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## The Wilhelmine E. Key 1997 Invitational Lecture



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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

**Table 1. Examples of recent publications relevant to marine conservation resulting from studies conducted in the U.S. by the National Research Council<sup>a</sup>**

Species- or taxon-specific reports	
1990	<i>Decline of the Sea Turtles</i>
1992	<i>Dolphins and the Tuna Industry</i>
1994	<i>An Assessment of Atlantic Bluefin Tuna</i>
1996	<i>Upstream: Salmon and Society in the Pacific Northwest</i>
Ecosystem and/or policy issues	
1990	<i>Managing Troubled Waters: The Role of Marine Environmental Monitoring</i>
1992	<i>Global Environmental Change</i> <i>Marine Aquaculture: Opportunities for Growth</i>
1993	<i>A Biological Survey for the Nation</i>
1994	<i>Restoring and Protecting Marine Habitat: The Role of Engineering and Technology</i>
1995	<i>Science and the Endangered Species Act</i> <i>Understanding Marine Biodiversity</i>
1996	<i>Stemming the Tide: Controlling Introductions of Nonindigenous Species by Ships' Ballast Water</i> <i>The Bearing Sea Ecosystem</i>
1997	<i>Sustaining Marine Fisheries</i>

<sup>a</sup> These books were published by the National Academy Press.

assay of DNA and proteins (Awise 1994; Ferraris and Palumbi, 1996; Hillis et al. 1996). Prominent among these have been mitochondrial (mt) DNA assays that permit a characterization of matrilineages within and among species, various nuclear assays (e.g., of allozymes, micro- and mini-satellite DNAs, nuclear RFLPs) that yield qualitative genotypic descriptions for particular Mendelian loci, direct nucleotide sequencing methods that in principle can be applied to any nuclear or cytoplasmic genes, and PCR procedures that permit recovery of DNA from even minute amounts of tissue. These molecular procedures have opened the entire biological world for genetic scrutiny. For marine (and other) organisms, molecular techniques permit genetic analyses that were unimaginable earlier in the century, when the primary access to information on particular genetic traits came either from captive pedigrees or (indirectly and insecurely) from morphological and other organismal-level appraisals.

To introduce these symposium proceedings, I will comment briefly on some of the unusual challenges as well as the special opportunities afforded by marine organisms for molecular genetic research in conservation biology. Marine turtles are not discussed elsewhere in this volume, so I will use these organisms as touchstones to illustrate several broader points that are echoed by symposium partici-

pants for other diverse marine taxa. [Note: All eight species of sea turtles are listed officially as threatened or endangered. In the past decade, these have been the subject of more than 120 research papers dealing with population genetics, conservation biology, molecular evolution, and related topics (Bowen 1996b). Detailed reviews are available on the biology (Bjornald 1995) and conservation genetics of marine turtles (Bowen and Awise 1996; Bowen and Witzell 1996), so only summary statements will be issued here.]

### Behavior, Demography, and Population Structure

Due to the nature of the environment occupied, many marine organisms are relatively inaccessible for direct field observations. Thus exceptional opportunities are afforded for genetic data to close real gaps in knowledge concerning organismal behaviors, natural histories, and current and past population demographic factors that in turn can be highly relevant to conservation efforts.

### Dispersal Behaviors and Genetics/Demography Connections

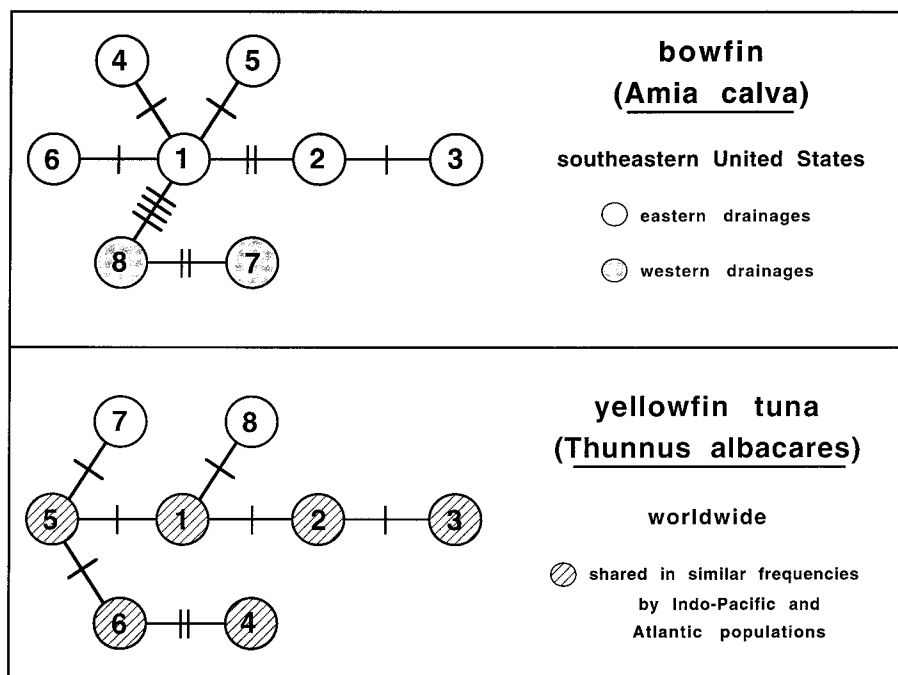
A long-standing question in marine turtle research has been whether females, after a sexual maturation process measured in tens of years and oceanic movements often measured in thousands of kilometers, return to nest at or near their natal beaches. Decades of field observations and physical tagging experiments have failed to answer this question. However, following the pioneering efforts of Bowen et al. (1989) and Meylan et al. (1990), several molecular surveys of mtDNA showed that conspecific rookeries of green turtles (*Chelonia mydas*), loggerheads (*Caretta caretta*), and hawksbills (*Eretmochelys imbricata*) within an ocean basin commonly display large or nearly fixed differences in matriline frequencies, a result strongly supportive of natal homing scenarios for adult females. Because females ultimately govern the reproductive output of a rookery, this natal-philopatric behavior signifies considerable demographic autonomy among turtle rookeries with regard to reproduction (Awise 1995). Thus natural recruitment from foreign rookeries is unlikely to compensate for mortality in heavily exploited rookeries or to reestablish over ecological time scales rookeries that have been extirpated by human activities or other causes.

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 Awise 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 (Awise 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).



**Figure 1.** Contrasting scales of mtDNA phylogeographic population structure in a freshwater fish, the bowfin, surveyed in the southeastern United States (from data in Bermingham and Avise 1986) and a pelagic marine fish, the yellowfin tuna, surveyed circumglobally (from data in Scoles and Graves 1993). Shown are parsimony networks connecting common genotypes (those observed in three or more individuals); lines across network branches indicate restriction site changes. Genotypes 7 and 8 in the yellowfin tuna were observed only in the Pacific, but in each case in only three assayed specimens. These two species were chosen for illustrative purposes because they match closely with respect to numbers of individuals assayed (68 and 88, respectively), numbers of restriction enzymes employed in the assays (13 and 12), and numbers of common mtDNA haplotypes observed (8 in each case). Yet both the phylogeographic depth and structure of the bowfin over spatial scales of a few scores of kilometers surpass those of the yellowfin tuna over global oceanic scales of many thousands of kilometers.

### 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 cetaceans) 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 oceanwide or even circumglobal 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 logistic challenge in population genetic studies of marine taxa is to conduct molecular surveys at spatial scales (sometimes glob-

al) 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 cetaceans (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 nonrecombining) 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 magnitudes of sequence divergence that distinguish 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 sunderings 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 agassizi*). 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 nonthreatened species and/or those harvested under "scientific"

**Table 2. Examples of conservation-relevant provisions from the *United Nations Convention on the Law of the Sea* (Platzöder 1994)<sup>a</sup>**

Article 61.2. The coastal State<sup>b</sup>, taking into account the best scientific evidence available to it, shall ensure through proper conservation and management measures that the maintenance of the living resources in the exclusive economic zone<sup>c</sup> is not endangered by over-exploitation.

Article 63.1. Where the same stock or stocks of associated species occur within the exclusive economic zones of two or more coastal States, these States shall seek . . . measures necessary to co-ordinate and ensure the conservation and development of such stocks.

Article 64.1. In regions for which no appropriate international organization exists, the coastal State and other States whose nationals harvest these species in the region shall co-operate to establish such an organization and participate in its work.

Article 66.1. States in whose rivers anadromous stocks originate have the primary interest in and responsibility for such stocks.

Article 67.1. A coastal State in whose waters catadromous species spend the greater part of their life cycle shall have responsibility for the management of these species and shall ensure the ingress and egress of migrating fish.

Article 119.1. In determining the allowable catch and establishing other conservation measures for the living resources in the high seas<sup>d</sup>, States shall: (a) take measures which are designed, on the best scientific evidence available to the States concerned, to maintain or restore populations of harvested species at levels which can produce the maximum sustainable yield . . . and (b) take into consideration the effects on species associated with or dependent upon harvested species with a view to maintaining or restoring populations of such associated or dependent species above levels at which their reproduction may become seriously threatened.

<sup>a</sup> Most of the 320 articles in the original document relate to nonbiological issues, such as rights of passage for maritime shipping. Other marine laws also exist, for example, the 1983 *U.N. Convention on Migratory Species* prohibits the taking of migratory endangered species on the high seas.

<sup>b</sup> The "State" is a country that has consented to be bound by the 1982 *U.N. Convention on the Law of the Sea*. As of December 1994, 155 nations had signed the agreement.

<sup>c</sup> The exclusive economic zone as defined in the *Law of the Sea* shall not extend beyond 200 nautical miles from the coastal state.

<sup>d</sup> The high seas are defined as all parts of the oceans not included within exclusive economic zones or territorial waters.

collecting permits) continue to appear in abundance in retail markets and restaurants in countries such as Korea and Japan. Here again molecular markers have found conservation applications, in the forensic identification to species (and sometimes to populations) of otherwise unlabeled animal products. In this issue, Palumbi describes how mtDNA sequences from PCR-based assays of retail-purchased "whale" meat ("kujira" in Japan or "gorae" in Korea) have been assigned genetically to a surprising diversity of cetaceans including species covered under the IWC hunting moratorium for more than a decade! In general, the forensic identification of marine animal products by molecular markers holds great promise for the law enforcement side of conservation biology.

Several conservation related provisions of international marine law (Table 2) require, for successful implementation, scientific information on population genetics and demography. These legal provisions were written primarily with marine fishes in mind, but in principle might be applied to other organisms as well, such as marine turtles.

For example, articles 66.1 and 67.1 of the *United Nations Convention on the Law of the Sea* (Table 2) prescribe that countries which provide developmental habitats for particular species hold primary interest and responsibility for conservation of those stocks. Marine turtles spend most

of their lives far removed from natal sites, and thus are exposed to harvest by foreign States. Genetic data often can identify the particular populations impacted by such harvests. Mentioned above was the genetically-estimated rookery composition of hawksbill turtles on a Puerto Rico feeding ground. Examples in which mtDNA markers have identified the rookery sources of marine turtles killed at sea include assignments of (1) more than 50% of juvenile loggerhead turtles in a Mediterranean longline fishery to nesting beaches in the Americas (Bowen 1995; Laurent et al. 1993), and (2) nearly all loggerhead turtles captured in the North Pacific driftnet and longline fisheries to rookeries in Japan (Bowen et al. 1995). These genetic assignments were made possible by the large frequency differences in mtDNA haplotype between rookeries, and by the availability of statistical procedures (originally developed for mixed-stock fisheries; Millar 1987; Pella and Milner 1987) to estimate proportional contributions from multiple source populations. Apart from the extraordinary migrational feats for marine turtles documented by these genetic studies, the findings also raise jurisdictional questions: for example, do the nations whose endangered turtle populations are impacted by high-seas fisheries have the legal right and/or obligation to seek or to enforce conservation agreements with the harvesting nations?

## Conclusions

The field of conservation genetics traditionally has been associated with concerns about levels of genetic variation and inbreeding depression in small, often captive animal populations (see discussion in Avise 1996a). However, with the advent of molecular approaches and their suitability as sources of polymorphic genetic markers for natural populations, a host of additional issues of conservation relevance can be addressed, ranging from studies of organismal behaviors, natural histories, and demographies, to assessments of the spatial and temporal aspects of population structure, to elucidations of systematics and phylogeny at any scale.

Norse (1994) lamented that "Marine conservation biology lags terrestrial conservation biology by about 20 years. It lacks central paradigms, graduate training programs, and substantial dedicated funding." On the other hand, the marine realm has provided some of the most exciting, imaginative, and innovative of available case studies in all of conservation genetics. I hope this issue may contribute to a wider appreciation of such efforts and also help to enthuse a new generation of widely versed biologists about this empirically and conceptually rich and important field.

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