia, New Zealand and Tonga) stocks in the Southern Oceans. Overall, our results demonstrate a striking degree of genetic structure both within and between oceanic populations of humpback whales, despite the nearly unlimited migratory potential of this species. We suggest that the humpback whale is a suitable demographic and genetic model for the management of less tractable species of baleen whales and for the general study of gene flow among long-lived, mobile vertebrates in the marine ecosystem.

Keywords: gene flow, humpback whale, mitochondrial DNA, population structure, stocks

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Introduction

The humpback whale is a cosmopolitan species estimated to have numbered more than 125 000 individuals prior to the onset of modern commercial whaling (Johnson &

Wolman 1985). Before protection by international agreement in 1966, the world-wide abundance of this species was reduced to less than 5000 and some regional populations were considered in danger of extinction. The distribution of humpback whales in the northern hemisphere is divided by continental land masses into two oceanic populations, the North Atlantic and the North Pacific (True 1904; Kellogg 1929). In the southern hemisphere, humpback whales form a single circumpolar population distributed throughout the southern oceans (Mackintosh 1965). Within each oceanic basin, humpback whales undertake annual migrations, averaging 10 000 km return, between summer feeding grounds in high latitude waters and winter breeding and calving grounds in low-latitude waters. Effective interchange between northern and southern hemisphere populations is prevented, or limited, by the seasonal opposition of this migratory cycle.

Within each major oceanic population, humpback whales are thought to form relatively discrete subpopulations which are not separated by obvious geographic barriers (Kellogg 1929; Chittleborough 1965; Mackintosh 1965; Baker *et al.* 1986; Katona & Beard 1990). In the southern hemisphere, discontinuous patterns of seasonal distribution and observations of migratory movement by Discovery-marked individuals suggest that humpback whales form five or six distinct subpopulations or 'stocks' which remain segregated year-round (Mackintosh 1942; Chittleborough 1965; Mackintosh 1965). Referred to as Groups I–VI, these stocks are distributed more or less discontinuously around the Antarctic continent during the austral summer feeding season. Each winter these groups migrate to discrete breeding and calving grounds along continental and insular coastlines in tropical latitudes of the southern hemisphere.

Population structure in the northern hemisphere oceans is more complex. Observations of naturally marked individuals in the western North Atlantic and the central and eastern North Pacific indicate that humpback whales consistently assort onto one of several geographically distinct coastal feeding grounds during summer months. Rates of exchange between even adjacent coastal feeding ranges are low and fidelity of return to a given region is high (Baker *et al.* 1986; Katona & Beard 1990). Individuals from discrete feeding grounds congregate to give birth and presumably to breed on common wintering grounds (Darling & McSweeney 1985; Baker *et al.* 1986; Mattila *et al.* 1989; Katona & Beard 1990). The term 'structured' stock has been used to refer to this pattern of seasonal segregation between feeding herds which share common wintering grounds (Baker *et al.* 1986). Geographically discrete wintering grounds near Mexico, Hawaii and the coast of Asia are thought to divide the North Pacific into three stocks. The North Atlantic is thought to be divided into a western stock which winters near islands and submerged banks of the West Indies and an eastern stock which winters near the Cape Verde Islands off Africa (Bannister *et al.* 1984).

Here we describe the hierarchical structure of humpback whale populations world-wide using restriction fragment length polymorphisms (RFLPs) of mitochondrial (mt) DNA from 230 individuals. This study extends the previous description of mtDNA variation among humpback whales from a more limited geographic range (Baker *et al.* 1990). First, we examine the distribution of mtDNA haplotypes in the three major oceanic populations, the North Pacific, the North Atlantic and the Southern Oceans. Second, we examine haplotype distributions within oceanic populations to assess genetic division between putative stocks. Finally, we examine haplotype frequencies from eleven seasonal habitats (i.e. winter breeding and summer feeding grounds) within putative stocks. We chose mtDNA for this analysis because of its maternal inheritance, absence of recombination and rapid rate of mutation (Brown 1983; Wilson *et al.* 1985; Avise *et al.* 1987). These characteristics make mtDNA analysis a powerful technique for describing demographic processes and the geographic patterns of genetic variation in natural populations. The maternal haploid inheritance of mtDNA has two important advantages over nuclear genetic markers. First, the phylogenetic relationship of mtDNA types reflects the history of distinct maternal lineages within a population or a species (Avise *et al.* 1987). Second, the effective population size of mtDNA genomes is one-fourth that of nuclear genes, leading to a higher rate of local differentiation by random drift (Birky *et al.* 1983). Local differentiation is also enhanced by the rapid rate of mtDNA evolution, generally considered to be five to ten times faster than nuclear DNA coding regions (Brown 1983; Wilson *et al.* 1985), although this rate may be slower for some cetaceans (Hoelzel & Dover 1991; Baker *et al.* 1993; Martin & Palumbi 1993).

Methods

Sample collection and DNA extraction

Samples for genetic analysis were available from 230 individual humpback whales representing three oceanic populations, six stocks and 11 seasonal habitats (Table 1). In keeping with traditional terminology, a 'stock' refers to an intraoceanic subpopulation, as originally defined by geographic distribution or demographic interchange, that is assumed to remain more or less isolated from other subpopulations year-round (Chapman 1974; Donovan 1991). The terms 'feeding grounds' and 'feeding herds' are used synonymously to refer to population divisions observed primarily during summer months in high latitude waters. The term 'wintering grounds' is used for di-

Table 1 Summary of tissue samples used for analysis of mtDNA variation among populations of humpback whales world-wide

Ocean/Stock	Region	Habitat	No. samples	Sex ratio (M:F)	Sampling periods
North Atlantic			90		
Western	Gulf of Maine	feeding	42	20:22	summers, 1988–89 (biopsy samples) fall, 1987 (necropsy)
	Newfoundland	feeding	18	10:8	summers, 1990–91
	Dominican Republic	wintering	30	16:13	winter, 1989
North Pacific			95		
Central	south-eastern Alaska	feeding	38	20:15	summers, 1987–88
	Hawaii	wintering	16	11:5	winter, 1988
Eastern	California	feeding	20	13:7	fall, 1988
	Mexico	wintering	21	18:3	winter, 1991
Southern Oceans			45		
Group I-VI	Antarctic Peninsula	feeding	3	n.a.	austral summer, 1989
Group IV	Western Australia	migration	15	12:1	austral spring, 1990
Group V	Eastern Australia	migration	14	9:4	austral spring, 1990
Group V	Tonga	wintering	13	5:9	austral winter, 1991
World Wide			230	134:87	

visions observed in low latitude waters. 'Migratory corridors' refer to regions, such as the eastern and western coasts of Australia, that are used primarily for migration between wintering and summering grounds.

Except for one beach-cast animal from eastern Australia, two individuals entrapped in fishing nets from Newfoundland and 10 victims of an unusual group mortality in the southern Gulf of Maine, samples of skin tissue were collected from free-ranging whales using a biopsy dart described in detail by Lambertsen (1987). The biopsy dart consisted of a commercially available aluminium crossbow bolt (arrow) and a stainless-steel cylindrical punch sharpened at its distal end. The punch was 9 mm in diameter and 2 to 2.4 cm in length with a 3 cm-wide metal flange at the base to control penetration of the skin by the dart and to provide recoil of the sample. The biopsy dart was shot from a crossbow fitted with a 125 or 150-lb draw fibreglass prod (bow). Each dart was fitted with a small collar of closed-cell neoprene for floatation and was retrieved from the water by hand (Mathews 1986). The biopsy punches were sterilized following each shot by immersing in 70% ethanol, flaming with a propane torch and coating the outside with a topical antibiotic. Extensive observations of whales before and after biopsy collection indicate no evidence of long-term disturbance or interruption of critical ongoing behaviour (Weinrich *et al.* 1991; Weinrich *et al.* 1992a).

Skin samples were stored without refrigeration in the field for periods of several days to several weeks in one of the following solutions (abbreviations and formulae for

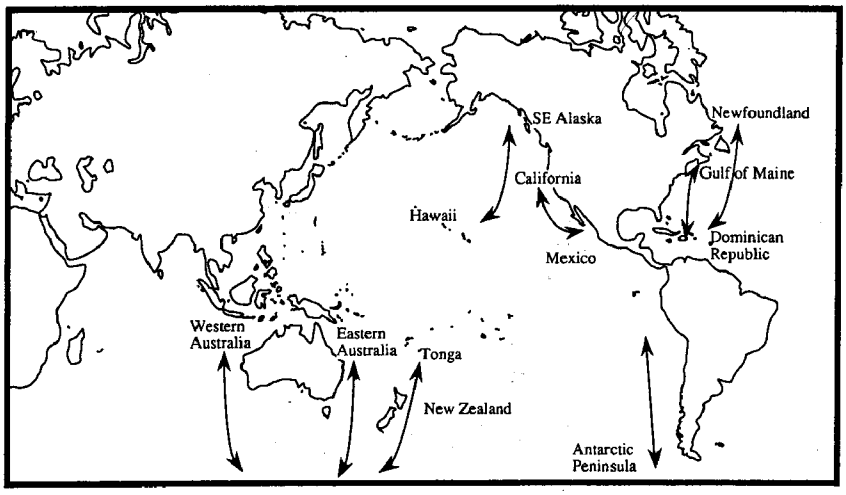

Fig. 1 Map of sample regions and inferred primary migratory connections between seasonal habitats of humpback whales.

standard molecular reagents follow Maniatis *et al.* (1982) unless otherwise noted): (i) 70% ethanol; (ii) 5-M NaCl, 10-mM EDTA and 10-mM Tris (pH 7.5); and (iii) solution #2 with the addition of 20% DMSO (Amos & Hoelzel 1991). When possible, each biopsy sample was scored with a sterile scalpel or razor blade to allow rapid penetration of the storage buffer. Samples were placed at –70 °C for long-term storage in the laboratory. Total cellular DNA was isolated from the pigmented outer epidermal layer of the skin biopsy by homogenization in a low molarity salt buffer and digestion with proteinase K (Davis *et al.* 1987). The homogenate was extracted twice with neutralized phenol–chloroform– isoamyl-alcohol (24:24:1), twice with chloroform–isoamyl-alcohol (24:1), precipitated with ethanol and dissolved in TE. The concentration of dissolved DNA was determined from its optical density at 260 nm. A typical biopsy sample yielded approximately 800 μg of high molecular weight, total cellular DNA.

Restriction fragment length polymorphisms of mtDNA

The mtDNA haplotype of each humpback whale was defined by restriction fragment length polymorphisms (RFLPs) revealed by a series of five restriction enzymes: two six-base cutters, *Dra*I and *Nco*I; and three degenerate or five-base cutters, *Acc*I, *Ava*I, and *Ava*II. These five enzymes were selected based on a previous survey of 82 individual humpback whales using 18 restriction enzymes (Baker *et al.* 1990). The remaining 13 restriction enzymes revealed no polymorphic sites in the previous survey and were thus considered uninformative for describing the geographic distribution of haplotypes. Restriction fragment analysis of mtDNA was based on Southern blotting of total cellular DNA and hybridization with a radioactively labelled probe, following the methods of Baker *et al.* (1990). Approximately 1.5 μg of total cellular DNA was incubated with 10 to 15 units of the restriction enzyme and reaction buffer under standard conditions. Restricted DNA was separated by electrophoresis in 0.8–1% TAE agarose gels and transferred overnight to nylon filters by Southern blotting in 10 × SSC. Filters were hybridized at 65 °C in 0.5-M sodium phosphate, 7% SDS, 1-mM EDTA and 1% BSA with radioactively labelled mtDNA from a Dall's porpoise (*Phocoenoides dalli*) that was cloned into a Lambda phage vector. Filters were washed at a final stringency of 0.1 × SSC, 0.5% SDS at 50 °C for 30 min and autoradiographed for 1–3 days.

Molecular genetic identification of sex

Molecular genetic identification of the sex of humpback whales followed the methods of Baker *et al.* (1991). Approximately 5–10 μg of genomic DNA was digested with 10–15 units of the restriction enzyme *Eco*RI and reaction buffer under standard conditions. Following gel electrophoresis and Southern blotting, nylon filters were hybridized at 55 °C in 0.5-M sodium phosphate, 7% SDS, 1-mM EDTA and 1% BSA with the radioactively labelled clone PDP1007 derived from the human Y chromosome (Page *et al.* 1987). Filters were washed at a final stringency of 0.1 × SSC, 0.5% SDS at 50 °C for 30 min and autoradiographed for 7–10 days with an intensifying screen. The sex-specific fragment patterns of humpback whales were consistent with those of other placental mammals. Males were identified by two restriction fragments, one 3.8 kb in length and another of 2 kb in length, while females were identified by a single 2-kb fragment observed at approximately twice the intensity of this band in the males.

Analysis of mtDNA variation

Inferred restriction site polymorphisms of mtDNA were used to define unique haplotypes among the sampled individuals and to estimate average nucleotide differences (i.e. genetic distance) between haplotypes using maximum-likelihood methods (Nei & Li 1979; Nei & Tajima 1983). Because the restriction enzymes used in this analysis of haplotypes were preselected, estimates of genetic distances are not representative of a random survey of the mtDNA genome. These estimates are valid only as indicators of relative nucleotide diversity or genetic distance within the overall survey presented here. The genetic relationship among populations of humpback whales was assessed by UPGMA clustering (Felsenstein 1991) using the estimated nucleotide differences between haplotypes weighted by sample size. The phylogenetic relationship of mtDNA haplotypes was described by parsimony analysis using the PAUP computer program (Swofford 1992). In most cases, the topology of these trees was verified by sequence information from a hypervariable section of the humpback whale mtDNA control region or D-loop (Baker *et al.* 1993).

The geographic differentiation of mtDNA variation was tested using three approaches: (1) the analysis of molecular variance model of Excoffier *et al.* (1992); (2) the analysis of gene identity model of Takahata & Palumbi (1985); and (3) a randomized χ^2 test of independence. The analysis of molecular variance procedure calculated standard variance components and an array of haplotypic correlation measures, referred to as ϕ-statistics, for each level of population subdivision (Excoffier *et al.* 1992). The significance of the observed variance components and ϕ-statistics were tested using a random permutation procedure available in the computer program AMOVA (courtesy of L. Excoffier). The permutation approach to significance testing avoids the parametric as-

sumptions of normality and independence that are not met by molecular distance measures (Mantel 1967; Smouse *et al.* 1986). Following the recommendation of Excoffier *et al.* (1992), we performed the AMOVA on the standard Euclidean distance matrix calculated from the number of restriction site differences between pairs of haplotypes.

Geographic differentiation of mtDNA within and between oceanic populations was also quantified using an analysis of gene identity (Wright 1943) as modified by Takahata and Palumbi (Takahata & Palumbi 1985) for the study of extranuclear differentiation in subdivided populations. The resulting coefficient of gene differentiation (G_{ST}) can be interpreted as the proportion of genetic variation that is explained by the categorical geographic divisions defined in the survey and thus is analogous to the variance component of the AMOVA analysis. Unlike the AMOVA, the analysis of gene identity is based on an explicit model of population genetics and provides an estimate of long-term migration according to the approximation, $G_{ST} = 1/(1 + 2N_m)$, where N_m is the effective number of females exchanged between populations per generation (Takahata & Palumbi 1985). Current formulation of this model, however, does not allow for the hierarchical or 'nested' analysis of population subdivisions available with the AMOVA. The statistical significance of an observed G_{ST} value was judged by a random permutation procedure (Palumbi & Wilson 1990).

Finally, differences in the regional frequencies of haplotypes were tested using contingency tables and a randomized chi-square Test of Independence (Roff & Bentzen 1989). This categorical analysis makes no assumptions about the genetic distance between haplotypes or the underlying genetic model of the population. As with the gene identity analysis, an observed χ^2 value was considered significant based on comparison to a null distribution of values generated from computer simulated resamplings of the data. Unless noted otherwise, comparisons considered to be significant by the G_{ST} analysis were also significant in a χ^2 test of independence. For all three analyses, the AMOVA, the G_{ST} analysis and the χ^2 test of independence, the significance of observed values were tested against the null distribution of the respective test statistic generated by 500 or 1 000 simulations.

Results

World-wide variation

The five restriction enzymes detected a total of 14 polymorphic sites defining 22 unique haplotypes among the 230 individual whales (Table 2). The 22 haplotypes included 11 of the 12 described previously (Baker *et al.* 1990). The twelfth haplotype ('B' type) found previously only in a heteroplasmic individual from Hawaii (i.e. an individual with two distinguishable mtDNA haplotypes) was not found again and the heteroplasmic individual was considered an 'A' type in all analyses reported here. Five haplotypes were unique to the North Pacific, six to the western North Atlantic and eight to the Southern Oceans. Two haplotypes, 'C' and 'J', were common to the western North Atlantic and the Southern Oceans and one haplotype, 'AE', was found in the North Pacific and Southern Oceans. No haplotype was common to all three oceanic populations. Direct sequencing of the mtDNA control regions from individuals representing the trans-oceanic types confirmed the similarity of the 'C' and 'J' types from different oceans but showed the 'AE' types from the North Pacific and Southern Oceans are not closely related (C. S. Baker, unpublished data).

A parsimony analysis of the 22 haplotypes in the world-wide sample proved uninformative. A large number of minimum length trees were generated using the heuristic search procedure with random addition of taxa (repeated 500 times with 10 trees saved during each search), available in the computer program PAUP. The resulting majority-rule consensus tree was poorly differentiated and its consistency index was low, suggesting reversals or parallel mutations among the restriction sites defining the haplotypes, as well as a large proportion of polymorphic sites unique to individual haplotypes (i.e.

Table 2 Matrix of presence or absence of 14 restriction sites defining 22 humpback whale mtDNA haplotypes

Haplotype no.	Restriction site matrix														Haplotype code
1	1	1	1	0	1	0	1	0	0	0	0	1	0	0	A
2	1	1	1	0	0	0	1	0	0	0	0	1	0	0	AA
3	1	1	1	0	0	0	1	1	0	0	0	1	0	0	BB
4	0	1	0	0	0	0	1	0	0	0	0	1	0	0	C
5	0	1	0	0	0	0	1	0	0	0	0	1	1	0	CA
6	0	1	0	0	0	0	1	0	0	0	0	0	0	0	CC
7	0	1	0	1	0	0	1	0	0	0	0	1	0	0	D
8	0	1	1	0	1	0	1	0	0	0	0	1	0	0	E
9	0	1	0	0	1	0	1	0	0	0	0	1	0	0	AE
10	0	1	0	0	0	1	1	0	0	0	0	1	0	0	F
11	0	1	1	0	0	0	1	0	0	0	0	1	0	0	G
12	0	0	1	0	1	0	1	0	0	0	0	1	0	0	H
13	0	1	0	0	0	0	1	1	1	0	0	1	0	0	I
14	0	1	0	0	0	0	1	1	0	0	0	1	0	0	ID
15	1	1	0	0	0	0	1	1	1	0	0	1	0	0	J
16	1	1	0	0	0	0	1	1	1	0	0	1	1	1	JJ
17	1	1	0	0	0	0	1	1	0	0	0	1	0	0	JB
18	1	1	0	0	0	0	0	1	1	0	0	1	0	0	K
19	1	0	0	0	0	0	1	1	1	0	0	1	0	0	L
20	1	1	0	0	0	0	1	0	0	0	0	1	0	0	M
21	0	0	0	0	0	0	1	0	0	1	0	1	0	0	N
22	0	1	0	0	0	0	1	0	0	0	1	1	0	0	O

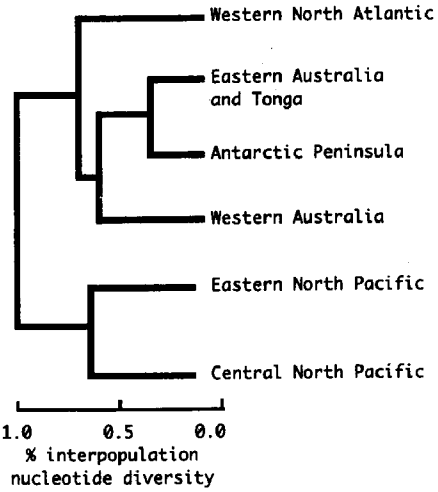

Fig. 2 Relationship between six sub-populations or 'stocks' of humpback whales, the western North Atlantic, eastern Australia and Tonga, Antarctic Peninsula, Western Australia, central North Pacific and eastern North Pacific, based on UPGMA clustering of average genetic distance between mtDNA haplotypes.

uninformative for cladistic analysis). This problem was not encountered in the parsimony reconstructions of haplotypes found within oceans (see below). To figuratively describe the genetic relationship of the geographic regions we used a UPGMA analysis based on the average genetic distance between regional samples of mtDNA haplotypes (Fig. 2). The Central and Eastern stocks of the North Pacific clustered together as did the Group IV and V stocks of the Southern Ocean. The Southern Oceans population was intermediate between the North Pacific and North Atlantic populations, while somewhat closer to the North Atlantic in average genetic distance.

The hierarchical analysis of mtDNA diversity showed a high degree of geographic differentiation within and among oceanic populations. Available formulations of the AMOVA program and limitations on the degrees of freedom at some levels of our analysis prevented a complete partitioning of molecular variance into the four levels of population structure present in our data: among oceans, among stocks within oceans, among regions within stocks and within regions. Instead, we tested the significance of different variance components using three sets of hierarchical analyses (Table 3). Overall, we found that nearly 60% of the molecular variance was explained by the nested population structure and that each population subdivision accounted for a significant portion of the overall haplotype diversity. In the analysis of stocks within oceans, for example, we found 38% of the haplotype diversity was explained by oceanic populations, 21% by stocks within oceans and 40% by diversity within stocks. The permutation procedure showed that the partitioning of variance within stocks (ϕ_{ST}) and among stocks within oceans (ϕ_{SC}) were highly significant. The significance of the variance among oceans, which is tested by permuting whole stock divisions randomly among oceans, could not be evaluated because of the small number of stock divisions. By nesting the 11 regions within oceans, however, we find a significant partitioning at all three levels (analysis 2, Table 3).

The gene identity analysis agreed with the results of the AMOVA, although providing somewhat lower estimates of the proportion of variance explained by population subdivisions (Table 4). The G_{ST} coefficient for the three oceans indicated that 30% of the variance in haplotype distributions is accounted for at the level of populations (three divisions, $G_{ST} = 0.301$; $P < 0.002$). Dividing the haplotypes into the six stocks explained an additional 11% of this variance (six divisions, $G_{ST} = 0.410$; $P < 0.002$). Assigning the haplotypes to their 11 seasonal habitats explained only slightly more of the variance than the six stock divisions (11 divisions, $G_{ST} = 0.420$; $P < 0.002$).

Table 3 The hierarchical analysis of molecular variance of mtDNA haplotypes among humpback whales, world-wide

	d.f.	% total variance	ϕ-statistic	*P*
Analysis 1				
Among Oceans	2	38.22	CT = 0.596	n.a.
Among Stocks/Oceans	3	21.22	SC = 0.345	0.001
Within Stocks	224	40.45	ST = 0.382	0.001
Analysis 2				
Among Oceans	2	49.26	CT = 0.609	0.001
Among Regions/Oceans	8	11.60	SC = 0.229	0.001
Within Regions	219	39.14	ST = 0.493	0.001
Analysis 3				
Among Stocks	5	55.81	CT = 0.587	0.001
Among Regions/Stocks	5	2.91	SC = 0.066	0.001
Within Regions	219	41.28	ST = 0.558	0.001

Note: The *P* value is reported as the probability of a more extreme variance component or ϕ-statistic than that observed, in comparison to a null distribution of these values based on 1 000 random permutations of the data matrix. In analysis 2, for example, ϕ_{ST} and the within-region variance component are tested by random permutations of individuals across the 11 regions. ϕ_{SC} and the among-regions/oceans variance component are tested by random permutations of individuals from a given ocean into regions within that ocean. ϕ_{CT} and the among-oceans variance component were tested by random permutations of whole regional samples across oceans.

Table 4 Summary of the G_{ST} coefficient from the gene identity analysis (Takahata & Palumbi 1985) and resulting indirect estimates of long-term average migratory exchange of females per generation (N_m) between regions based on the comparisons of humpback whale mtDNA haplotypes in each oceanic population

Regional Comparison	Population divisions	G_{ST}	N_m
World Wide			
Oceanic Populations	3	0.301**	1.17
Stocks	6	0.410**	0.72
Regional Habitats	11	0.420**	0.69
North Pacific Ocean			
South-eastern Alaska to Central California	2	0.411**	0.72
Hawaii to Mexico	2	0.037	13.00
Central North Pacific to Eastern North Pacific	2	0.070**	6.64
North Atlantic Ocean			
within the Gulf of Maine	2	0.156*	n.a.
Gulf of Maine to Newfoundland	2	0.000	166.20
Southern Ocean			
Eastern Australia to Tonga	2	0.076	6.08
Group IV to V	2	0.154**	2.75

Note: Significance of G_{ST} coefficient tested by 500 random permutations. Values not exceeded by more than 2.5% of the 500 simulations are noted by * and those not exceeded in any simulation by **. The minimum number of female migrants exchanged between populations per generation N_m, was calculated from the approximation, $G_{ST} = 1/(1 + 2N_m)$ (Takahata & Palumbi 1985). No rates of migratory exchange were calculated for the within Gulf of Maine analysis since the tested population divisions were not geographic.

To test for possible sex-biases in dispersal among seasonal habitats, we identified the sex of most individual whales in our sample. Molecular genetic identification of each individual's sex showed a significant bias towards males in the world-wide sample (134:87, $\chi^2 = 10.0$, $P < 0.005$; Table 1). This bias, however, was not specific to seasonal habitats (e.g. feeding or wintering grounds) or significant for most regional samples. Males predominated on the Hawaiian wintering grounds while females predominated on the Tongan wintering grounds, although these differences were not significant with the present sample size. The sex ratio was nearly equal on the south-eastern Alaskan, Newfoundland and Gulf of Maine feeding grounds but biased toward males in Central California. Significant regional biases towards males were found only on the Mexican wintering grounds ($\chi^2 = 10.7$, $P < 0.005$) and the Western Australia migratory corridor ($\chi^2 = 9.3$, $P < 0.005$).

The central and eastern North Pacific

Background. Based on an examination of logbooks from 19th-century whalers, Kellogg (1929) suggested that humpback whales in the North Pacific were divided into two stocks. He proposed that an Asian stock winters in tropical waters south of Japan and travels north to feeding areas in the Sea of Okhotsk and along the Kamchatka Peninsula. An American stock was thought to breed in the waters off the west coast of Mexico and travel northward along the coast of North America to feeding grounds in the Gulf of Alaska, the Bering Sea and near the Aleutian Islands. Although Rice (1974) suggested that whales from the Hawaiian wintering grounds are part of an extended American stock, Kellogg (1929) did not consider this group and may have been unaware of its existence (Herman 1979).

Observations of naturally marked individuals now demonstrate that individuals from Alaskan feeding grounds migrate primarily to wintering grounds around the windward islands of Hawaii (Darling & Jurasz 1983; Darling & McSweeney 1985; Baker *et al.* 1986). In the eastern North Pacific, individuals from the central California feeding ground migrate primarily to wintering grounds along the coast of Mexico (Urban & Aguayo 1987; Calambokidis *et al.* 1990). Although the majority of data on migratory movement of naturally marked individuals suggest a demographic division between the central and eastern component of the North Pacific population (Perry *et al.* 1990), important exceptions have been noted. A few whales from Alaska have been observed in Mexico and one whale from central California has been observed in Hawaii (Baker *et al.* 1986). Movement between wintering grounds by individual whales has also been documented, although these occurrences are infrequent (Darling & Jurasz 1983; Darling & McSweeney 1985; Baker *et al.* 1986). Finally, the winter song of the humpback whale, a presumed male mating display, changes from year to year but remains similar on the two wintering grounds (Payne & Guinee 1983), indicating some acoustic contact between these groups.

Genetic analysis. We tested differences in haplotype frequencies among seasonal habitats and between the central and eastern stocks of the North Pacific population using samples from 95 humpback whales (Fig. 3a): 38 from south-eastern Alaska, 20 from central California, 16 from Hawaii and 21 from Mexico. Among the 95 individuals surveyed, there were 6 haplotypes differing from each other by between 1 and 4 restriction sites. The 'A' type was unanimous on the south-eastern Alaskan feeding ground, dominant on the Hawaiian wintering ground and common on the Mexican wintering grounds. The 'E' type was common on the central California feeding

ground and the coastal Mexican wintering ground. The 'F' type was dominant in central California, present in low numbers in Mexico and represented by a single individual in Hawaii. The 'G' and 'H' types were represented by single individuals in central California and the 'AE' type by two individuals in Mexico.

Considerable geographic structure is obvious in the overall distribution of mtDNA haplotypes among the four regional habitats of the central and eastern North Pacific ($G_{ST} = 0.278$, $P < 0.002$). Haplotype frequencies showed a categorical (i.e. fixed) segregation between the south-eastern Alaska and central California feeding grounds ($G_{ST} = 0.414$, $P < 0.002$) and a strong connection between south-eastern Alaska and the Hawaiian wintering grounds, as noted previously (Baker *et al.* 1990). Mexico, however, shared similarities in haplotype frequencies with both feeding grounds. Differences between the Hawaiian and Mexican wintering grounds were significant with the randomized Test of Independence ($\chi^2 = 12.68$, $P < 0.002$) but not the analysis of gene identity ($G_{ST} = 0.037$, $P > 0.10$).

To test differences between the central and eastern components of the North Pacific population, samples from Hawaii and Alaska were combined and compared to the combined samples from central California and Mexico. We chose to test the genetic significance of this population subdivision based on historical descriptions of stocks (e.g. Kellogg 1929), longitudinal geographic distances and the current understanding of migratory movement among naturally marked individuals (e.g. Perry *et al.* 1990). The analysis of gene identity showed that this stock division was highly significant ($G_{ST} = 0.0976$, $P < 0.002$), although accounting for substantially less variation than the complete partitioning into seasonal habitats.

The western North Atlantic

Background. Humpback whales in the western North Atlantic congregate each winter to give birth and presumably to breed in the shallow waters over submerged banks and along the coastlines of islands in the West Indies (Whitehead 1982; Martin *et al.* 1984; Mattila *et al.* 1989; Katona & Beard 1990). During summer months, individual whales predictably return to only one of four geographically distinct coastal feeding grounds (Katona & Beard 1990): Iceland, western Greenland, Newfoundland (including the coast of Labrador), and the southern Gulf of Maine. Movement between feeding grounds is restricted and fidelity to a particular feeding ground is high (Katona & Beard 1990). An eastern North Atlantic stock of humpback whales is thought to migrate from feeding grounds along the coast of northern Europe to winter grounds near the Cape Verde Islands, but little is known of the current status of this group (Bannister *et al.* 1984).

Genetic analysis. We tested differences in haplotype frequencies between feeding grounds and between feeding and wintering grounds in the western North Atlantic using samples from 90 humpback whales (Fig. 3b): 42 from the Gulf of Maine, 18 from Newfoundland and 30 from the Dominican Republic. Among the 90 individuals surveyed there were 8 haplotypes differing from each other by between 1 and 6 restriction sites. Two of these types, 'JJ' and 'JB', were not described in a previous survey of 28 individuals from the Gulf of Maine (Baker *et al.* 1990). Of the eight total haplotypes found in the combined western North Atlantic samples, 'JJ' and 'L' were found only in the Gulf of Maine, 'JB' was found only in the Dominican Republic, 'K' was common to only the Gulf of Maine and the Dominican Republic, and 'C', 'D' and 'I' were common to all three regions. No haplotype was unique to Newfoundland.

There was little evidence of distinct geographic structure among the three seasonal habitats of the western North Atlantic. An analysis of gene identity indicated no significant differences between the Gulf of Maine and Newfoundland (two regions, $G_{ST} = 0.001$, $P = 0.78$). Given the absence of significant differences between these two feeding grounds, the samples were pooled and compared to the Dominican Republic. A Test of Independence showed significant heterogeneity in this comparison ($\chi^2 = 15.01$, $P < 0.03$) although the analysis of gene identity did not (three regions, $G_{ST} = 0.001$, $P = 0.90$).

Although there was no evidence of a division between the two feeding grounds, a surprising degree of heterogeneity was found between two distinct samples collected within the Gulf of Maine (Baker *et al.* 1994). The first sample was collected during necropsies of ten victims of an unusual group mortality during the winter of 1987–88. Geraci *et al.* (1989) reported that these animals died suddenly after ingesting Atlantic mackerel containing elevated levels of saxotoxin, a dinoflagellate neurotoxin responsible for paralytic shell-fish poisoning in humans. This sample was dominated by 'C' and 'D' haplotypes. The second sample of 32 individuals was collected by biopsy darting in the southern Gulf of Maine during the summers of 1988–89. This sample was dominated by 'I' and 'J' haplotypes. The partitioning of these two sampled groups indicated significant genetic structure ($G_{ST} = 0.156$, $P = 0.018$) or heterogeneity within the Gulf of Maine.

The Southern Oceans

Background. Historically, the two most extensively studied stocks of humpback whales in the world are those of

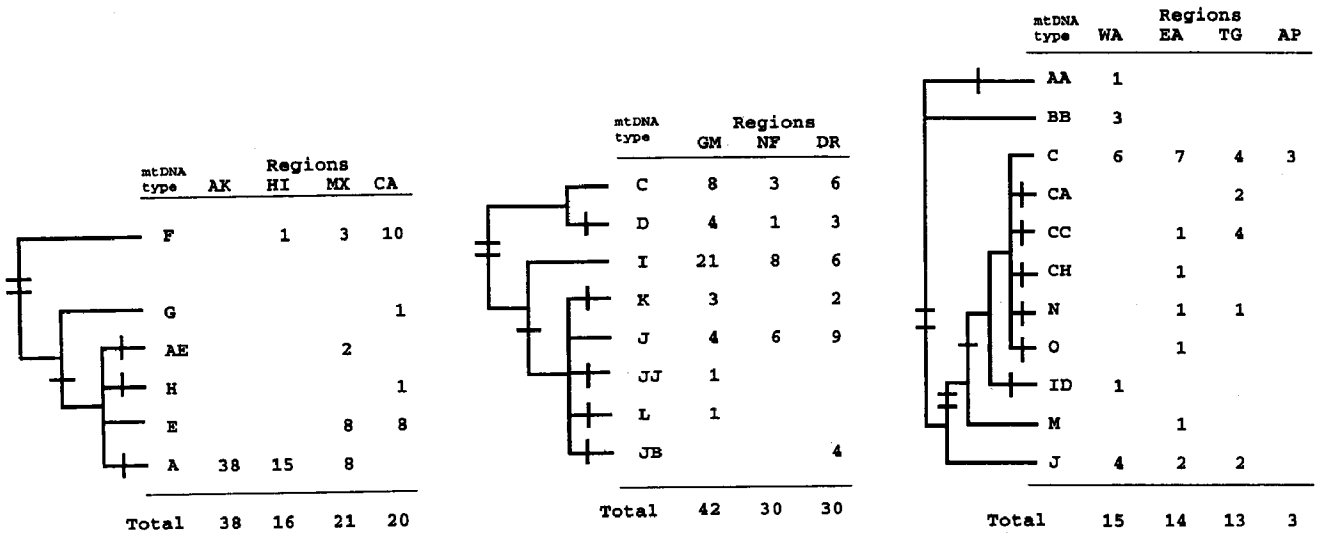

Fig. 3 (a) Genealogy and frequency of mtDNA haplotypes in the central California (CA), Mexico (MX), Hawaii (HI) and south-eastern Alaska (SEA) regions of the central and eastern North Pacific. Genealogy is based on a majority rule consensus of four equally parsimonious trees (length = 6; Consistency Index = 0.833) found in a branch and bound search of the data using the computer program PAUP. Perpendicular bars along the tree indicate inferred restriction site changes. (b) Genealogy and frequency of mtDNA haplotypes in the southern Gulf of Maine (GOM), Newfoundland (NF), and Dominican Republic (DR) regions of the western North Atlantic. Genealogy is based on a majority rule consensus of four equally parsimonious trees (length = 9; Consistency Index = 0.889) found in a branch and bound search of the data using the computer program PAUP. Perpendicular bars along the tree indicate inferred restriction site changes. (c) Genealogy and frequency of mtDNA haplotypes in the Western Australia (WA), Eastern Australia (EA), Tonga (TG) and Antarctic Peninsula (AP) regions of the Southern Ocean. Genealogy is based on a majority rule consensus of 21 equally parsimonious trees (length = 12; Consistency Index = 0.833) found in a branch and bound search of the data using the computer program PAUP. Perpendicular bars along the tree indicate inferred restriction site changes.

Antarctic Groups IV and V (Chittleborough 1965; Dawbin 1966). The approximate geographic boundaries of the Group IV and V humpback stocks in Antarctic waters have been defined by the distribution of catches and the interpretation of Discovery marking results (Chittleborough 1965). After a period of summer aggregation, Group IV humpback whales migrate along the coast of Western Australia to wintering grounds off the northwest coast of Australia. Group V humpbacks segregate along two major corridors during migration to wintering areas in tropical latitudes. The eastern component migrates along the coastline of New Zealand and is presumed to winter primarily near islands in the Southwest Pacific including Tonga, the Cook Islands, Niue, Samoa, and Fiji (Townsend 1935; Dawbin 1966). The western component of the Group V stock migrates along the coast of eastern Australia and is thought to winter in coastal waters inshore of the Great Barrier Reef (Paterson & Paterson 1989).

Genetic analysis. We tested differences in haplotype frequencies between the eastern and western migratory components of Group V and between Group IV and V using samples from 42 individuals collected in the Southern Ocean (Fig. 3c): 15 individuals from Western Australia, a migratory corridor for Group IV, 14 from eastern Australia, a migratory corridor for the western component of Group V and 13 from Tonga, the presumed wintering ground for the eastern component of Group V. Three individuals from the Antarctic Peninsula, a feeding ground for Groups I–VI, are included for comparison but the sample size is considered too small for statistical analysis. Among the 45 individuals surveyed, there were 11 haplotypes differing from each other by between 1 and 5 restriction sites. Of the 11 total haplotypes, 'BB', 'ID', and 'AA' were unique to Western Australia, 'M', 'O' and 'OH' were unique to eastern Australia, 'CA' was unique to Tonga and 'CC' and 'CA' were common to eastern Australia and Tonga. The two haplotypes with the broadest distributions, 'J' and 'C', were indistinguishable at this level of genetic resolution from types found in the western North Atlantic.

The potential for genetic divisions or heterogeneity within Group V, i.e. between eastern Australia and Tonga, was tested first because of the historic inclusion of these two geographically distant regions as a single stock. An analysis of gene identity suggested that geographic location explained about 7% of the variation in the samples but this difference was not significant with the available sample size (two regions, $G_{ST} = 0.0763$, $P = 0.42$).

Based on the absence of significant differences between eastern Australia and Tonga, samples from these two regions were pooled and compared to Western Australia (Group IV). An analysis of gene identities indicated significant differences between the Group IV and V regions (two regions, $G_{ST} = 0.1539$, $P < 0.002$). Analysis of unpooled samples from Western Australia, eastern Australia and Tonga also gave significant results (three regions, $G_{ST} = 0.1440$, $P < 0.002$).

Discussion

Oceanic population divisions

Humpback whale maternal lineages are highly subdivided among the three major oceanic populations despite the nearly unlimited dispersal potential of this species, as evidenced by a long-distance seasonal migration exceeding 16 600 km annually (Stone *et al.* 1990). Of the 22 mtDNA haplotypes found in the world-wide survey of 230 individuals, only three were found in more than one ocean and none were found in all three oceans. Maternal lineages within oceanic populations are further segregated into stocks which are not separated by obvious geographic barriers. In the North Pacific, these stocks are further structured by seasonal migration, with maternal lineages showing greater segregation on summer feeding grounds than on winter breeding grounds. The AMOVA suggests that 60% of the world-wide haplotype diversity can be explained by the described population subdivisions. Individual variance components were significant for each of the three hierarchical levels tested, among oceans, among stocks within oceans and among regions within stocks. By comparison, a similar hierarchical analysis of mtDNA haplotype diversity among 10 human ethnic populations grouped into five larger geographic regions explained only 26% of the total molecular variance (Excoffier *et al.* 1992).

Under the assumptions of neutral theory and the island model of gene flow, the gene identity analysis can be used to estimate long-term rates of migration among populations or subpopulations (Table 4). The observed G_{ST} value of 0.30 for the world-wide population of humpback whales suggests that gene flow between oceans is limited to about one female per generation ($N_m = 1.17$). This value is comparable to that derived for human continental populations using a high resolution restriction mapping of mtDNA (Stoneking *et al.* 1990) and low resolution restriction site approach (Merriwether *et al.* 1991) similar to our own. For stocks of humpback whales, the observed G_{ST} value of 0.41 suggests that gene flow is further restricted to less than one female per generation at this level of population subdivision ($N_m = 0.72$).

The average genetic distance between stocks showed a good agreement with their geographic distribution. Stocks cluster by ocean in the UPGMA tree and the western North Atlantic shows a closer relationship to the contiguous Southern Ocean than to the North Pacific which is separated by continental land masses. It was not possible, however, to construct a world-wide phylogeny of mtDNA haplotypes using RFLP data. The parsimony analysis of the world-wide sample indicated a considerable degree of homoplasy in the restriction-site changes used to define the 22 haplotypes. This problem was not encountered in the parsimony reconstructions of RFLP haplotypes within oceans, perhaps because lineages within oceans have not diverged sufficiently to accumulate parallel site changes or reverse mutations. Greater molecular resolution of haplotypes is needed to reconstruct, with reasonable confidence, the world-wide phylogenetic relationship of mtDNA lineages (Baker *et al.* 1993).

Within-ocean divisions

The North Pacific. The complexity of population structure in the central and eastern North Pacific emphasizes the importance of a hierarchical sampling design for genetic analysis of whale populations. Here, the distribution of mtDNA haplotypes revealed a profound segregation between maternal lineages on the two sampled feeding grounds, south-eastern Alaska and central California (Baker *et al.* 1990). The G_{ST} analysis suggests an interchange of fewer than one female per generation between these two coastal feeding grounds ($N_m = 0.72$, Table 4). As expected from previous mtDNA analysis and the migratory movement of naturally marked individuals, Hawaii was closely related to south-eastern Alaska and distantly related to the central California feeding grounds. The Mexican wintering grounds, however, were dominated by haplotypes common to both feeding grounds. Despite the intermingling of haplotypes in Mexico, the G_{ST} analysis supports the division of the North Pacific into a central stock which feeds in Alaskan waters and winters predominantly in Hawaii, and an eastern or 'American' stock that migrates between feeding grounds along the coast of California and wintering grounds along the coast of Mexico. Estimated gene flow between these two stocks was higher than that observed for some other population divisions but low by demographic standards ($N_m = 6.64$).

The western North Atlantic. The distribution of mtDNA haplotypes in the southern Gulf of Maine and Newfoundland provides little evidence of profound geographic segregation among maternal lineages. The G_{ST} analysis indicates that less than 1% of the observed genetic variation was explained by these regional divisions and examination of the parsimony tree shows that four of the seven resolved haplotypes are represented in both regions. The

heterogeneity between haplotypes on the two sampled feeding grounds and the wintering grounds near the Dominican Republic, however, implies some genetic divisions among regions of the western North Atlantic. Since the Caribbean wintering congregation includes individuals from all known feeding grounds (Mattila *et al.* 1989; Katona & Beard 1990), the observed heterogeneity may reflect differences between the westerly continental feeding grounds sampled here, and insular feeding grounds to the east (e.g. Greenland and Iceland).

A more surprising result of the western North Atlantic survey is the evidence of a distinct genetic heterogeneity within the southern Gulf of Maine feeding grounds. The sample of victims from an unusual dinoflagellate poisoning were dominated by two mtDNA types ('C' and 'D') which were uncommon in the sample of whales collected by biopsy darting. A G_{ST} analysis of these two samples indicated genetic differences as large as those observed between stocks (e.g. Groups IV and V of the Southern Oceans). Such differential mortality among maternal lineages can accelerate the loss of genetic variation in small or highly structured populations and violates some of the basic assumptions of the 'coalescent' approach to the genetic investigation of small populations (Tajima 1983). This result suggests a surprising degree of fine-scale genetic structure in whale populations and demonstrates the need to evaluate unusual mortality events within the context of the genetic mosaic of natural populations (O'Brien & Evermann 1988). The underlying causes of this local heterogeneity are not known but may include preferred social affiliations between individuals of common maternal descent (i.e. a 'group' bias due to maternal kinship), local habitat or prey preference among matrilines, and temporary emigration due to seasonal migratory patterns (Hammond 1990; Weinrich *et al.* 1992b; Baker *et al.* 1994).

The Southern Oceans. Historic descriptions of stock differentiation between Groups IV and V (Chittleborough 1965; Mackintosh 1965; Dawbin 1966) were supported by the observed distribution of mtDNA haplotypes of humpback whales migrating past Western Australia (Group IV), eastern Australia (Group V, western component) and the Tongan archipelago (Group V, eastern component). Although the two most common haplotypes were found in all three regions, three haplotypes were unique to Western Australia and six haplotypes were unique to eastern Australia and Tonga. Estimated gene flow between the Group IV and combined Group V divisions (N_m = 2.75) was less than half that observed in the comparable analysis of the eastern and central stocks of the North Pacific, although considerably larger than that estimated for the south-eastern Alaska and central California feeding grounds. Genetic differences between the eastern and western components of Group V were not significant given current samples sizes. However, the presence of at least one unique haplotype in Tonga and five in eastern Australia, and the moderately large G_{ST} value argue for a more detailed survey of these regions and other described wintering grounds in the south-west Pacific.

Maternally directed migratory fidelity

Given the tremendous mobility of humpback whales and the apparent absence of geographic barriers within oceanic basins, the formation of significant genetic divisions between stocks indicates strong fidelity to migratory destinations. The demonstrated ability of individual whales to visit alternate wintering grounds and, on occasion, to move between feeding grounds (Baker *et al.* 1986) argues against a strict behavioural imprinting or site-specific genetic programming underlying this fidelity. Instead, the life history strategy of humpback whales suggests a likely mechanism for a 'cultural' transmission of migratory destinations (Baker *et al.* 1990). Calves are born on or near the wintering grounds and complete a round-trip migration to the feeding grounds before separating from their mothers (Matthews 1937). The continued regional return of individual whales identified during their first year of life suggests that migratory fidelity develops as a result of a calf's early maternal experience (Martin *et al.* 1984; Baker *et al.* 1987; Clapham & Mayo 1987). The prolonged suckling period of humpback whale calves, relative to other balaenopterid whales (Brown & Lockyer 1984), could facilitate and reinforce this maternal, cultural inheritance of migratory destinations. Similarly, the reported ability of a calf to learn idiosyncratic feeding strategies from its mother (Weinrich *et al.* 1992b), provides additional evidence of cultural transmission of behaviour in humpback whales.

Although apparently maternally directed, the migratory fidelity of humpback whales cannot accurately be described as 'natal' (e.g. Bowen *et al.* 1989; Bowen *et al.* 1992). In the central and eastern North Pacific, where a complete hierarchical analysis of feeding and wintering grounds was possible, segregation of haplotypes was strongest between the two feeding grounds. The two wintering grounds, where calves are presumed to be born, showed evidence of migratory interchange of haplotypes. This seasonally structured pattern of migration suggests an evolutionary strategy that takes advantage of the social or genetic benefits of both philopatry and dispersal. Strong maternally directed fidelity to particular feeding grounds could be reinforced by the opportunity to form cooperative foraging associations among close relatives or familiar partners (Baker 1985; Weinrich 1991), as well as the more obvious advantages of learning local patterns of prey availability (Baker *et al.* 1992). Conversely, the

apparent intermingling of mtDNA types on the Hawaiian and Mexican wintering grounds could reflect a strategy for outbreeding and intrasexual competition for mates during the winter breeding season (Tyack & Whitehead 1983; Baker & Herman 1984).

Among many mammalian species, natal fidelity is often biased towards females while juvenile dispersal is often biased towards males (Greenwood 1983). In extreme cases, this could lead to different patterns of mtDNA haplotype distributions in the sexes, although evidence of male dispersal would be lost during each generation since even reproductively successful male immigrants would leave no mtDNA heirs. Among our samples of humpback whales, however, we found no obvious evidence of sex biases in dispersal or fidelity. On the south-eastern Alaskan and central Californian feeding grounds, where strong migratory fidelity maintains categorical segregation of maternal lineages, the dominant haplotypes included both males and females. On the Hawaiian and Mexican wintering grounds, where individuals from different feeding grounds may intermingle, most haplotypes were represented by both sexes; the anomalous 'F' type found on the Hawaiian wintering grounds was a female, and the 'A', 'E' and 'F' types on the Mexican wintering grounds included at least one female each. The dominance of males in samples from Western Australia and Mexico is more likely attributable to known differences in the timing of migration among age–sex classes of humpback whales (Dawbin 1966), behavioural characteristics that make males more accessible to biopsy collection (Baker *et al.* 1991) and permit conditions limiting or prohibiting the collection of samples from cow-calf pairs, than to sex-bias dispersal. A specific test of possible sex biases in dispersal or habitat use will require a substantially larger and more systematic collection of regional samples.

Implications for management

The concept of baleen whale stocks, or population divisions, has a long history of controversy (e.g. Chapman 1974; Donovan 1991). Nevertheless, the assumption of biologically significant subdivisions within oceanic populations has been, and continues to be, fundamental to management schemes of exploited (Donovan 1991) and protected (NMFS 1991) species. For exploited species, an understanding of stock boundaries is critical for estimating abundance, setting catch limits and interpreting catch statistics and life-history parameters. For protected species, stock boundaries are important for assessing population changes, establishing territorial jurisdiction and identifying critical habitats.

In an attempt to sort through the history of the stock concept in baleen whales, Donovan (1991) provides the following working definition: 'a relatively homogeneous and self contained population whose losses by emigration and accessions by immigration, if any, are negligible in relationship to the rates of growth and mortality'. Given this demographic definition, it is clear that significant genetic differences between population subunits should be considered strong evidence for stocks and that these population subdivisions should be afforded independent management status. Between south-eastern Alaska and central California, for example, we detected no common mtDNA haplotypes and our estimate of Nm, based on the G_{ST} analysis, was less than one female per generation. Between Group IV and V of the Southern Oceans, we detected both common and unique haplotypes in significantly different frequencies and our estimate of Nm was approximately three. With such low rates of migratory interchange, it is obvious that the harvest, or recovery, of whales in one region will have little effect on the population status of the other region across a management time scale.

The absence of significant genetic differences, however, should not be considered conclusive proof of demographic homogeneity (Palumbi *et al.* 1991). Genetic differences among populations accumulate slowly by demographic standards and the effects of gene flow are independent of population size. Thus, long-term rates of migratory exchange as low as a few females per generation are likely to maintain relatively homogeneous frequencies of mtDNA haplotypes among populations at equilibrium (Birky *et al.* 1983; Slatkin 1987). Among populations of even moderate sizes (> 1000 individuals each), migratory rates an order of magnitude greater than this would still be negligible in relation to rates of growth and mortality.

Finally, it should be noted that the baleen whale stock concept has generally involved the assumption of reproductive isolation. We have addressed here only genetic differences attributable to the segregation of maternal lineages, as reflected in the distribution of mtDNA haplotypes. Observations of migratory interchange between wintering grounds by naturally marked whales and our own descriptions of intermingling between haplotypes on the Hawaiian and Mexican wintering grounds suggest that the structure of nuclear DNA variation may be more complex. Further investigation of nuclear DNA markers are necessary to address questions concerning the mating system of humpback whales and the possibility of reproductive isolation between stocks and oceanic populations (Baker *et al.* 1993). As the description of nuclear and mitochondrial DNA variation in the green sea turtle has shown, different genetic structures can coexist within a single species (Karl *et al.* 1992). The humpback whale, with its seasonal pattern of long-distance migration and complex social organization in-

volving a competitive mating system and cooperative or non-competitive foraging strategies (Baker 1985), is likely to have evolved a similarly complex population genetic structure (Palumbi & Baker 1994). A more thorough understanding of genetic and demographic divisions among humpback whales could provide a comparative model for managing less tractable species of baleen whales, as well as a more general understanding of gene flow and population structure in the marine ecosystem.

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This world-wide survey is the result of international collaboration between researchers involved in regional studies of humpback whales and those involved in the application of molecular techniques to questions concerning the social organization, migration and population structure of this and other endangered species. Our common interests are the understanding and conservation of genetic resources in the marine ecosystem.
