Genetic Structure of Cetacean Populations in Sympatry, Parapatry, and Mixed Assemblages: Implications for Conservation Policy

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Many cetaceans have a wide distribution in one or more oceans, and in some species, individuals migrate over an extensive range. When breeding sites are geographically distant from foraging grounds, as for a number of baleen whales, genetic stocks may be geographically isolated during a breeding season and together in a mixed assemblage during a separate feeding season. These assemblages can be spatially and temporally dynamic and pose a special problem for managers when whales are hunted on feeding grounds (as is typical). For other species seasonal migrations are less pronounced, but the same effect of locally mixing genetic stocks can develop through other mechanisms. Examples are described where intraspecific foraging specializations appear to be important in limiting gene flow between sympatric and parapatric populations. It is proposed that learning could be important in the generation and maintenance of these specializations. The effective conservation of genetic diversity in these species will require further data on both spatial and temporal components of population genetic structure.

Overview of Cetacean Phylogeography

Cetaceans are highly mobile and can range over vast distances. In some cases their prey is also widely distributed, while in other cases it is regionally abundant. In the latter case, some species, especially among the baleen whales, can fast for long periods between feeding bouts and travel great distances in the interim. These are some of the factors creating the potential for complex patterns of population structure. A few species, such as the fin whale (*Balaenoptera physalus*), blue whale (*B. musculus*), and sei whale (*B. borealis*) have extensive ranges, but their migration patterns are poorly understood. Several baleen whales, however, are famous for their predictable and extensive migrations, including the grey whale (*Eschrichtius robustus*), humpback whale (*Megaptera novaeangliae*), and southern right whale (*Eubalaena australis*). For these species, migrations are between very localized breeding and feeding grounds that the whales return to each year. Some of the dolphin species, in contrast, range over relatively finite geographic areas. For example, local populations of the bottlenose dolphin (*Tursiops truncatus*), such as the "aduncas type" off the coast of South Africa, have been described (Ross 1977),

and some members of the family Platanistidae (the river dolphins) have narrowly defined ranges within local river systems. Other odontocetes such as killer whales and harbor porpoise have a very wide distribution in the worlds oceans, though both proximate and distant populations can become genetically differentiated (Hoelzel et al., 1998; Hoelzel and Dover 1991a; Rosel et al. 1995; Wang et al. 1996).

Various studies have investigated the population genetics of cetacean species (see reviews in Hoelzel 1992, 1994). In an extensive study based on the analysis of up to 45 allozyme loci (on a total of nearly 18,000 samples taken during whaling expeditions), four species were investigated in detail: fin, minke (*B. acutorostrata*), brydes (*B. edeni*), and sei whales (Wada and Numachi 1991). Each of these are pelagic species that are known to travel long distances, but there are also important distinctions. Three (the fin, minke, and sei whales) were caught primarily on feeding grounds in the Antarctic and in the North Atlantic, but the brydes whale has a very different distribution, limited to warm temperate and tropical waters. This species was hunted in populations from Madagascar to Peru.

The least genetic differentiation was between fin whales sampled from a nearly

circumpolar distribution in the southern hemisphere, and from across the North Pacific from the Kamchatka Peninsula (Russia) to British Colombia. Pairwise comparisons among nearly 500 whales from across this range gave Nei genetic distances in the range of 0.0004 to 0.0007; too low to imply any clear distinction. Three putative populations were identified in the Antarctic, the North Pacific, and off the coast of Spain. Most of the variation found could be explained by variation within populations ($G_{ST} = 0.071$). Sei whales were sampled over a very similar range, but without any samples from Spain. Comparing all samples, the pairwise Nei distance was an order of magnitude greater than that for fin whales (0.0084), and there was evidence for greater differentiation between putative populations in the southern and northern hemispheres ($G_{ST} = 0.165$).

The minke whales were sampled over a similar range in the Antarctic, though further south for the most part. In the northern hemisphere minkes were sampled from three nearshore populations: the coast of Brazil near Recife, the southeastern coast of Korea, and the northeastern coast of Japan. The Brazilian sample was analyzed for fewer loci than for the other three samples (14 compared to 43 or 37) and showed a very similar allele distribution to the Antarctic sample. Comparisons of the other three putative populations showed much greater variation ($G_{ST} = 0.558$) than had been seen for either sei or fin whales, including differentiation between the proximate Korean and Japanese minke whale stocks ($D = 0.0125$). Genetic distance between the northern and southern Pacific stocks was greater than that seen between sei and brydes whales (0.0885 versus 0.0567). Based on this study and consistent genetic studies using other markers (Hoelzel and Dover 1991b; Wada et al. 1991), it has been proposed that the northern and southern hemisphere minke whales be classified as separate species. Hoelzel and Dover (1991b) also found high levels of differentiation between minke whales in the North Atlantic and those in the North Pacific.

Wada and Numachi (1991) compared brydes whales from five putative populations: south of Madagascar, Indonesia, Fiji, the North Pacific, and the Peruvian coastal stock. In addition, there were six samples from the Solomon Islands of a "small form" of the species. The latter had been recognized as a local race, but the genetic analysis showed a genetic distance from other brydes whale stocks ($D = 0.47–0.52$) that was comparable to the largest genetic distances between species within the genus. Sequence data from the mitochondrial DNA (mtDNA) control region confirmed this distinction, with samples of the small form clustering in a distinct lineage within a brydes and sei whale clade (Dizon et al. 1996). Pairwise distances for allozymes between other brydes populations were similar to that seen for fin whales ($G_{ST} = 0.047$), though the geographic range was not as great (Wada and Numachi 1991). A mtDNA control region study indicated greater substructure in the region between the Indian Ocean and the Pacific than among oceanic samples in the Pacific (Pastene et al. 1996a).

The above examples illustrate the need to investigate patterns of phylogeography further in other populations and for other species, and how geographic distance and genetic differentiation are not necessarily well correlated for cetacean species [see Hoelzel (1991a) for further discussion]. In this article I focus on the other end of the spectrum and discuss patterns of intraspecific genetic differentiation within a geographic region. There are several ways these patterns could come about. First, differentiation could occur in sympatry or parapatry. Second, populations could reconverge following differentiation in allopatry. This may occur, for example, as a consequence of habitat division during an ice age, or following range expansion reflecting a shift in environmental conditions. If prezygotic isolating mechanisms had developed in isolation, but crosses were still fully viable, the perpetuation of the population distinction in sympatry may depend on adaptations or behavior that developed in allopatry. Finally, populations that have differentiated in allopatry may mix in temporary assemblages, for example, when breeding populations of a migratory mysticete species mix on seasonal feeding grounds.

The concept of differentiation in sympatry is most controversial, though there are a number of possible examples in the literature [see reviews in Bush (1994) and Otte and Endler (1989)]. It has been suggested that this would be most likely to occur when "traits important in isolation are correlated with traits important in resource use" (Skulason and Smith 1995; cf. Rice and Hostert 1993). Further, resource specializations often begin with specializations in behavior (Metcalfe 1993; West-Eberhard 1989). I suggest that this may be an important mechanism for the genera-

tion of genetic differentiation among some sympatric and parapatric populations of cetacean species.

Resource Polymorphisms and Genetic Differentiation

Resource polymorphisms are discrete, intraspecific specializations reflecting differential niche use. They have been described for a broad diversity of species (some examples are listed in Table 1). These can be manifest in various ways, including morphological, life-history, and behavioral specializations (see reviews by Skulason and Smith 1995; Smith and Skulason 1996). In some cases, when differences in resource use lead to assortative mating or physical separation within a local environment, these specializations can lead to genetic differentiation, and possibly speciation in sympatry (see Smith and Skulason 1996). There are numerous examples of resource polymorphisms among fish species, often involving both morphological and behavioral variation. For example, several species of cichlids show prey choice specializations, including one genus (*Perissodus*) where individuals eat scales from either the right or the left side of live fish (Hori 1993). A frequency dependent selection model was proposed to explain the coexistence of these two strategists (Hori 1993). Specialists for benthic versus open water foraging exist for charr (McLaughlin and Grant 1994), trout (Ferguson and Taggart 1991), sticklebacks (Cresko and Baker 1995), and various other species, and often involve morphotypes adapted to each type of foraging (for example, benthic feeders typically have a mouth that faces downward). A number of fish species show differentiation between littoral and pelagic specialists. For example, individual bluegill sunfish in single North American freshwater lakes feed on either zooplankton in open water or on larvae clinging to vegetation in the littoral zone (Ehlinger and Wilson 1988). A specific strategy is required for efficient foraging in each environment, and it has been shown that individual fish require 3–5 days to learn to feed by each strategy (Ehlinger 1990).

A variety of preconditions have been proposed for the facilitation of resource specialization. These include the existence of "open" or underutilized niches and diminished interspecific competition (see Smith and Skulason 1996). The marine environment is homogeneous enough to support the distribution of a species

Table 1. Examples of resource specialization in vertebrate species

Species	Habitat and prey type	References
Fish		
Brown trout (*Salmo trutta*)	Benthivory, planktivory, piscivory	Ferguson and Taggart 1991; McVeigh et al. 1995
Stickleback (*Gasterosteus aculeatus*)	Benthivory, planktivory	Cresko and Baker 1995; McPhail 1994
Bluegill sunfish (*Lepomis macrochirus*)	Littoral, pelagic	Ehlinger 1990; Ehlinger and Wilson 1988
Pumpkinseed sunfish (*L. gibbosus*)	Littoral, pelagic	Robinson et al. 1993
Cichlid (*Cichlasoma mickleyi*)	Feeding on snails, plants	Kornfield et al. 1982
Birds		
Pacific reef heron (*Egretta sacra*)	Different hunting techniques	Rohwer 1990
Oystercatcher (*Haematopus ostralegus*)	Different hunting techniques	Goss-Custard and Dit Durell 1983
Cocos finch (*Pinaroloxias inornata*)	Feeding behavior and prey choice	Werner and Sherry 1987
African finch (*Pyrenestes ostrinus*)	Soft seeds, hard seeds	Smith 1987
Hookbilled kite (*Chondrohierax uncinnatus*)	Small snails, large snails	Smith and Temple 1982
Mammals		
Norway rat (*Rattus norvegicus*)	Feeding on limpets, crabs	Navarrete and Castilla 1993
Minke whale (*Balaenoptera acutorostrata*)	Different foraging strategies	Hoelzel et al. 1989
Killer whale (*Orcinus orca*)	Feeding on marine mammals, fish	Bigg 1982; Hoelzel 1991a, 1993
Bottlenose dolphin (*Tursiops truncatus*)	Nearshore, offshore, prey choice	Hersh and Duffield 1990; Mead and Potter 1995
Spotted dolphin (*Stenella attenuata*)	Nearshore, offshore	Douglas et al. 1984

over a broad geographic range, but local variations in habitat could also facilitate the development of local niche specializations. For example, the habitat in the marine littoral zone is very different from the offshore habitat, and in a given geographic location the marine habitat can vary considerably with increasing depth.

A simplified schematic of the types of environmental variation likely to be experienced by cetacean species is given in Figure 1. For the purpose of illustration, they are divided into factors related to habitat and prey type, though these are not necessarily independent. Over a very broad geographic scale oceanic features change, especially in relation to the character and depth of thermoclines, the effect of prevailing winds, and the consequent currents and upwelling. There are some cetacean species that are only found in polar regions, such as the monodontids [the beluga (*Delphinapterus leucas*) and narwhal (*Monodon monocerus*)], and others found primarily in tropical [e.g., spinner dolphins (*Stenella longirostris*)] or temperate regions [e.g., right whale dolphins (*Lissodelphis* sp.)]. Other species are distributed over a broad geographic range that can include tropical, temperate, and polar regions [e.g., the killer whale (*Orcinus orca*)]. Prey are relatively sparsely distributed in the tropics, and individual cetaceans feeding in this habitat range over large areas in search of food. Prey of all types are abundant in boreal and polar regions where cold, nutrient rich waters are brought to the surface by upwellings. However, maintaining body temperature in cold polar waters is energetically costly. Some species solve this problem by migrating between polar regions where they feed and temperate or tropical regions where they breed.

On a finer geographic scale, there are species that are found only in fresh water (most of the river dolphins, Platanistoidea), primarily in coastal waters [e.g., Peale's dolphin (*Lagenorhynchus australis*) and humpback dolphins (*Sousa* sp.)], or only in deep waters [e.g., the clymene dolphin (*Stenela clymene*) and rough-toothed dolphin (*Steno bredanensis*)]. A number of other species are found in both coastal and open-water habitats [e.g., killer whales, bottlenose dolphins (*T. truncatus*), Atlantic spotted dolphins (*S. frontalis*), and common dolphins (*D. delphis*)]. Franciscana (*Pontoporia blanvillei*) has a narrow distribution along the coastal waters from Peninsula Valdez in Argentina to the mouth of the Doce River in Brazil. Along this range franciscana are found in both coastal and estuarine habitats. Such distributions that include a range of marine habitats could lead to local intraspecific specializations.

One well-studied example of habitat specialization is that of the bottlenose dolphin, which occurs in coastal and offshore populations throughout its range. In the western North Atlantic, the nearshore and offshore forms have been described in some detail. Mead and Potter (1995) describe a number of distinguishing features based on a sample of 15 voucher offshore samples and 90 stranded dolphins. There was little variance among the cranial measures for the voucher offshore samples, and on this basis 18 of the stranded samples were classified as offshore for further comparisons. The relative width of the nasal bones (ratio between the internal nares and the condylobasal length) was consistently greater for the offshore form, with very little overlap. The offshore form also had a greater body and skull length, though there was considerable overlap for these two measures. There were also consistent differences in the stomach contents and parasite load. The nearshore form fed primarily on four species of
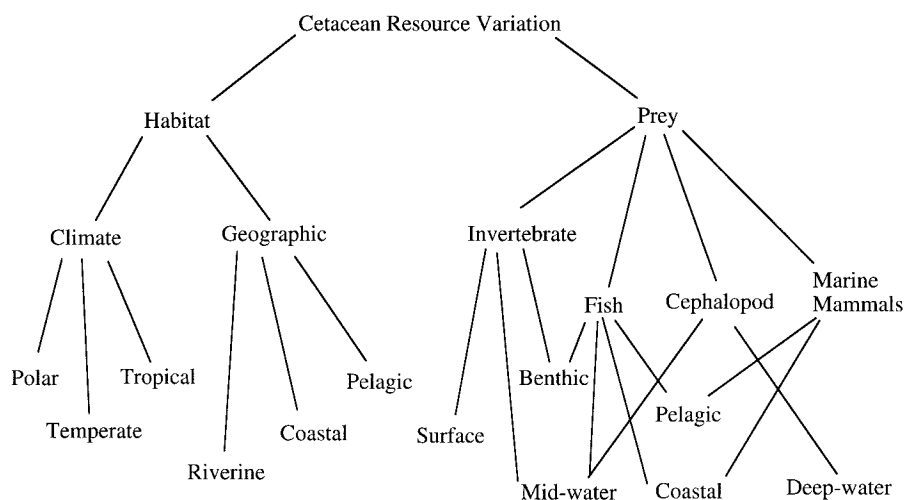

Figure 1. Schematic depicting some of the types of resource variation experienced by cetacean species. Multiple categories are relevant for some species.

coastal fish, while the offshore form fed on different pelagic fish species and squid. Lesions from the parasitic nematode Crassicauda were found in 74% of the samples classified as offshore and only 1.6% of those classified as nearshore.

Hoelzel et al. (in press) conducted a genetic study of these putative nearshore and offshore populations using both mtDNA and microsatellite DNA markers. Significant allele frequency differences and R_{ST} distances (after Slatkin 1995) were found from comparisons between nearshore and offshore populations at five microsatellite loci. Sequence comparisons at the mtDNA control region locus also indicated that a high proportion of the variation could be explained by differences between populations ($\emptyset_{ST} = 0.6$). The $\emptyset_{ST}$ statistic incorporates both haplotype frequency and sequence divergence into a measure of genetic differentiation (Excoffier et al. 1992). A value of 0.6 implies a genetic migration rate of approximately $Nm = 0.33$, where $Nm = (1/\emptyset_{ST} - 1)/2)$, or roughly one female genetic migrant every three generations. These results are consistent with earlier studies showing differences between the type and concentration of hemoglobin between putative nearshore and offshore forms (Duffield et al. 1983).

Other studies of nearshore and offshore forms also indicate morphological and in some cases genetic distinctions. For example, nearshore and offshore forms of spotted dolphin (*S. attenuata*) can be distinguished by tooth and jaw structure (Douglas et al. 1984). Two forms of common dolphin (*D. delphus*) have been classified by the length of the beak. In this case, ranges overlap, and both forms are sometimes found in the nearshore habitat. Rosel et al. (1994) compared a small sample of the two forms (8 short-beaked common dolphins from California and 10 from other populations with 11 long-beaked common dolphins from California) and found a net mtDNA sequence divergence of 1.78% between forms in California and no shared haplotypes.

Most of the above examples involve putative populations that occupy parapatric ranges. These habitats differ in a number of ways, including depth, prey diversity, and prey species composition. Both differences in nasal morphology (Mead and Potter 1995) and hemoglobin type (Duffield et al. 1983) in the bottlenose dolphin have been proposed to reflect differences in diving behavior, possibly related to prey choice and the propensity for the off-

Table 2. Differences between resident and transient killer whale pods

Character	Resident type	Transient type
Prey	Mostly fish	Mostly marine mammals
Range	Seasonally predictable and correlated with salmon runs in regions of the eastern North Pacific.	Less predictable (with some exceptions) and apparently extending over a larger geographic area.
Group size	Typically 5 to 80	Typically 1 to 15
Dispersal behavior and pod stability	No evidence of recruitment by immigration in long-term study of pod composition. Males remain in natal pod into sexual maturity. Pod composition highly stable.	Pod composition relatively fluid.
Acoustic behavior	Complex vocal repertoire. Tend to be vocal while foraging.	Relatively simple vocal repertoire. Tend to be silent while hunting.
Morphology	Variable "saddle patch" pigmentation; rounded dorsal fin common.	Relatively invariant saddle patch; pointed dorsal fin common.

Data used in table were derived from Baird and Stacey (1988), Baird and Dill (1995), Bigg et al. (1987, 1990), Guinet (1992), Hoelzel and Osborne (1986).

shore form to prey on deep-water species such as squid. However, in other species, intraspecific foraging specializations also occur in sympatry. The best known example is that of the killer whale.

Killer whales have an extremely broad distribution and, combining reports from various parts of the world, have been reported to forage on a wide variety of prey species (see Hoyt 1984). In coastal populations where they have been studied in detail, social groups (pods) of two types have been described (see Baird and Dill 1995; Bigg 1982; Bigg et al. 1987). These have been referred to as "transients," which feed primarily on marine mammals, and "residents," which feed primarily on fish (Bigg 1982). Apart from foraging specialization, resident and transient pods differ in a number of respects (summarized in Table 2). This includes morphological distinctions (Baird and Stacey 1988), but with the exception of the two local forms described in the Antarctic (Berzin and Vladimirov 1983), these are not as pronounced as those seen in bottlenose, spotted, and common dolphins.

Genetic studies have consistently shown a high degree of differentiation between the two sympatric forms of killer whales (Hoelzel et al. 1998; Hoelzel and Dover 1991a). Hoelzel et al. (1998) described differentiation at the mtDNA control region and three microsatellite DNA loci between transients and residents in the eastern North Pacific. There were no mtDNA haplotypes shared between the two groups, and 91.1% of the variation at this locus could be explained by differences between transients and residents. Microsatellite allele frequency differences and R_{ST} distance measures between the two populations were also highly significant. In spite of this substantial differen-

tiation between foraging specialists in the eastern North Pacific, comparisons within and across types between different geographic regions did not support the possibility that there are two species distributed worldwide, one specializing on marine mammals and the other on fish (Hoelzel and Dover 1991a).

These populations could have differentiated in allopatry and then reconverged, however, this seems unlikely for the following reasons. In all locations where killer whales occur, both types of prey are found, and there are killer whales in those locations that forage on each prey type. Specialization has only been established in regions where the populations have been extensively studied (as in the eastern North Pacific) or killed in large numbers as part of a fishery (as in the Antarctic). However, in each case there was clear evidence for individual prey specificity and only occasional evidence for individuals or pods taking both prey types (which could be opportunistic). Glacial incursions have in the past partitioned some of the nearshore habitat that forms the seasonal range for some populations. However, killer whales range over large areas (based on resighting data, see Ford et al. 1994) including areas that would not have been affected.

If killer whale populations are differentiating in sympatry, there are a number of possible mechanisms. Various selection models have been proposed for the generation of conspecific differentiation in sympatry. These include directional selection correlated with mate choice that is dependent on habitat type (see Bush 1994), sexual selection through the reversal of female mate preference, given a stable equilibrium in male trait genotype (Turner and Burrows 1995), character dis-

placement through competition (see Robinson and Wilson 1994), and balancing selection (see Diehl and Bush 1989). One model involving balancing selection suggests a complementary mechanism based on the incorporation of beneficial mutations with habitat-specific effects. When these mutations have fitness effects that differ between habitats, there could be indirect selection favoring habitat choice over random dispersal (Kawecki 1996). A controversial proposed mode of differentiation involves reproductive isolation resulting from the development of alternative social organizations (see West-Eberhard 1989). An example of incipient speciation by this mechanism was recently described for the fire ant (*Solenopsis invecta*), where barriers to gene flow were established between colonies with one (monogyny) versus multiple (polygyny) queens (Shoemaker and Ross 1996).

For a species with a high capacity for learning and a complex social structure, such as the killer whale (and other dolphin species), an alternative mechanism based entirely on learning may be possible. This hypothesis is based on a number of assumptions: (1) that learning to forage efficiently by each strategy requires substantial investment in time and effort, (2) that efficient foraging is necessary to meet energetic demands, (3) that individuals learn from other members of the social group, and (4) that different foraging strategies necessitate differences in the structure of the social group and the behavior of individuals in the group. In this way, social traditions could serve to pass the relevant information from one individual to another, and the consequence may be that individuals tend to disperse primarily between like groups.

In the case of the killer whale, there is evidence for long-term associations with the natal pod in both resident and transient pods (Bigg et al. 1987), and likely examples of training juvenile animals in hunting skills (Guinet and Bouvier 1995; Hoelzel 1991a). Both of these studies on hunting behavior further suggest that adults invest in this training through loss of efficiency in the hunt (Hoelzel 1991a) and long-term associations during "practice" hunting behavior (in the absence of prey; Guinet and Bouvier 1995; Hoelzel 1991a). The genetic data for both mtDNA and nuclear DNA markers indicates that dispersal between pod types is rare (Hoelzel et al., in press). Further, some differences in the structure of the two pod types, such as group size, have been re-
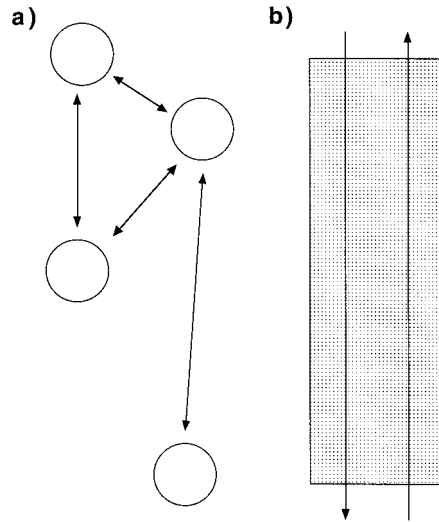
lated to differences in foraging strategy (Hoelzel 1991a, 1993). In addition to learning how to capture prey (and the strategies are sometime complex, often involving multiple members of the pod; see Hoelzel 1991a, 1993; Smith et al. 1981), the different strategists need to learn where and when to find prey. For example, differences in the patch dynamics of salmonid and pinniped prey in the eastern North Pacific would require very different patterns of movement (Figure 2). This could also lead to the spatial and temporal isolation of the two pod types within a geographic area. Finally, differences in group size could lead to differences in reproductive strategy. For example, the smaller, more dynamic transient pods may be more suitable to a serial polygynous male strategy than the larger, more stable resident pods. Each of these factors could contribute to the diminished dispersal between pod types.

Temporary Mixed Assemblages

A number of cetacean species migrate between clearly defined winter breeding grounds and summer feeding grounds. This is especially true of the baleen whale species, but it is also observed in some odontocetes, such as the beluga (Brennin et al. 1997). When migrating individuals are philopatric, returning to their natal breeding grounds, there is the potential for mixing between differentiated stocks in temporary assemblages on seasonal feeding grounds. This is another mechanism whereby there can be genetically differ-
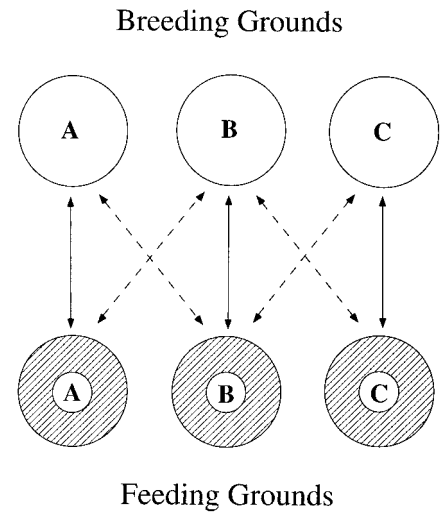
entiated sympatric populations. The coexistence of the populations is temporary, but if this is when stocks are hunted (as is typically the case), then the effective management and conservation of these stocks will need to take this factor into account (Hoelzel 1991b).

A clear example for a different marine taxon has been reported for the loggerhead turtle (*Caretta caretta*). Loggerheads show strong female phylopatry, and consequently, pronounced mtDNA genetic structure between breeding beaches (Bowen et al. 1993). However, they sometimes travel great distances to feeding grounds, and in the west Mediterranean basin, stocks from the Atlantic and eastern Mediterranean mix and are taken as a bycatch in longline fisheries, thereby impacting two stocks, neither of which breed in the area of impact (Laurent et al. 1993).

For migratory cetacean stocks, there are a number of possible patterns of distribution and movement, depending on the species and the local environment; for example, primary movement may be between "private" breeding and feeding grounds, with some possible movement across areas (Figure 3). In this case, stock structure may be expected to be partitioned between both breeding and feeding grounds. A possible example has been described for the humpback whale in the North Pacific (Baker et al. 1990, 1993). Photographic identification studies have indicated migration between the western North Pacific and the Bering Sea, Hawaii and Alaska, and Baja and Central California (Calambokidis et al. 1996; Medrano-
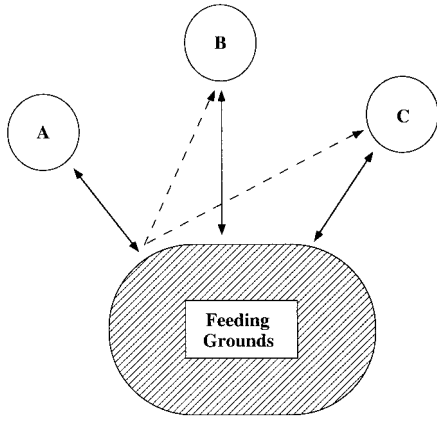

Figure 2. Schematic of the distribution of prey resource and movement patterns (arrows) of killer whales with respect to the resource for **(a)** pinniped and **(b)** salmonid prey in the eastern North Pacific.

Breeding Grounds

Feeding Grounds

Figure 3. Hypothetical migration pattern for three populations where primary movement is between separate pairs of feeding and breeding grounds. Dashed lines indicate low-level secondary patterns of movement.

Figure 4. Migration between three hypothetical breeding populations (A, B, and C) and a single feeding ground. Back migration to nonnatal breeding grounds is indicated by dashed lines (shown for population A only).

Figure 5. Schematic representation of a migration system similar to that expected for the Antarctic stocks. Hypothetical breeding populations (A–D) migrate to feeding grounds that overlap to an undetermined extent in a circumpolar distribution.

Gonzalez et al. 1995). Baker et al. (1993) investigated mtDNA variation among whales from the two eastern North Pacific stocks and found substantial differentiation between them. However, further studies using both mtDNA and nuclear genetic markers suggested that in both the North Pacific and the North Atlantic, males may move between migration routes more than females (Larsen et al. 1996; Palumbi and Baker 1994).

The occurrence of multiple breeding stocks that converge on a single feeding area (Figure 4) is of greater concern from the perspective of genetic conservation and management. In this case differentiated breeding stocks mix in temporary assemblages, and the pattern of mixing can vary on both spatial and temporal scales. This could affect the differential impact of exploitation on the component stocks. For example, hunting in a given location for an extended period could result in takes from more than one stock as they move through the area. An example of both mixing stocks and temporal change in the pattern of mixing has been reported for the minke whale (Goto and Pastene 1996; Wada 1991). Minke whale stocks on either side of Japan (the Korean versus the western North Pacific stocks) are genetically differentiated at both allozyme (Wada 1991) and mtDNA loci (Goto and Pastene 1996). Both studies found evidence for the seasonal mixing of these stocks on feeding grounds in the Okhotsk Sea. Further, at the location where samples were taken (in the southern end of the Okhotsk Sea) there was evidence for mixing primarily in April, during the early part of the season (Goto and Pastene 1996; Wada 1991). Later in the s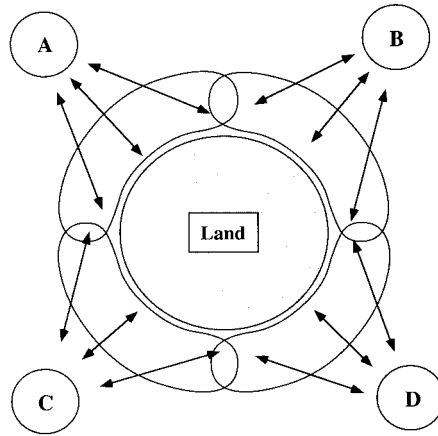eason the genotype of whales from this area matched that of the western North Pacific stock. In another example involving minke whales, a temporal mixing of two genetic stocks, primarily in the early part of the feeding season, was reported for samples from the Antarctic (management areas IV and V; see Donovan 1991), based on mtDNA variation (Pastene et al. 1996b). Genetic studies (based on mtDNA) of minke whales in the North Atlantic and North Sea, where they are currently hunted in a Norwegian fishery, show no clear distinction between stocks off Norway and off Iceland, but in each location there are two distinct mtDNA lineages (Bakke et al. 1996; Palsboll 1990), which may represent different breeding stocks.

The Antarctic poses a special challenge for the assessment of stock structure. The density of prey is high and there is a broad, circumpolar area to which whales migrate to feed (see schematic in Figure 5). The pattern of stock mixing will depend on the number, position, and range of migrating breeding stocks, but for most species these data are not known. Most species compared among broad geographic areas in the Antarctic show high levels of variation but little evidence of geographic structure (e.g., Wada and Numachi 1991). In some cases this could mean that breeding stocks are mixing freely over extended ranges. More data on the genetic structure of putative breeding stocks is needed, but for some species, such as the minke whale, even identifying the breeding stocks is difficult.

Conclusions

Studies to date have indicated a complex pattern of population genetic structure for most cetacean species investigated. Seasonal patterns of movement and the possibility of extremely large-scale dispersal, or local isolation (sympatric or parapatric) between populations, generate a mosaic of genetic diversity that cannot easily be determined from an intuitive assessment of geography. Resource specializations may be one important mechanism whereby cetacean populations differentiate in sympatry and parapatry. The special problem of multiple genetic stocks within a single geographic area is likely to be quite common from a conservation perspective, as it involves species that are important in fisheries and in areas of high impact from other human activity. This complicates the identification of management units and necessitates the inclusion of temporal as well as spatial considerations. It is clear that more research is required to identify these population distinctions and assess the dynamics of the system. This is necessary to ensure that genetically depauperate stocks are not depleted through an unknown and indirect impact on the population and that natural levels and patterns of diversity can be conserved. Such studies should include both mitochondrial and nuclear genetic markers to facilitate the discrimination of male and female dispersal patterns and to maximize resolution.

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