9-1998

Molecular insights into the population structures of cosmopolitan marine fishes

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Molecular Insights Into the Population Structures of Cosmopolitan Marine Fishes

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Many marine fishes are cosmopolitan, occurring in continuous (e.g., circumtropical) or discontinuous (e.g., antitropical) distributions. Little is known of the genetic basis of population structure of these species, even though several support extensive fisheries. To develop a database that would facilitate comparison of the population structures among cosmopolitan fishes we consistently included restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA) as a common approach to our investigations of these species. This article presents a review of those analyses. Considerable intraspecific genetic variation was revealed within all cosmopolitan marine species. Continuously distributed species displayed population structures ranging from a lack of significant heterogeneity between ocean samples to shallow but significant structuring within an ocean basin. In general, greater intraspecific genetic divergence was revealed within discontinuously distributed fishes. Levels of population structuring ranged from species comprising conspecific populations with no mtDNA haplotypes in common to those comprising populations with homogeneous distributions of mtDNA haplotypes across ocean basins. The close affinity of haplotypes among conspecific populations of all discontinuously distributed species was consistent with contact since the Pleistocene. Although general patterns of genetic population structure were similar among continuously and discontinuously distributed cosmopolitan marine species, there were some striking differences. These differences underscore the need for a thorough understanding of the genetic basis of population structure of each species for proper management.

Several species of pelagic marine fishes are broadly distributed, inhabiting the tropical and subtropical surface waters of the world's oceans (Briggs 1960). Some of these species, including tunas, billfishes, swordfish, dolphin fish, and several sharks, support extensive commercial and recreational fisheries throughout their ranges. Little is known of the population genetic structure of any of these truly international fishery resources, although such information is critical to the delineation of fishery management units, the evaluation of fishery interactions, and on a longer time scale, the conservation of genetic variation (Allendorf et al. 1987; Avise 1996).

Over the past several years our laboratory has investigated the stock structure of many continuously distributed pelagic fishes. Preliminary studies employing restriction fragment length polymorphism (RFLP) analysis of mitochondrial DNA (mtDNA) revealed less genetic divergence between Atlantic and Pacific populations of skipjack tuna (Graves et al. 1984) and albacore (Graves and Dizon 1989) than was reported between populations of terrestrial organisms separated by as little as tens or hundreds of kilometers (e.g., Avise et al. 1979). Although the small sample sizes employed in those studies limited the power of the analyses to critically test the null hypothesis that Atlantic and Pacific populations shared a common gene pool, we were impressed by the absence of consistent genetic differences between samples of skipjack tuna and albacore from different oceans, and suggested that the relative lack of genetic divergence might be attributed to either recent isolation or a low level of contemporary gene flow. The latter would be facilitated by the presence of a continuous circumtropical habitat, the occurrence of spawning over a broad spatial and temporal range, and the species' potential for intraspecific gene flow mediated by passive larval dispersal or the high vagility of adults.

In the 1980s there were few mtDNA-based population genetic analyses of ma-

From the Virginia Institute of Marine Science, P.O. Box 1346, Gloucester Point, VA 23062. I am indebted to my colleagues Jan McDowell, Dan Scoles, Jan Cordes, Catherine Goodbred, and Bruce Collette who coauthored the manuscripts upon which this review is based. I gratefully acknowledge the many individuals who assisted in sample collection. This manuscript benefited from the critical reading of Vince Buonaccorsi, David Carlini, Kimberly Reece, and two anonymous reviewers. Funds for this study were provided by the National Marine Fisheries Service and the Billfish Foundation. VIMS contribution no. 2133. Address correspondence to Dr. Graves at the address above or e-mail: graves@vims.edu. This paper was delivered at a symposium entitled "Conservation and Genetics of Marine Organisms" sponsored by the American Genetics Association at the University of Victoria, Victoria, BC, Canada, June 7, 1997.

 89:427–437

rine fishes with which to compare our results. Because of the large potential for gene flow in the pelagic environment, we felt that there was limited value to comparisons of the population structures of highly vagile cosmopolitan marine fishes with those of freshwater fishes or terrestrial animals which often have greatly reduced dispersal abilities and encounter formidable barriers to gene flow within their ranges. Therefore, to develop a more appropriate database with which to compare our continuing studies of circumtropical pelagic fishes, we initiated investigations of the population genetic structure of broadly distributed pelagic marine fishes with disjunct populations. Several species of temperate marine fishes are known to comprise geographically isolated conspecific populations north and south of the tropics (Briggs 1974). We assumed that, relative to continuously distributed pelagic fishes, those with antitropical distributions would display more population genetic structure, but not nearly as much as that reported among most conspecific populations of freshwater fishes or terrestrial animals. In addition, the ability to estimate a time of divergence for isolated conspecific populations of temperate fishes using analyses of allozymes (Grant and Leslie 1996; Stepien and Rosenblatt 1996) or mtDNA (Bowen and Grant 1997) would provide temporal reference points to evaluate genetic divergences among populations of continuously distributed pelagic fishes.

Cosmopolitan Marine Fishes

This review focuses on studies of four "species" with circumtropical distributions: yellowfin tuna (Scoles and Graves 1993), white/striped marlin (Graves and McDowell 1994, unpublished data), blue marlin (Graves and McDowell 1995, unpublished data) and sailfish (Graves and McDowell 1995; McDowell JR and Graves JE, unpublished data); and four species of cosmopolitan temperate fishes with disjunct distributions: bluefish (Goodbred and Graves 1996) and three species of mackerels (Scoles et al., in press).

Yellowfin Tuna

Yellowfin tuna (*Thunnus albacares*) occur throughout the tropical and subtropical waters of the Atlantic, Indian, and Pacific Oceans (Figure 1a), rarely entering areas with surface water temperatures below 18°C (Collette and Nauen 1983). Spawning occurs throughout the year over a broad

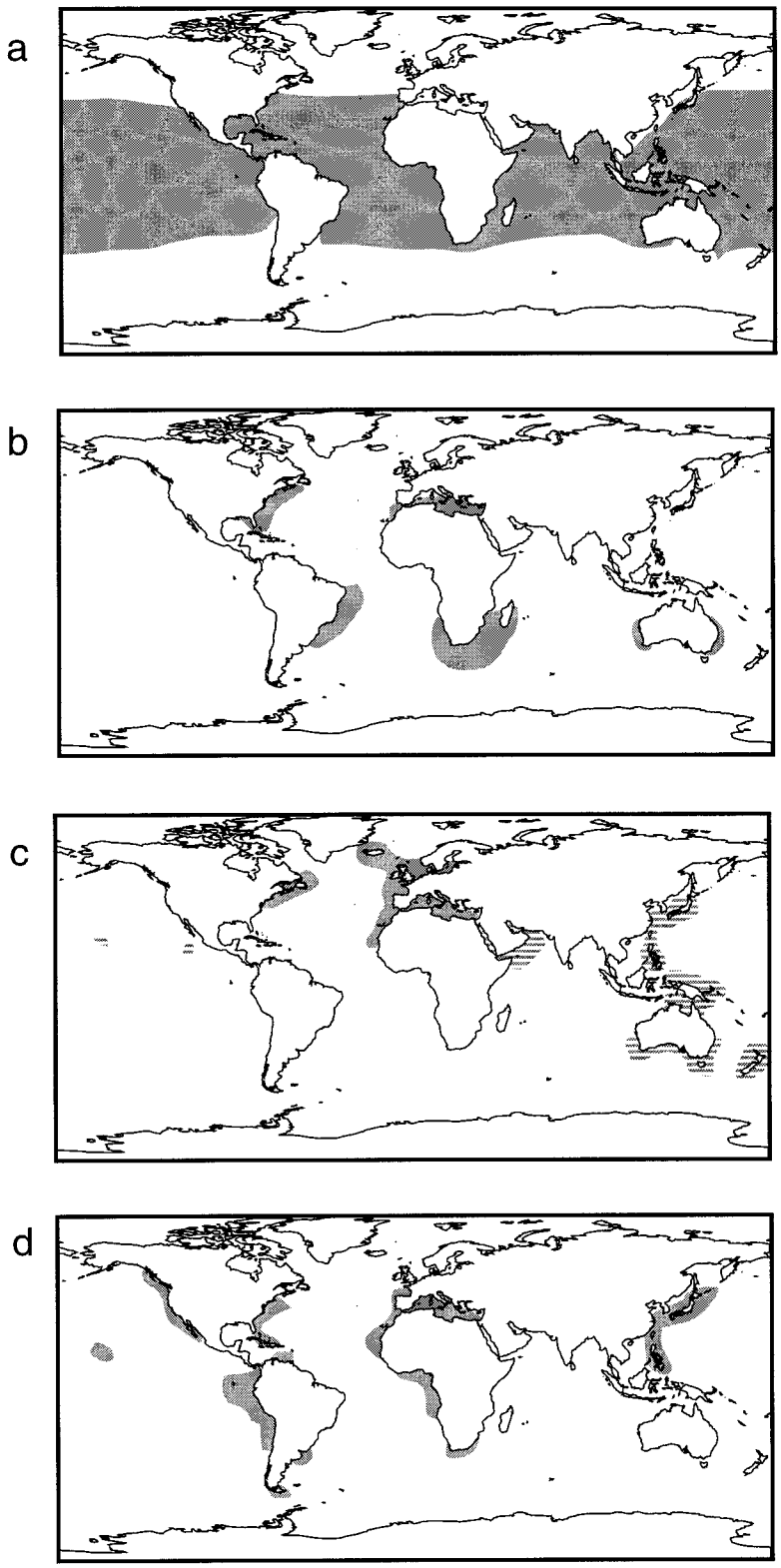

Figure 1. Distribution of cosmopolitan marine fishes. **(a)** Circumtropical distributions. The shaded area reflects the distribution of yellowfin tuna (*T. albacares*), blue marlin (*M. nigricans*), sailfish (*I. platypterus*), striped marlin (*T. audax,* Indo-Pacific Oceans), and white marlin (*T. albidus,* Atlantic Ocean). The distributions of yellowfin tuna, striped marlin, and white marlin extend a little further into subtropical waters than those of blue marlin or sailfish. **(b)** Bluefish (*P. saltatrix*). **(c)** Atlantic mackerel (*S. scombrus,* stippled shading) and spotted chub mackerel (*S. australasicus,* lined shading). **(d)** Chub mackerel (*S. japonicus*).

area in the tropical oceans. Individuals exhibit relatively rapid growth, attaining a length of 100 cm at the end of 2 years. Yellowfin tuna are typically mature by the end of their second year and may live for at least 8 years (Inter-American Tropical Tuna Commission 1991). Yellowfin tuna are vagile, and tagging studies indicate that some individuals undertake extensive movements, including trans-Atlantic migrations (Scott et al. 1990), although the majority of fish are recovered within several hundred kilometers from the point of release (Hunter et al. 1986).

Istiophorid Billfish

The family Istiophoridae comprises three genera: *Makaira* (blue marlin and black marlin), *Tetrapturus* (white marlin, striped marlin, and at least three species of spearfish), and *Istiphorus* (sailfish). All are epipelagic predators with extensive ranges in tropical and subtropical marine waters.

The striped marlin (*Tetrapturus audax*) and the white marlin (*T. albidus*) have ranges that extend a little further into subtropical waters than the other istiophorids (Figure 1a; Nakamura 1985). The white marlin is restricted to the Atlantic Ocean and reaches a maximum size of approximately 80 kg, while the striped marlin occurs in the Indian and Pacific Oceans and reaches a maximum size of approximately 200 kg. Little is known of the spawning habits of either species, although ripe individuals and early life-history stages have been found over a broad region in tropical waters. Tagging studies indicate that individuals of both species are capable of extended movements, including trans-Atlantic migrations of white marlin and recoveries in Hawaii of striped marlin tagged off California (Scott et al. 1990; Squire 1987). As with the other isotiophorids, a large fraction of white and striped marlin are recaptured near the site of release even after several years. Trends in tag-recapture data reveal seasonal movements within areas, some of which may be related to spawning in tropical waters (Squire and Suzuki 1990).

The blue marlin (*Makaira nigricans*) is an epipelagic predator occurring throughout tropical oceans (Figure 1a). Various authors have separated blue marlin into an Atlantic and an Indo-Pacific species (Nakamura 1985); however, recent genetic data support the existence of a single species (Finnerty and Block 1992; Graves and McDowell 1995). Blue marlin exhibit very rapid growth and reach a total length of almost 2 m by the end of their first year (Prince et al. 1991). It is estimated that individuals may live in excess of 20 years. A strong sexual dimorphism is evident in the species, with males typically reaching maximum sizes of less than 120 kg, while females may exceed 800 kg (Nakamura 1985). Tagging studies reveal that most fish are recaptured near their site of release, despite several years of freedom (Witzell and Scott 1990). Some individuals have been known to undertake extensive movements within ocean basins, and in two instances, between oceans (NMFS 1994). Little is know of spawning in the blue marlin. Mature individuals and larvae have been captured over a broad range in the tropics (Matsumoto and Kazama 1974; Strasburg 1969). However, evidence for distinct spawning cycles has been reported in some areas near island chains (Hopper 1990).

The sailfish (*Istiophorus platypterus*), like the blue marlin, exhibits a circumtropical distribution (Figure 1a) and has been recognized by some authors as comprising Atlantic and Indo-Pacific species (Nakamura 1985). Genetic data are consistent with the existence of a single species (Graves and McDowell 1995). Sailfish tend to be distributed more coastally than blue marlin, although they are taken on longline gear in commercial fisheries throughout the tropical oceans. The maximum size reached by individuals varies among locations within and between oceans. Maximum sizes of approximately 60 kg and 100 kg have been reported for the Atlantic and Pacific Oceans, respectively (Nakamura 1985). The recapture of a tagged fish 16 years after release indicates that individuals can be long-lived. Tagging studies also demonstrate the potential for extended movements (in excess of 2000 km), although the majority of recaptures are in the same area as the release (Scott et al. 1990). Sailfish are multiple spawners, and spawning has been reported in offshore waters as well as a number of locations throughout the species' range. In some areas spawning activity occurs throughout the year, while in other regions it is restricted to a period of several months (Nakamura 1985).

Bluefish

The bluefish (*Pomatomus saltatrix*) is a pelagic predator commonly found in temperate coastal marine waters at temperatures between 15°C and 25°C (Wilk 1977). The species comprises at least six geographically distinct populations and is found in most ocean basins except the eastern Pacific (Figure 1b). Bluefish attain a maximum size in excess of 10 kg, and individuals typically reach sexual maturity during their second year (Wilk 1977). Depending on the population, spawning may occur inshore or in waters extending to the edge of the continental shelf. Larvae exist in the plankton for up to 30 days and in some areas rely on cross-shelf transport to arrive in estuarine nursery areas (Hare and Cowen 1993). Seasonal migrations are common within each population, and tagged individuals have been reported to travel in excess of 1300 km (Lund and Maltezos 1970). It is not known if migration occurs among geographically distinct populations.

Mackerel

Three species of mackerels are recognized in the genus *Scomber*. The Atlantic mackerel (*S. scombrus*) is found in the North Atlantic (Figure 1c), spotted chub mackerel (*S. australasicus*) is found in the Indian and Pacific Oceans (Figure 1c), and the chub mackerel (*S. japonicus*) is found in the temperate waters of all three oceans (Figure 1d). Each species comprises multiple, disjunct populations. Comprehensive biological information is not available for all three species, or for the different geographical populations of each species. In general, mackerels are coastal, schooling fishes that feed on plankton and small fishes. Maximum size for each species is approximately 50 cm fork length (generally less than 2 kg), and sexual maturity is reached in 2–3 years (Collette and Nauen 1983). All three species are serial spawners and the duration of the larval stage is 3–4 weeks (Hunter and Kimbrell 1980; Ware and Lambert 1985).

Genetic Analyses

A wide variety of molecular genetic techniques are currently available to population geneticists (Avise 1994), and several have been used to survey variation of nuclear and mitochondrial loci within pelagic fishes. The large number of techniques and loci available for genetic analyses enables the selection of genetic loci and analytical methods that are best suited to reveal population structure within the particular species of interest. Unfortunately this same diversity reduces the opportunity for comparative studies of population structure across taxa as, more often than not, different studies have surveyed different loci with different techniques. Realizing the need for comparative studies with-

in the discipline, we have consistently employed RFLP analysis of the entire mtDNA genome as one approach in our investigations of genetic variation within cosmopolitan marine fishes.

Table 1. Sample sizes, the number of geographically distant collection locations in the Atlantic (A), Pacific (P), and Indian (I) Oceans, and genetic variation of cosmopolitan marine fishes

Species	Collection locations	*N*	Haplotype diversity, *h* (sample range)	Mean nucleotide sequence diversity, π (sample range)
Yellowfin tuna	1A, 5P	120	0.84 (0.82–0.87)	0.28% (0.28–0.39%)
Striped marlin	4P	166	0.82 (0.69–0.84)	0.30% (0.20–0.32%)
White marlin	4A	235	0.78 (0.54–0.90)	0.15% (0.06–0.15%)
Blue marlin	3A, 3P	424	0.91 (0.58–0.97)	0.59% (0.14–0.80%)
Sailfish	2A, 1P, 1I	109	0.59 (0.28–0.73)	0.40% (0.22–0.66%)
Bluefish	4A, 1P, 1I	150	0.92 (0.10–0.92)	1.09% (0.05–0.71%)
Atlantic mackerel	2A	40	0.58 (0.28–0.85)	0.18% (0.07–0.29%)
Spotted chub mackerel	4P, 1I	93	0.86 (0.59–0.86)	1.90% (0.13–0.77%)
Chub mackerel	4A, 4P	276	0.96 (0.64–0.95)	2.48% (0.29–0.50%)

Methodology

Detailed descriptions of sample collections and analytical protocols for each species are provided in the primary publications. For most specimens mtDNA was purified from heart and gonad tissue dissected from individuals within 8 h of capture using the equilibrium density gradient centrifugation protocols of Lansman et al. (1981). In cases where yields of purified mtDNA were low, mtDNA-enriched genomic DNA was isolated using the protocols of Chapman and Powers (1984). The mtDNA samples for each species were individually digested with a suite of 9 to 12 restriction endonucleases and the resulting fragments were separated electrophoretically overnight on agarose gels. Fragments of purified mtDNA were end-labeled with ^{35}S radionucleotides prior to electrophoresis and subsequently visualized by autoradiography (Sambrook et al. 1989). Gels containing digestions of mtDNA-enriched genomic DNA isolations were transferred to a solid support (Southern transfer) and hybridized with a biotin-labeled probe DNA consisting of mtDNA purified from conspecifics or the entire yellowfin tuna mtDNA molecule cloned as four fragments into a plasmid vector.

Each different fragment pattern produced by a restriction endonuclease was assigned a letter, and relationships among patterns were inferred from completely additive fragment sizes. A composite mtDNA haplotype consisting of 9 to 12 letters representing the fragment patterns generated by each restriction endonuclease was compiled for every individual. Haplotype diversity (*h*), which represents the probability of encountering different haplotypes in multiple draws from a sample, was calculated following Nei (1987). Nucleotide sequence divergence (*d*) between mtDNA haplotypes was estimated from a restriction site presence/absence matrix using the approach of Nei and Miller (1990). Mean nucleotide sequence diversity within samples (π), which is the weighted sequence divergence among haplotypes within a sample, and the mean nucleotide sequence divergence between samples corrected for within-sample diversity (δ) were calculated following Nei (1987). The distribution of haplotypes among collections was evaluated for homogeneity using the chi-square randomization method of Roff and Bentzen (1989). All of the above calculations were performed with the restriction enzyme analysis package (REAP) of McElroy et al. (1992).

Population Genetic Structuring Within Cosmopolitan Species With Discontinuous Distributions

Bluefish

Samples of bluefish were obtained from six geographically isolated populations; four within the Atlantic Ocean (U.S., Portugal, Brazil, and South Africa), one from the Pacific Ocean (eastern Australia), and one from the Indian Ocean (western Australia). RFLP analysis of mtDNA employing nine informative restriction endonucleases revealed a broad range of within-sample diversities among locations (Table 1). Five of the six bluefish collections exhibited relatively high levels of variation, with haplotype diversities in excess of $h = 0.66$. However, the two collections of 19 fish each obtained from eastern Australia in 1991 and 1995 displayed greatly reduced genetic variation. Both collections comprised two haplotypes, one of which was represented by 18 individuals in each sample, resulting in similar haplotype diversities of $h = 0.10$.

No haplotypes were shared among any of the six isolated collections of bluefish, although geographically proximate collections often contained haplotypes that differed by the gain or loss of a single restriction site. Bluefish from the western and eastern North Atlantic (U.S. and Portugal) were closely related ($\delta = 0.26\%$), as were those from eastern and western Australia ($\delta = 0.42\%$) (Figure 2). The South African collection was most closely associated with those from the western and eastern North Atlantic ($\delta = 0.38\%$ and 0.35%, respectively). Bluefish from the western South Atlantic (Brazil) were distantly related to all other geographically isolated populations of bluefish. Pairwise comparisons of the Brazilian bluefish with the five other populations resulted in net mean nucleotide sequence divergences greater than $\delta = 1.38\%$.

Atlantic Mackerel

Collections of 20 Atlantic mackerel each were obtained from the western North Atlantic (U.S.) and eastern North Atlantic (England). Within-sample variation revealed by RFLP analysis of mtDNA using 12 restriction enzymes was greater in the western Atlantic ($h = 0.85$) than the eastern Atlantic ($h = 0.28$) (Table 1). A single haplotype was common to both samples, occurring in a majority of individuals from the eastern North Atlantic (0.85) and at a lower frequency in the U.S. collection (0.35), but the distribution of haplotypes was not homogeneous between the samples. The rare haplotypes in both collections were closely related to the common haplotype (differing by the gain or loss of one or two restriction sites), resulting in a net nucleotide sequence divergence of $\delta = 0.01\%$ (Figure 2).

Spotted Chub Mackerel

Five collections of 15 to 21 spotted chub mackerel were obtained from the western North Pacific (Japan), eastern North Pacific (Mexico), western South Pacific (Australia and New Zealand), and Red Sea (Israel). Haplotype diversities (*h*) were fairly similar among the samples, varying between 0.59 and 0.85 (Table 1), but the mean nucleotide sequence diversities of the Australia and New Zealand collections ($\pi = 0.75\%$ and 0.77%, respectively) were elevated relative to those from Japan, Mexico, and the Red Sea ($\pi = 0.30\%$, 0.13%, and 0.41%, respectively). This difference resulted from the presence of two divergent mtDNA lineages within the Australia and New Zealand samples. The haplotypes from the different lineages differed

by an average nucleotide sequence divergence of $d = 1.34\%$. One of the lineages was unique to the samples from Australia and New Zealand. Three haplotypes were common to those samples and the distribution of haplotypes between the two locations was not significantly heterogeneous.

Collections of spotted chub mackerel from Japan and Mexico in the North Pacific shared two haplotypes, one of which occurred at elevated frequencies in both samples. Although the two samples were separated by a small net nucleotide divergence of $\delta = 0.02\%$, the distribution of haplotypes was not homogeneous between the samples ($P = .013$).

One haplotype was common to all four Pacific samples of spotted chub mackerel, occurring at low frequencies in the South Pacific and elevated frequencies in the North Pacific. A net nucleotide sequence divergence of $\delta = 0.54\%$ separated the combined North Pacific and South Pacific samples (Figure 2), reflecting the presence of the divergent mtDNA lineage in the South Pacific samples.

The Red Sea collection of spotted chub mackerel possessed haplotypes that were intermediate to those of Pacific spotted chub mackerel and Atlantic chub mackerel. The Red Sea sample was most closely related to the South Pacific samples of spotted chub mackerel ($\delta = 0.51\%$), in particular, the mtDNA lineage that was unique to the Australia and New Zealand samples. The Red Sea mackerel collection was originally described as chub mackerel (*S. japonicus*) based on morphology and the reported distribution of the species of *Scomber* (Matsui 1967). However, both RFLP analysis of mtDNA and sequencing of the mitochondrial cytochrome-*b* gene revealed that the Red Sea mackerels were more closely aligned with spotted chub mackerel. A subsequent morphological examination of mackerel from the Red Sea and northern Indian Ocean has resulted in a reassignment to *S. australasicus* (Baker and Collette, 1998).

Chub Mackerel

Eight collections of chub mackerel were analyzed, five from the Atlantic Ocean and three from the Pacific Ocean. Several haplotypes were common to two or more samples within the Atlantic. Along the western Atlantic, samples from the United States and Argentina shared one haplotype and were separated by a small net nucleotide divergence ($\delta = 0.04\%$), but the distribution of haplotypes was significantly heterogeneous between the two samples. In the eastern Atlantic the distribution of haplotypes among collections from the Mediterranean Sea, Ivory Coast, and South Africa was not significantly heterogeneous. Similarly, heterogeneity was not observed between samples from Argentina and the Ivory Coast, across the South Atlantic.

Net nucleotide sequence divergences greater than $\delta = 1.17\%$ separated all Atlantic and Pacific samples of chub mackerel (Figure 2). Within the western North Pacific the distribution of haplotypes was not significantly heterogeneous between collections from Taiwan and Japan. Four haplotypes were common to these collections, three of which occurred in more than one individual in each sample. The combined western North Pacific samples exhibited one fixed restriction site difference relative to the sample from California, and were separated by a net nucleotide sequence divergence of $\delta = 0.30\%$.

Population Genetic Structuring Within Cosmopolitan Species With Continuous Distributions

Yellowfin Tuna

Five collections of 20 yellowfin tuna each from the Pacific (Mexico, Ecuador, Hawaii, Papua New Guinea, and Australia) and one from the Atlantic (U.S.) were analyzed with 12 restriction enzymes. Variation was strongly conserved across all samples. Haplotype diversities (h) ranged from 0.82 to 0.87, and mean nucleotide sequence diversities (π) varied from 0.28% to 0.39%. Several haplotypes were shared among all collections of yellowfin tuna, including those from different oceans (Table 2). The two most common haplotypes were represented by approximately one-half of the individuals in each sample. The distribution of haplotypes among the five samples of yellowfin tuna within the Pacific Ocean and the single Atlantic sample was not significantly heterogeneous, and the net nucleotide sequence divergences (δ) between samples were quite small, ranging from 0.01% to 0.10% (Figure 3).

Striped Marlin

Four Pacific collections of approximately 40 striped marlin from Mexico, Ecuador, Hawaii, and Australia, each exhibited about the same level of within-sample variation. Haplotype diversities (h) varied between 0.69 and 0.84, and mean nucleotide sequence mean diversities (π) ranged between 0.20% and 0.32% (Table 1). Although the level of variation was similar among samples, the distribution of haplotypes was not. Several haplotypes occurred at elevated frequencies either in single collections or in combined collections from the eastern Pacific or western/central Pacific (Table 2). Values of net nucleotide sequence divergence (δ) between samples were very low, ranging from 0.01% to 0.06% (Figure 3). This resulted from the relatively high levels of within- sample variation and the close affinity of most haplotypes, which typically differed by the gain or loss of one or two restriction sites.

White Marlin

Four relatively large collections of white marlin were obtained from geographically distant locations within the Atlantic Ocean (U.S., Caribbean, Brazil, and Morocco). RFLP analysis of mtDNA employing 12 restriction endonucleases revealed substantial within-sample variation ($h = 0.54$–0.90) but reduced nucleotide sequence diversities ($\pi = 0.15$–0.30%) due to the very close relationships of the haplotypes. No spatial partitioning of genetic variation was evident among the four collection locations. Seven haplotypes were represented by four or more individuals in the pooled sample of 235 white marlin, and six of these were common to all four geographically distant samples. No major discontinuities in haplotype frequencies were noted between samples across the Atlantic or across the equator, and net genetic divergences (δ) between samples were all less than 0.01%.

White/Striped Marlin

Ten restriction endonucleases were common to the RFLP analyses of white and striped marlin, allowing an evaluation of interocean genetic divergence between the two species. Surprisingly, two haplotypes were common to both species, one of which occurred in white marlin at a frequency of 0.73 and in striped marlin at a frequency of 0.13. Furthermore, the most common white marlin haplotype differed by a single site change from the most common striped marlin genotype. Neighbor-joining and parsimony analyses revealed no clustering of haplotypes by ocean (species), and the white marlin and striped marlin were separated by a net nucleotide sequence divergence of 0.12% (Figure 3).

Blue Marlin

Blue marlin collections from the Atlantic Ocean (U.S., Jamaica, and Brazil) and Pacific Ocean (Mexico, Ecuador, Hawaii, and Australia) exhibited high levels of within-sample variation (Table 1). Atlantic sam-

Table 2. Distribution of mtDNA haplotypes among collections of yellowfin tuna (YFT) and striped marlin (STM)

Genotype	MEX	ECU	HAW	AUS	PNG	ATL
YFT-1	6	7	7	8	8	7
YFT-2	5	2	3	4	3	3
YFT-3	—	3	1	—	1	1
YFT-4	1	1	—	2	—	2
YFT-5	—	—	—	1	1	2
YFT-6	—	1	1	—	—	1
YFT-7	1	2	—	—	—	—
YFT-8	2	—	—	1	—	—
Minor	5	4	8	4	7	4
Total	20	20	20	20	20	20
STM-1	12	20	14	12		
STM-2	6	6	7	3		
STM-3	8	9	4	1		
STM-4	—	2	10	8		
STM-5	—	1	2	7		
STM-6	—	1	—	11		
STM-7	6	—	—	—		
STM-8	—	—	3	—		
Minor	4	1	3	5		
Total	36	40	43	47		

Minor haplotypes occurred in two or fewer individuals in the pooled sample.

ples of blue marlin consistently exhibited higher mean nucleotide sequence diversities than Pacific collections (pooled Atlantic π = 0.74%, pooled Pacific π = 0.18%). This was due to the presence of two genetically distinct mtDNA lineages within the Atlantic samples, only one of which was represented in Pacific collections. The unique Atlantic haplotypes typically differed from the "ubiquitous" haplotypes by five or more restriction site differences, and an average nucleotide sequence divergence of 1.23%.

No significant geographic population structuring was revealed among blue marlin samples within the Atlantic or Pacific Oceans. Almost all haplotypes represented by more than a few individuals were common to two or more collections, and no significant heterogeneity was observed in the distribution of haplotypes among collections within an ocean.

Significant heterogeneity was evident, however, in the distribution of haplotypes between collections of blue marlin from the Atlantic and Pacific Oceans. This was due primarily to the presence of the unique lineage of haplotypes within the Atlantic which occurred in approximately 40% of the Atlantic blue marlin. A net nucleotide sequence divergence of 0.15% separated the Atlantic and Pacific collections (Figure 3).

Sailfish

Sailfish collections from the Atlantic (U.S. and Brazil), Pacific (Mexico), and Indian Oceans (Australia) exhibited a range of within-sample diversities (Table 1), with the Pacific sample exhibiting values considerably lower than the other collections. Two genetically distinct clades of haplotypes were present within Atlantic samples, with only one occurring in samples from the Pacific or Indian Oceans. The Atlantic clade haplotypes occurred in approximately 80% of the Atlantic sailfish and were separated from ubiquitous clade haplotypes by an average nucleotide sequence divergence of 0.65%. A mean nucleotide sequence divergence of 0.27% separated Atlantic and Indo-Pacific collections (Figure 3).

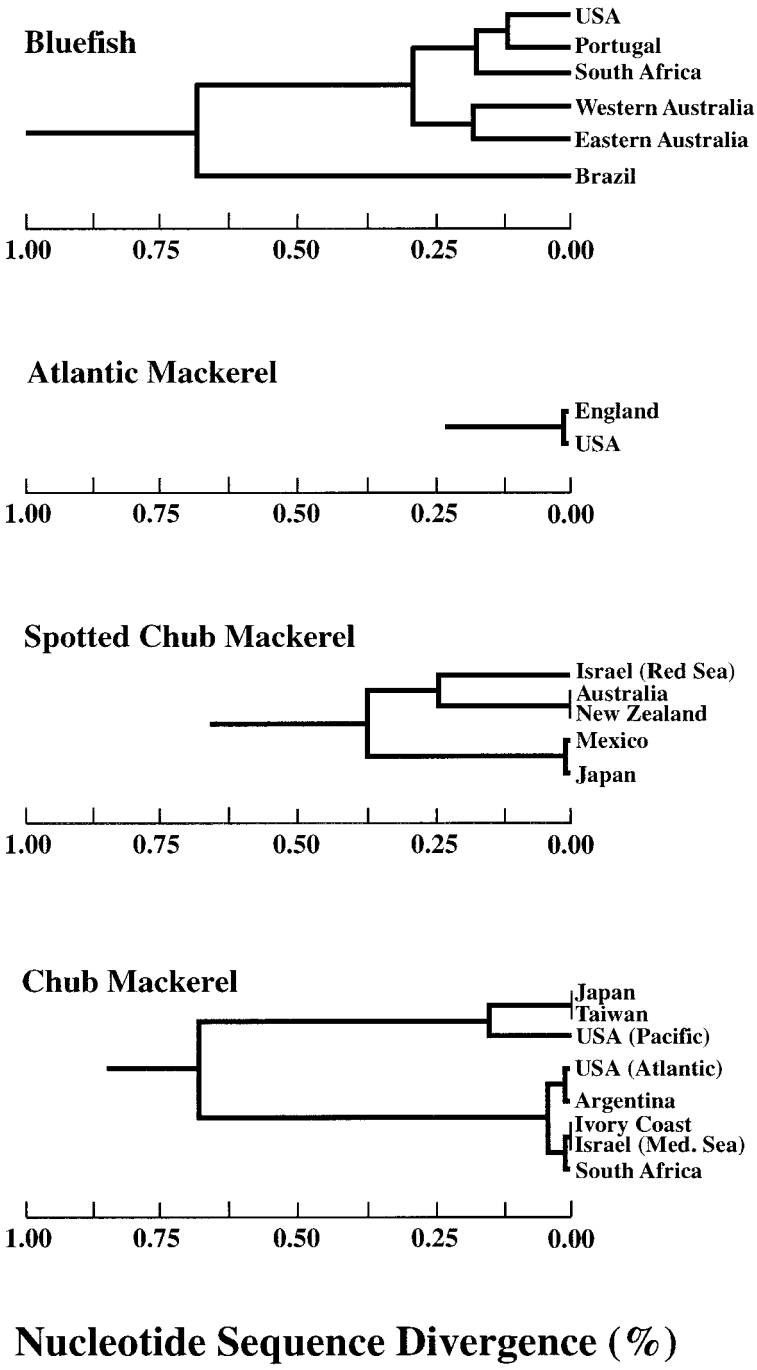

Figure 2. UPGMA clustering of net mean nucleotide sequence divergences (δ) among populations of four species of discontinuously distributed pelagic marine fishes: bluefish (*P. saltatrix*), Atlantic mackerel (*S. scombrus*), spotted chub mackerel (*S. australasicus*), and chub mackerel (*S. japonicus*).

Phylogeographic Patterns Among Cosmopolitan Species

Cosmopolitan Species With Discontinuous Distributions

Conspecific populations of bluefish, Atlantic mackerel, and chub mackerel all exhib-

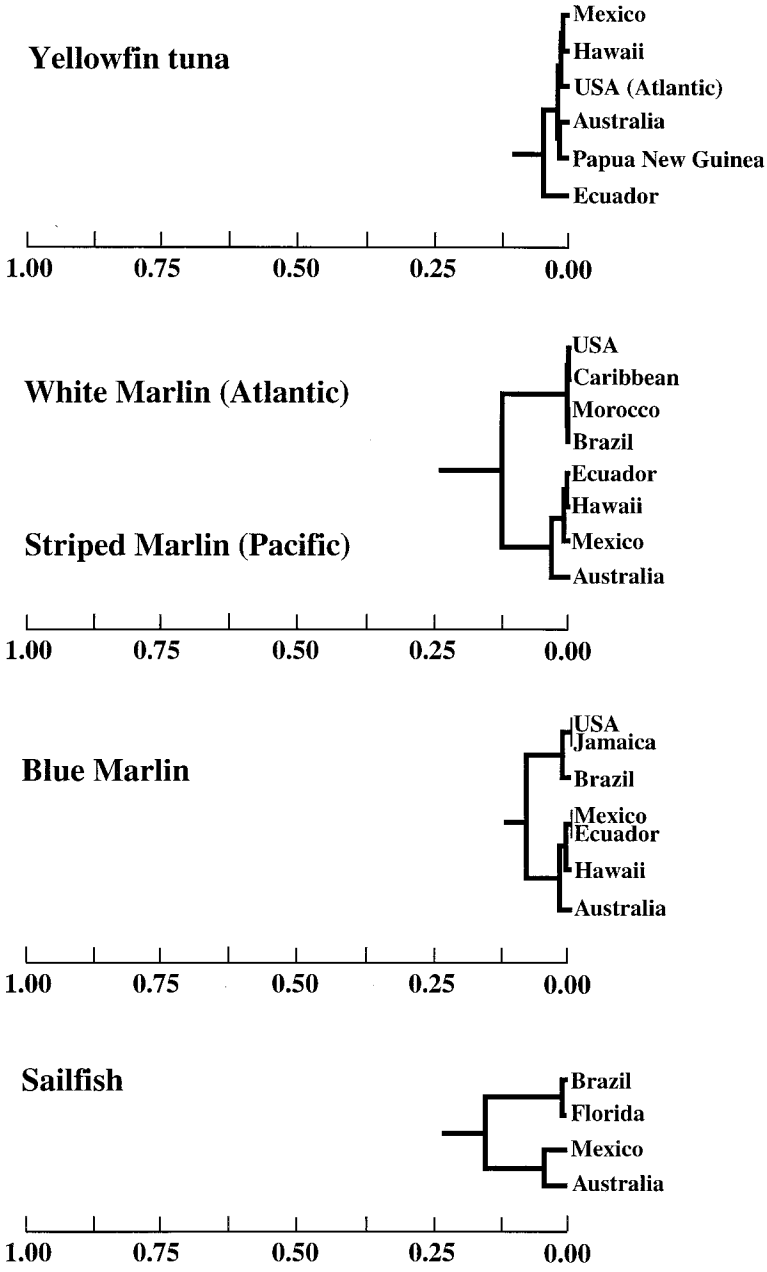

Figure 3. UPGMA clustering of net mean nucleotide sequence divergences (δ) among geographically distant collections of four "species" of continuously distributed pelagic marine fishes: yellowfin tuna (*T. albacares*), white marlin/striped marlin (*T. audax*/*T. albidus*), blue marlin(*M. nigricans*), and sailfish(*I. platypterus*).

ited close genetic relationships across the North Atlantic, although there was a considerable range in genetic affinities among species. Haplotypes were shared among conspecific populations of Atlantic mackerel and chub mackerel, but not among bluefish samples, and net nucleotide sequence divergences between conspecific populations of the three species ranged from 0.01% (Atlantic mackerel) to 0.26% (bluefish) (Table 3). Values of mtDNA sequence divergence can be converted to estimates of divergence times by the application of a molecular clock, although it is realized that evolutionary rates may vary among and within lineages over time (Avise 1994), and that stochastic variation in the accumulation of relatively small numbers of substitutions may represent a substantial source of error (Hillis et al. 1996). Using a rate of 2% nucleotide sequence divergence per million years for the entire mtDNA molecule (Brown et al. 1979), estimates of divergence times between conspecific populations in the North Atlantic range from 5,000 years for Atlantic mackerel to 130,000 years for bluefish. Although caution must be used in the application of divergence times, these data demonstrate a difference in the genetic connectivity of Atlantic mackerel, chub mackerel, and bluefish across the Atlantic.

Over the past million years the distribution of tropical and temperate water masses has changed dramatically (Dansgaard et al. 1993; Savin et al. 1975), and even as recently as 18,000 years ago, during the last ice age, temperatures may have cooled sufficiently in some tropical areas to allow contact (or colonization) of isolated populations of temperate fishes (CLIMAP 1976). The range of genetic divergences among conspecific populations of cosmopolitan temperate fishes suggests that there has been multiple opportunities for contact. Differences in dispersal abilities, or the stochastic nature of dispersal, could be responsible for the observed range in divergence times across temperate species. In addition, slight differences in temperature preferences between species, combined with historical temperature fluctuations, may have presented some species with a greater opportunity for gene flow.

Comparisons of patterns of genetic relationships among distant populations of bluefish and mackerels from other areas within the Atlantic Ocean were less congruent than those in the North Atlantic due to the fact that bluefish from the western South Atlantic (Brazil) were distantly related ($\delta > 1.3\%$) to all other geographically isolated conspecific populations. Large divergences were not observed between other bluefish populations or among conspecific populations of chub mackerel within the Atlantic Ocean. A similar phylogeographic pattern was not evident for chub mackerel in the Atlantic Ocean. Chub mackerel from Argentina exhibited close genetic affinities with all other Atlantic samples (Table 3), and no significant heterogeneity was observed in the distribution of haplotypes between collections from Argentina and the Ivory Coast. The relative isolation of Brazilian bluefish is puzzling and may simply reflect the stochastic nature of long-distance dispersal of temperate species across the tropics.

Crosetti et al. (1994) employed RFLP analysis of the entire mtDNA genome to study the global phylogeography of grey

Table 3. Comparison of within-ocean net nucleotide sequence divergence (δ) among conspecific populations of discontinuously distributed pelagic fishes

Species	Populations	δ
North Atlantic (west/east)		
Bluefish	U.S./Portugal	0.26
Atlantic mackerel	U.S./England	0.01
Chub mackerel	U.S./Israel (Mediterranean)	0.14
South Atlantic (west/east)		
Bluefish	Brazil/South Africa	1.66
Chub mackerel	Argentina/Ivory Coast	0.03
	Argentina/Israel (Mediterranean)	0.07
	Argentina/South Africa	0.10
Atlantic Ocean (north/south)		
Bluefish	U.S./Brazil	1.48
	Portugal/South Africa	0.35
Chub mackerel	U.S./Argentina	0.04
	Israel (Mediterranean)/Ivory Coast	0.00
	Israel (Mediterranean)/South Africa	0.01
North Pacific (west/east)		
Chub mackerel	Japan/U.S.	0.32
Spotted chub mackerel	Japan/Mexico	0.02

All values were estimated using RFLP analysis of mtDNA employing 9 to 12 restriction endonucleases.

mullet (*Mugil cephalus*), which occurs in discontinuous distributions throughout temperate and tropical waters, and reported a net nucleotide divergence between eastern and western Atlantic samples of 1.78%. This value is comparable to those between bluefish from Brazil and other Atlantic conspecific populations. However, genetic divergences between all grey mullet populations were consistently larger than those between bluefish (excluding Brazil), chub mackerel, or spotted mackerel populations. This suggests a greater time of isolation among grey mullet populations, and the potential for a different isolating mechanism.

Close genetic affinities were revealed between conspecific populations of spotted chub mackerel and chub mackerel across the North Pacific. Samples of spotted chub mackerel from Japan and Mexico (two haplotypes in common, $\delta = 0.02\%$) were more closely related than chub mackerel from Japan and California (no haplotypes in common, $\delta = 0.30\%$). Estimated divergence times for the conspecific populations of the two species are 10,000 years and 150,000 years, respectively. Genetic relationships between sardines (*Sardinops sagax*) across the North Pacific (Japan and California) based on sequence analysis of the mitochondrial control region (Bowen and Grant 1997) and cytochrome-*b* gene (Grant et al., in press) correspond to an isolation time of a few hundred thousand years, similar to that estimated for chub mackerel across the North Pacific.

The genetic relationships among conspecific populations of bluefish and mackerels are consistent with divergences during or after the Pleistocene, suggesting that dispersal events have been an important factor in shaping the current genetic relationships among conspecific populations. Dispersal could be promoted within these temperate species by both larval drift and adult movements. Bluefish are capable of extended movements (Lund and Maltezos 1970) and large schools of mackerel are encountered well offshore (Collette and Nauen 1983), providing a possible mechanism for dispersal across ocean basins. Within the North Atlantic, entrainment of larvae into the Gulf Stream could provide a mechanism for transport, as has been suggested for bluefish (Hare and Cowen 1993). The potential for larval transport may be important in other current systems as well.

The role of dispersal is clearly important for establishing new populations, and the possibility of recent colonization events was suggested for populations of bluefish and spotted chub mackerel. In contrast to other conspecific collections, bluefish samples from eastern Australia were nearly monotypic, and the haplotypes present were most closely related to those in western Australia. These data are consistent with a recent colonization of eastern Australia by western Australian bluefish, most likely via the Great Australian Bight during a period of elevated water temperatures.

A similar reduction of variation relative to other conspecific populations was noted for the spotted chub mackerel sample from Mexico. Spotted chub mackerel do not occur along the mainland coast of North or South America, and the Revillagigedo Islands represent the furthest penetration of the species into the eastern Pacific. The reduction in genetic diversity of the Revillagigedo Island sample, and its close affinity to the western Pacific populations (Taiwan and Japan) is consistent with the interpretation that the Revillagigedo Islands population may be the result of a recent colonization event.

Continuously Distributed Cosmopolitan Fishes

As expected, cosmopolitan marine fishes with continuous distributions exhibited far less genetic structuring than species with discontinuous distributions (compare Figures 2 and 3). However, the level of intraspecific structuring within circumtropical species ranged from a lack of genetic differences between ocean populations to significant but shallow structuring within an ocean.

The distribution of mtDNA haplotypes among five samples of yellowfin tuna from geographically distant locations in the Pacific Ocean was not significantly heterogeneous, nor was heterogeneity observed when a sixth sample from the Atlantic Ocean was included. Ward et al. (1994) also found negligible partitioning of mtDNA variation among samples of yellowfin tuna from the Pacific Ocean, although they did report statistically significant differences at an allozyme locus between pooled western and eastern Pacific samples.

Blue marlin, white marlin, and sailfish, like yellowfin tuna, exhibited a lack of population structuring within oceans. For all three billfish species, conspecific collections from geographically distant sites within an ocean exhibited distributions of mtDNA haplotypes that were not significantly heterogeneous. Therefore, the null hypothesis of a common gene pool could not be disproved. A similar observation was reported for swordfish (*Xiphias gladius*) in the North Pacific by Grijalva-Chon et al. (1994). Their RFLP analysis of mtDNA revealed no significant differences among large collections of swordfish from Mexico, Hawaii, and Japan.

The lack of significant heterogeneity in the distribution of mtDNA haplotypes among collections of pelagic fishes across broad regions is consistent with some gene flow between geographically distant areas. Theoretically, gene flow on the order of a few individuals per generation would be sufficient to prevent the accumulation of significant genetic drift between geographically distant locations

(Hartl and Clark 1989). Tagging studies have demonstrated the capacity for long-range dispersal in many pelagic species (Hunter et al. 1986; Scott et al. 1990). Coupled with continuous suitable habitat across oceans, and the occurrence of protracted spawning over a broad geographic area, the occurrence of some intraocean gene flow does not seem problematic. In the case of yellowfin tuna, interocean gene flow would be possible around the Cape of Good Hope during the austral summer. The existence of yellowfin tuna and other circumtropical species in this area has been demonstrated (Talbot and Penrith 1962).

In contrast to yellowfin tuna, both blue marlin and sailfish exhibited significant genetic differences between samples from the Atlantic and Pacific Oceans. The mtDNA haplotypes of Atlantic collections of each species comprised two genetically divergent lineages, only one of which was represented in Pacific samples. However, average nucleotide sequence divergence between "Atlantic" and "ubiquitous" haplotypes of blue marlin was almost twice that of sailfish (d = 1.23% and 0.65%, respectively), and the Atlantic clade of haplotypes was represented in approximately 80% of Atlantic sailfish, while the Atlantic clade occurred in less than 40% of Atlantic blue marlin. Finnerty and Block (1992) also noted the presence of two divergent mtDNA lineages in blue marlin based on their analysis of 26 mitochondrial cytochrome-*b* sequences.

Divergent mtDNA lineages also have been reported for swordfish in the Atlantic Ocean. Sequence analyses of the swordfish mtDNA control region demonstrated the presence of a genetically divergent lineage of mitochondrial haplotypes that was most frequent in swordfish from the Mediterranean and occurred at decreasing frequencies in the samples from the North Atlantic, South Atlantic, and Pacific, respectively (Alvarado-Bremer et al. 1996; Rosell and Block 1996).

Based on the phylogeographic structuring exhibited between conspecific populations of blue marlin and sailfish from the Atlantic and Pacific Oceans, one would expect an even greater genetic divergence between white marlin and striped marlin. This was not the case (Figure 3). The two species shared two mtDNA haplotypes, and genetically divergent mtDNA lineages characteristic of Atlantic samples of blue marlin and sailfish were not present in white marlin. The net genetic divergence between white marlin and striped marlin (δ = 0.12%) was only twice the maximum value found between geographically distant samples of striped marlin within the Pacific Ocean (δ = 0.06%), and lower than the divergences between conspecific samples of blue marlin and sailfish from the Atlantic and Pacific Oceans (δ = 0.15% and 0.27%, respectively). Sequence analysis of the mitochondrial cytochrome-*b* gene by Finnerty and Block (1995) also revealed a high genetic similarity between white and striped marlin. Together these data suggest that a reexamination of the taxonomic status white marlin and striped marlin is warranted.

Within the Pacific Ocean striped marlin exhibited significant heterogeneity among geographically distant collections. Although the phylogeographic structuring among striped marlin collections was relatively shallow (Figure 3), the data suggest very limited gene flow among striped marlin from distant areas. This was not expected as the natural history of the species would appear conducive to gene flow. Striped marlin are continuously distributed across the Pacific Ocean, exhibit a protracted spawning season over a large geographic area, and individuals are capable of undertaking extensive movements (Squire 1987). The observed spatial partitioning of genetic variation among widely separated collections of striped marlin could be the product of ephemeral evolutionary "noise" due to a large variance in female reproductive success of these prolific spawners (Hedgecock 1994), or it could result from spawning site fidelity. Distinct seasonal movements associated with spawning have been reported for striped marlin off the coast of Mexico (Squire and Suzuki 1990).

Intraspecific Phylogenies

A range of intraspecific population structures was exhibited by the cosmopolitan fishes investigated in this study, and as expected, species with discontinuous distributions displayed greater divergence among geographically distant samples than continuously distributed fishes. Relative to similar analyses of freshwater fishes or terrestrial organisms, the magnitude of population structuring exhibited by pelagic marine fishes is extremely small (Avise 1994).

In general, haplotypes within a species were closely related, differing by the gain or loss of a few restriction sites. In only three instances—Australian and New Zealand spotted chub mackerel, Atlantic blue marlin, and Atlantic sailfish—was there evidence of a deeper genetic architecture. For each of these species, two genetically distinct mtDNA lineages were present in a geographically restricted area, a pattern consistent with a period of isolation and secondary contact (Avise et al. 1987). The average nucleotide sequence divergence between haplotypes of the divergent clades (d = 0.65–1.34%) suggests an isolation event dating to the Pleistocene.

The high haplotype diversities and close genetic similarities among haplotypes observed in cosmopolitan species is consistent with reports for several marine fishes (Shields and Gust 1995) and has been interpreted as evidence for recent population expansion (Rogers 1995). Grant and Bowen (1998) reported high haplotype diversities and close genetic relationships among haplotypes for several species of anchovies and sardines. They suggested that such a pattern could result from periodic extinctions and recolonizations, likely events for species which occupy upwelling zones that may be geologically ephemeral (Hayward 1997). Such an explanation cannot account for the phylogeographic pattern found for many of the tropical cosmopolitan species examined in this study, as tropical marine waters are believed to have been a relatively constant environment for millions of years, resulting in high species diversities (Briggs 1974). Other factors must also be responsible for the relatively high diversity and recent coalescence of mtDNA haplotypes of cosmopolitan marine fishes.

Implications for Management and Conservation

Effective management and conservation of fisheries resources requires an understanding of the population structure of the exploited species, and these studies have provided information to refine existing management models. In the Atlantic Ocean, blue and white marlin are managed by the member nations of the International Commission for the Conservation of Atlantic Tunas (ICCAT). Both blue marlin and white marlin are overexploited, and the biomass of each species is less than 25% of that necessary to support maximum sustainable yield (SCRS 1997). ICCAT previously assumed that each species comprised two stocks, north and south of 5°N latitude. However, the lack of significant genetic differences between conspecific collections of blue marlin and white marlin from the North and South Atlantic is consistent with the existence of a single

Atlantic stock for each species. The genetic results are supported by fishing records indicating the presence of white marlin and blue marlin across 5°N latitude throughout the year, the occurrence of continuous spawning activity over a broad area across the tropics, and tag and recapture data demonstrating movements of individuals of both species across 5°N latitude. To effect a rebuilding of these species, conservation efforts will have to be applied throughout the Atlantic Ocean.

Because time and funds are limited, it has not been possible to evaluate the genetic basis of population structure of all pelagic species, and management agencies have had to make assumptions regarding the population structure of some species based on information gained from other species that are either taxonomically related or ecologically similar. The large variation in population structures observed among cosmopolitan marine fishes suggests that such assumptions are inappropriate. The assumption of a single stock when multiple stocks exist could result in management measures allowing the overharvest of a genetic unit, and conceivably the loss of unique genetic variation. This underscores the need to obtain a thorough understanding of the genetic basis of population structure for each species for proper management or, in the absence of such information, a serious consideration of the effects of proposed management decisions on alternate population structures.

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Corresponding Editor: Fred W. Allendorf