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Conservation Genetics in the Marine Realm

J. C. Avise

Techniques for DNA and protein assay make possible genetic studies on any species. In recent years, molecular methods have been applied to a number of conservation-relevant genetic issues for marine organisms ranging from zooplankton to whales. To introduce these symposium proceedings, I will mention some of the unusual challenges and opportunities afforded by marine taxa for genetic research in conservation. Marine organisms often are less accessible for behavioral and natural history observation than are their terrestrial counterparts. Many marine organisms have exceptional dispersal and migratory capabilities. Species’ ranges can be vast. Life histories may include high fecundities and explosive reproductive potentials. Many marine species of conservation concern are harvested commercially or illegally and thus economic, social, jurisdictional, and forensic matters often arise in population management, in addition to biological considerations. For a diversity of marine taxa, molecular markers have uncovered previously unknown aspects of behavior, natural history, and population demography that can inform conservation and management decisions. The studies compiled in this volume highlight the scope and imaginative uses of genetic information for conservation challenges in the marine realm.

If not for the fact that about 70% of the Earth’s surface is covered by oceans, the long-term prospects might be even more dim for the biosphere’s eventual recovery from global environmental crises precipitated by human overpopulation (World’s Scientific Academies 1994). The oceans have resisted permanent human settlement, and their vast size and composition provide some buffer against global environmental insults by man. Yet even in the relatively untouched marine realm, human impacts on biodiversity have been profound. Populations of many of the world’s largest and most spectacular marine mammals, reptiles, birds, fishes, and invertebrates have been depleted severely or forced to extinction by human harvesting (Malakoff 1997). These and many other marine organisms, including the magnificent invertebrate assemblages that comprise and inhabit coral reefs, also are under threat from human activities that pollute or otherwise modify saltwater environments. Human-mediated introductions of alien marine species, intentional and inadvertent (e.g., in ballast water from ships; Carlton and Geller 1993; Lodge 1993), present another growing problem. Concerns about human effects on marine biodiversity are reflected, for example, in more than 25 studies conducted in this decade by the U.S. National Research Council on endangered species in the sea, or on environmental policies and practices whose influences often extend to the marine realm (examples in Table 1).

Conservation issues for marine organisms have attracted the attention of geneticists also. For example, two recent volumes on conservation genetics (Avise and Hamrick 1996; Smith and Wayne 1996) included chapters on marine and anadromous organisms in addition to discussions of broader genetic issues germane to these and to nonmarine taxa. This special issue of the *Journal of Heredity* presents case histories that provide further indications of the diverse applications of genetic data to conservation efforts in the marine realm. These articles are an outgrowth of a symposium sponsored by the American Genetic Association at the annual meetings of the Society for Conservation Biology, held in Victoria, British Columbia, on June 7, 1997.

The explosion of interest in conservation genetics was made possible by the deployment in the past 3 decades of usable laboratory techniques for the direct
These books were published by the National Academy Press.

### Table 1. Examples of recent publications relevant to marine conservation resulting from studies conducted in the U.S. by the National Research Council

<table>
<thead>
<tr>
<th>Year</th>
<th>Title of Publication</th>
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<tbody>
<tr>
<td>1990</td>
<td>Decline of the Sea Turtles</td>
</tr>
<tr>
<td>1992</td>
<td>Dolphins and the Tuna Industry</td>
</tr>
<tr>
<td>1994</td>
<td>An Assessment of Atlantic Bluefin Tuna</td>
</tr>
<tr>
<td>1996</td>
<td>Upstream: Salmon and Society in the Pacific Northwest</td>
</tr>
</tbody>
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Ecosystem and/or policy issues

<table>
<thead>
<tr>
<th>Year</th>
<th>Title of Publication</th>
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<tbody>
<tr>
<td>1990</td>
<td>Managing Troubled Waters: The Role of Marine Environmental Monitoring</td>
</tr>
<tr>
<td>1992</td>
<td>Global Environmental Change</td>
</tr>
<tr>
<td>1993</td>
<td>A Biological Survey for the Nation</td>
</tr>
<tr>
<td>1994</td>
<td>Restoring and Protecting Marine Habitat: The Role of Engineering and Technology</td>
</tr>
<tr>
<td>1995</td>
<td>Science and the Endangered Species Act</td>
</tr>
<tr>
<td>1996</td>
<td>Stemming the Tide: Controlling Introductions of Nonindigenous Species by Ships' Ballast Water</td>
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Molecular genetic markers also have been used to decipher movement and association patterns of marine turtles at other stages of the life cycle. Marine turtles spend most of their lives on oceanic journeys or on feeding grounds that may be far removed (hundreds or even thousands of kilometers in some cases) from rookery sites. Several studies have employed rookery-characteristic mtDNA markers to assign individuals captured on feeding grounds or during migration to rookeries of origin. An emerging generality is that particular assemblages of nonnesting marine turtles often derive from multiple rookery sites. Thus, with regard to mortality sources at non-nesting phases of the life cycle, different rookeries can be jointly impacted demographically. This too can have conservation ramifications.

For example, the shells of hawksbill turtles are highly prized for “tortoiseshell” jewelry and ornamental products. Although a moratorium exists on international trade in hawksbill shell, in 1992 Cuba announced its intent to resume harvest of hawksbills within its territorial waters. Genetic analyses of mtDNA from a nearby feeding population (Mona Island, Puerto Rico) and from several nesting colonies throughout the Caribbean (Bass et al. 1996; Bowen et al. 1996) demonstrated that hawksbill turtles within a feeding assemblage can derive from multiple rookeries across a broad area (review in Bowen 1996c). By logical extension, Cuban harvests of hawksbill turtles within its sovereign waters might be expected to have demographic impact on multiple rookeries beyond its own. Several other population genetic studies on the rookery origins of nonnesting turtles have been conducted that have similar relevance to conservation efforts (reviews in Avise and Bowen 1994; Bowen 1995, 1996c).

Another genetics-demography link applies to marine animals such as oysters with high fecundities and a “sweepstakes” mode of reproduction and survival. Such species have billions of individuals and large ranges, yet often display two paradoxical aspects of genetic variation: (1) vastly lower genetic variation than expected under neutrality theory based on their abundances (Avise et al. 1988; Nei and Graur 1984), and (2) “chaotic patchiness” involving seemingly stochastic genetic heterogeneity over small spatial and temporal scales. Huge variances in family reproductive success may account in part for both phenomena (Hedgecock et al., 1982, 1992).
Spatial and Temporal Scales: Phylogeography

The spatial scales of organismal dispersal and population structure in the sea often are vastly greater than those typifying most terrestrial animals. Many marine species (e.g., pelagic turtles, fishes, and cephalopods) are remarkably vagile as adults, passively mobile over huge distances (e.g., zooplankton), or highly dispersive as gametes or at early life-history stages (including species such as corals and mollusks that may be sessile or demersal as adults). Exceptionally high dispersal potentials sometimes translate into minimal or modest “phylogeographic” (Avise 1998) divergence over vast areas. For example, several of the billfish and tuna species described in this issue (Graves) show ocean-wide or even circumpolar levels of mtDNA differentiation comparable to or lower than those reported (Figure 1) among populations of terrestrial vertebrates or freshwater fishes within small continental regions such as the southeastern United States (Avise 1996b). Thus a special logistical challenge in population genetic studies of marine taxa is to conduct molecular surveys at spatial scales (sometimes global) commensurate with population genetic patterns that might be possible given the dispersal potentials of the organisms involved and any plausible historical connections between the water masses they inhabit.

On the other hand, a growing appreciation from studies of marine organisms is that high dispersal potential frequently does not translate into high levels of realized gene flow (even as registered in presumably “neutral” molecular markers) (Palumbi 1996). Many examples have come to light in which population genetic subdivisions in marine species are pronounced despite high intrinsic organismal vagility. Such population structure may result in part from behavioral philopatry during the life cycle, as for example in the natal-homing behavior of female sea turtles (mentioned above) and anadromous salmon (Waples, in this issue); social organization into kinship groups, as in some cephalopods (Hoelzel, Palumbi); or habitat restrictions and historical or contemporary physical partitions of suitable marine environments, as in sardines and anchovies (Grant and Bowen). The magnitudes as well as the ecological and evolutionary processes responsible for a realized population genetic structure nearly always bear direct relevance to any conservation or management plans for the particular species involved.

Moritz (1994) has formalized an important distinction concerning the varying temporal “depths” of population genetic structure possible within a species. He defines “evolutionarily significant units” (ESUs; see also Dizon et al. 1992; Ryder 1986; Waples 1991) as relatively deep historical population subdivisions, and distinguishes them from “management units” (MUs) that represent shallower but nonetheless differentiable population segments connected by little or no contemporary gene flow. Suggested empirical guidelines for the genetic identification of intraspecific population segments that should qualify as ESUs (as opposed to MUs) center on four conceivable aspects of “genealogical concordance” (Avise 1996b; Avise and Ball 1990): (1) concordance (in the putative population units identified) across multiple sequence characters within a nonrecombining segment of DNA; (2) concordance in such genealogical partitions across multiple independent (unlinked and nongenetic) loci; (3) concordance in the geographic positions of intraspecific gene-tree partitions across multiple codistributed species; and (4) concordance between gene-tree partitions and historical geographic boundaries as inferred from traditional (nonmolecular) biogeographic evidence.

Studies on marine turtles exemplify nicely the distinction between ESUs and MUs, and also illustrate how both can be relevant to population stewardry and conservation. Consider, for example, global phylogeographic patterns in mtDNA displayed by green turtles and loggerheads (Bowen et al. 1992, 1994; comparative review in Bowen 1996a). As already mentioned, conspecific nesting rookeries of both species often show highly significant differences in matriline frequencies within ocean basins and therefore qualify as MUs. However, these genetic differences typically are “shallow” with respect to the magnitude of sequence divergence that distinguishes the rookery-specific mtDNA haplotypes. By contrast, rookeries from separate ocean basins, notably the Atlantic-Mediterranean versus the Indian-Pacific, usually show much larger mtDNA sequence differences. Furthermore, the inferred times of separation based on a testudine-specific molecular clock are in general agreement for both species with...
plausible historical population sunders via rise of the Isthmus of Panama some 3 million years ago. Thus, as gauged by concordance criteria (1), (3), and (4) listed above, with only minor exceptions the Atlantic-Mediterranean rookeries within each species empirically comprise one ESU and the Indian-Pacific rookeries constitute another. Individual rookeries are important as MUs because the matrilineal differences imply demographic reproductive independence over ecological time scales, whereas the ESUs are important also because they register the deeper historical genetic subdivisions within each species that should warrant special conservation recognition.

**Taxonomy and Conservation Priority**

Discussions of phylogeographic population structure often grade into deliberations about systematics, taxonomy, and conservation prioritization (Vane-Wright 1991). The marine turtles again provide illustrations. In the eastern Pacific, a dark-colored form of the green turtle sometimes has been afforded taxonomic recognition as a distinct species, the black turtle (*Chelonia agassizii*). However, in terms of placement within the global mtDNA phylogeny for *C. mydas*, black turtles proved essentially indistinguishable from other members of the Indian-Pacific green turtle clade (Bowen et al. 1992). This result, interpreted in conjunction with other lines of evidence, appears to be inconsistent with species-level recognition for the “black turtle” (Bowen and Karl 1996).

Similar molecular studies of another complex of marine turtles provided a contrasting outcome. The Kemp’s ridley turtle (*Lepidochelys kempi*) was suspect taxonomically because of near morphological identity to the olive ridley (*L. olivacea*), and because of an unusual distribution that at face value made little biogeographic sense (Carr 1967). The Kemp’s ridley was described from a single nesting location (Tamaulipas, Mexico) in the western Gulf of Mexico, whereas rookeries of the olive ridley occur nearly worldwide in suitable waters. Nonetheless, a molecular survey of mtDNA revealed that assayed populations of *L. olivacea* from the Atlantic and Pacific Oceans were considerably less differentiated from one another than either was from *L. kempi*, and that the Kemp’s ridley was slightly more distinct on average from these olive ridleys than were any conspecific populations of green turtles or loggerheads to one another (Bowen et al. 1991). In this case the genetic results bolstered the biological rationale for taxonomic recognition of the Kemp’s ridley, and thus for the focused international conservation efforts that had been directed toward it.

In this current issue, case studies similar in spirit describe molecular genetic analyses relating to the behaviors, natural histories, population structures, biogeographic histories, and systematics of several groups of marine taxa: crustaceans (Bucklin), fishes (Gold, Grant and Bowen, Graves, Seeb, and Waples), and cetaceans (Hoelzel, Palumbi). Many of these studies address spatial and temporal aspects of population differentiation, consider behavioral and demographic processes responsible for observed genetic patterns, and implicitly or explicitly distinguish MUs and ESUs.

**Economics, Legalities, and Jurisdictions**

In terrestrial and freshwater conservation biology, management attention typically is focused on species that by virtue of rarity have little economic clout (except, perhaps, indirectly through ecotourism dollars or through legislative restrictions on businesses). In contrast, many depleted marine species of special management concern have huge economic constituencies. The marine fishing and shellfishing industries are among the few remaining arenas of human enterprise to exploit natural (as opposed to domesticated or captive) populations as major commercial sources of food and other animal products. The logistics of marine harvest are such that a viable fishery can (and often does) collapse economically well before the target species becomes imminently threatened with biological extinction (Botsford et al. 1997). Such target species may, however, be thought of as “ecologically extinct” when depleted to the point at which they no longer perform their former roles in marine ecosystems (Bowen 1997).

Perhaps the majority of conservation genetic studies in the marine realm thus far have been directed toward commercially important rather than “endangered” species. Described in this issue are examples from the tunas and billfishes (Graves), rockfishes (Seeb), red drums and relatives (Gold), and sardines and anchovies (Grant and Bowen). A common goal is to distinguish genetic “stocks” (ESUs and MUs) and thereby assist in formulating guide-lines and allotment quotas for commercial harvest. A related objective for some species such as salmon (Waples) has been to genetically distinguish hatchery-reared from native fishes for purposes of assessing the population consequences of artificial propagation and supplementation programs, or to identify dwindling wild strains that might qualify for legal protection under the Endangered Species Act. As elaborated elsewhere (Allendorf and Waples 1996; National Research Council 1996), genetics-based recommendations for the management of economically important fishes are prone to entanglement in a complex nexus of considerations from legal, commercial, recreational, and cultural interests.

In some large marine animals, an exceptionally high economic value for individual specimens can promote commercial harvests even when population numbers become dangerously low. For example, a single giant bluefin tuna in good condition can be worth tens of thousands of dollars in sushi markets. In such cases, as the demand and supply curves adjust, an economic collapse of a fishery could be approximately coincident with biological extinction itself. Many marine mammals and seabirds also have fallen into this category. For example, the Stellar’s sea cow was exterminated by Russian hunters in 1768, and in recent centuries several other marine mammals including the northern elephant seal, fur seals, sea otters, and several whale species were hunted to the verge of extinction (Haley 1979). Among seabirds, the great auk met its demise by collectors in 1844 (Birkhead 1994) and the Labrador duck in 1878 (Ehrlich et al. 1992). Populations of many other seabirds likewise have been under duress from excessive harvests of eggs or adults, human-mediated introductions of exotic predators such as rats, and/or overt destruction of nesting habitats (Diamond 1982).

Centuries of systematic hunting, exacerbated in the 20th century by the invention of steam-powered vessels and the exploding harpoon, have driven many species of cetaceans to perilously low levels, to the point that most of the larger mysticete (baleen) and odontocete (toothed) whales are listed as threatened or endangered (World Conservation Union 1993). In 1982, the International Whaling Commission (IWC) voted to impose an indefinite moratorium on commercial hunting. Yet whale and dolphin products (ostensibly derived from nontreated species and/or those harvested under “scientific”
This is a text from a document discussing conservation genetics, focusing on the marine realm. The text mentions the United Nations Convention on the Law of the Sea and its provisions related to the conservation of marine resources. It highlights the importance of molecular markers and DNA analysis in identifying species and tracking their movements, particularly in migratory species. The text also touches on the role of international agreements and organizations in ensuring conservation efforts. Several case studies are mentioned, including the conservation of marine turtles and whales. The text concludes with a discussion on the future of conservation genetics in the marine realm, emphasizing the need for continued research and collaboration. References to scientific works are included, providing a foundation for the discussed topics.
netics: case histories from nature. New York: Chapman & Hall.


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