Shallow Population Histories in Deep Evolutionary Lineages of Marine Fishes: Insights From Sardines and Anchovies and Lessons for Conservation

W. S. Grant and B. W. Bowen

Most surveys of mitochondrial DNA (mtDNA) in marine fishes reveal low levels of sequence divergence between haplotypes relative to the differentiation observed between sister taxa. It is unclear whether this pattern is due to rapid lineage sorting accelerated by sweepstakes recruitment, historical bottlenecks in population size, founder events, or natural selection, any of which could retard the accumulation of deep mtDNA lineages. Recent advances in paleoclimate research prompt a reexamination of oceanographic processes as a fundamental influence on genetic diversity; evidence from ice cores and anaerobic marine sediments document strong regime shifts in the world's oceans in concert with periodic climatic changes. These changes in sea surface temperatures, current pathways, upwelling intensities, and retention eddies are likely harbingers of severe fluctuations in population size or regional extinctions. Sardines (*Sardina, Sardinops*) and anchovies (*Engraulis*) are used to assess the consequences of such oceanographic processes on marine fish intrageneric gene genealogies. Representatives of these two groups occur in temperate boundary currents on a global scale, and these regional populations are known to fluctuate markedly. Biogeographic and genetic data indicate that *Sardinops* has persisted for at least 20 million years, yet the mtDNA genealogy for this group coalesces in less than half a million years and points to a recent founding of populations around the rim of the Indian–Pacific Ocean. Phylogeographic analysis of Old World anchovies reveals a Pleistocene dispersal from the Pacific to the Atlantic, almost certainly via southern Africa, followed by a very recent recolonization from Europe to southern Africa. These results demonstrate that regional populations of sardines and anchovies are subject to periodic extinctions and recolonizations. Such climate-associated dynamics may explain the low levels of nucleotide diversity and the shallow coalescence of mtDNA genealogies. If these findings apply generally to marine fishes, management strategies should incorporate the idea that even extremely abundant populations may be relatively fragile on ecological and evolutionary time scales.

From the Conservation Biology Division, Northwest Fisheries Science Center, NOAA, Seattle, Washington, and the Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, Florida. We thank A. Bass, A. Clark, and A. Garcia for technical support, and R. Leslie and A. Payne (Sea Fisheries Research Institute, Cape Town, South Africa), T. Kobayashi (National Research Institute of Fisheries Science, Yokohama, Japan), S. Jablanski (SUDEPPE, Rio de Janeiro, Brazil), and J. Shaklee (CSIRO, Canberra, Australia) for generously providing samples for the various studies reviewed in this article. K. Bailey, J. Gold, S. Karl, T. Streelman, F. Utter, and R. Waples provided insightful comments on the manuscript. Genetic studies of sardines and anchovies were supported by the U.S. National Science Foundation and by the Foundation for Research Development, Pretoria, South Africa. Address correspondence to Dr. Grant, Northwest Fisheries Science Center, 2725 Montlake Boulevard East, Seattle, WA 98112-2097, or e-mail: stew.grant@noaa.gov. 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.

 89:415–426

A recurring debate in evolutionary biology is over the extent to which microevolutionary processes operating within a species can be extrapolated to explain macroevolutionary differences among species . . .
Avise et al. (1987, p. 489)

To understand the dynamics of marine fish populations, researchers must identify the conditions that regulate reproduction, population growth, and persistence. On short (ecological) time scales, a variety of factors, including nutrient cycles, food-chain processes, spawning, predation, recruitment, and climate have been proposed as primary regulators of abundance (Butler 1991; Parrish and Mallicoate 1995; Smith et al. 1992; Watanabe and Kuroki 1997). Although several early hypotheses about population regulation are now discounted on the basis of field studies, other hypotheses remain untested because of the lack of an appropriate tool. Recent advances in sampling technology and satellite imagery show considerable promise, demonstrating, for example, that in the California Current egg and larval production is contingent on small upwelling plumes along the coast (Lo et al. 1996).

One emerging generalization from molecular analyses is that marine fishes are often characterized by shallow population genetic architectures, even though genetic divergence from sister taxa indicates sep-

arations of millions of years. In a review of mitochondrial DNA (mtDNA) diversity in widely distributed marine fishes, Shields and Gust (1995) noted a recurring pattern of a single or a few prevalent haplotypes with numerous rare haplotypes that were one or two mutations removed from the common haplotype. These starlike phylogenies characterize regional populations of haddock (*Melanogrammus aeglefinus*; Zwanenburg et al. 1992), Atlantic cod (*Gadus morhua*; Carr and Marshall 1991; Smith et al. 1989), cape hake (*Merluccius capensis*; Becker et al. 1988), deepwater hake (*M. paradoxus*; Becker et al. 1988), Atlantic herring (*Clupea harengus*; Kornfield and Bogdanowicz 1987), Pacific herring (*C. pallasi*; Schweigert and Withler 1990), red drum (*Sciaenops ocellatus*; Gold et al. 1993), black drum (*Pogonias cromis*; Gold et al. 1994), greater amberjack (*Seriola dumerili*; Richardson and Gold 1993), red snapper (*Lutjanus compechanus*; Camper et al. 1993), Spanish sardine (*Sardinella aurita*; Tringali and Wilson 1993), orange roughy (*Hoplostethus atlanticus*; Baker et al. 1995; Ovenden et al. 1989; Smolenski et al. 1993), Atlantic capelin (*Mallotus villosus*; Dodson et al. 1991), albacore tuna (*Thunnus alalunga*; Graves and Dizon 1989), and skipjack tuna (*Katsuwonus pelamis*; Graves et al. 1984). Shallow haplotype divergences atop long lineages are also clearly illustrated in Figures 4 and 5 of Bermingham et al. (1997) for species of damselfish isolated about 3 million years ago by the formation of the Panama isthmus. Explanations for this widespread pattern include a large variance in reproductive success that leads to the propagation of only a few haplotypes (Shields and Gust 1995), overharvesting (Camper et al. 1993), the physical nature of the pelagic realm (Graves 1995), recent habitat reductions (Shulman and Bermingham 1995), population bottlenecks (Gold et al. 1994), or other "demographic events" (Dodson et al. 1991).

This phenomenon is also apparent in sardines (*Sardina, Sardinops*) and anchovies (*Engraulis*). Both groups are globally distributed in temperate zones and have representative species or populations in most of the world's temperate boundary current systems (Figure 1). These populations are isolated by vast expanses of open ocean or by warm tropical waters that restrict movement across the equator. Sardines and anchovies are a perennial concern to marine resource managers because they represent the majority of the clupeoid biomass in highly productive

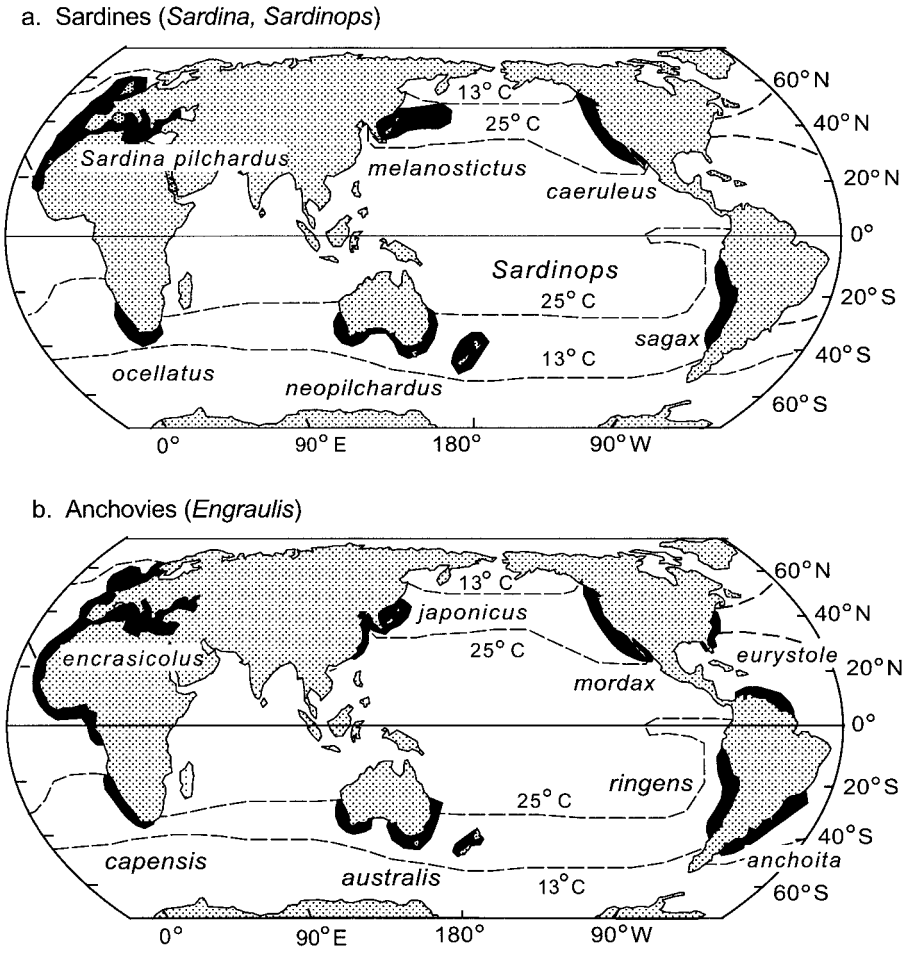

Figure 1. Geographical distributions of sardines (*Sardina, Sardinops*) and anchovies (*Engraulis*) with 13°C and 25°C isotherms (dashed lines).

boundary current systems, and because regional populations of both groups show strong fluctuations in abundance that have been attributed to high levels of exploitation (Murphy 1966, 1967). For example, the biomass of sardines (*Sardinops caeruleus*) in the California Current peaked at an estimated 3,600,000 metric tons (MT) in the 1930s (Murphy 1966) then declined during a period of intensive harvests to about 5,000–6,000 MT in 1975 (Barnes et al. 1992; Wolf 1992). The biomass of California anchovies (*Engraulis mordax*) has also fluctuated from lows in the 1950s to a high in the 1970s (Lo and Methot 1989). All of the regional populations of sardines and anchovies have similar histories of declines and partial recoveries which are attributed to harvests or to climatic and oceanographic changes (Lluch-Belda et al. 1989).

Here we review genetic evidence from allozyme and mtDNA datasets for sardines and anchovies that may bear imprints of population collapses (bottlenecks), metapopulation dynamics (extinctions and recolonizations), founder events, dispersals, and divergence between isolated populations. These case histories are used to evaluate the hypotheses that have been forwarded to explain shallow gene genealogies in other marine fishes. The forces that attenuate mtDNA diversity may be a key to understanding population regulation in marine fishes. Hence these shallow intraspecific phylogenies carry implications for microevolution and marine biogeography as well as resource management in the face of climatic change and high exploitation (Hansen et al. 1981; Santer et al. 1996).

Long-Term Climatic Variability and Population Abundance Cycles

It is widely accepted that climatic changes are capable of limiting abundances, but the impact of these changes on marine biodiversity has only recently been appreciated (Hayward 1997; Roemmich and McGowan 1995; Watson et al. 1996). Rapid changes in oceanic temperature over the

last few tens of thousands of years, corresponding to major climatic shifts, have been recorded in ice cores from Greenland (Dansgaard et al. 1993; GRIP Members 1993) and Antarctica (Jouzel et al. 1993; Lorius et al. 1985). These regime shifts, some of which have occurred on a time scale of only a few decades, drastically altered major ocean circulation and temperature patterns (Lehman and Kiegwin 1992). Recent decade-scale shifts in the Kuroshio Current led, in part, to a rapid decline of Japanese sardines in the 1940s (Kawasaki 1993; Kawasaki and Omori 1995).

On scales of centuries and millennia, abundances of sardines and anchovies in the California Current have fluctuated greatly. Based on scale deposition rates in anaerobic sediments, Baumgartner et al. (1992) identified nine population declines and recoveries over the last 1,700 years. During this interval the estimated abundance of the California sardine fluctuated from less than 1 million MT to at least 4 million MT. These fluctuations predate fishing activity along the California coast and thus are attributable entirely to natural biotic, climatic, and oceanic changes.

The earth's climate oscillates on several time scales with various amplitudes. For example, the population fluctuations documented by Baumgartner et al. (1992) for sardines occurred during a period of relatively minor climatic shifts. Over the preceding 100,000 years, the amplitude of global climatic oscillations, as recorded in Greenland ice cores, was much greater (GRIP Members 1993). These North Atlantic changes corresponded to temperature and salinity shifts in many of the world's oceans (Broecker 1995). Imprints of temperature fluctuations in ice cores reaching back about 250,000 years also indicate strong climatic variability (Dansgaard et al. 1993). On yet a deeper temporal scale, climates have greatly fluctuated during the four major Pleistocene glaciations reaching back 1.7 million years. These changes have undoubtedly led to population crashes and expansions, and possibly to extinctions of some regional sardine and anchovy populations in the major boundary currents of the world.

Sardines (*Sardina, Sardinops*)

Northwest Atlantic and Indian–Pacific sardines are divided into two genera. *Sardina* in European waters consists of a single species, *S. pilchardus,* that extended in historical times from West Africa to the North Sea in the Atlantic and from the western Mediterranean to the western margin of the Black Sea (Figure 1a). *Sardinops* inhabits five upwelling zones of the Indian–Pacific Ocean characterized by high levels of primary and secondary productivity, including southern Africa, Australia–New Zealand, Chile–Peru, west-central North America, and Japan. In the light of recent molecular data, the taxonomy of these regional populations is uncertain, and we will refer to them by their traditional species names: *S. ocellatus* (S. Africa), *S. neopilchardus* (Australia), *S. sagax* (Chile), *S. caeruleus* (California), and *S. melanostictus* (Japan). The geographic distributions of the regional populations are generally bounded by the 13°C and 25°C isotherms, since temperatures above 27°C are lethal to adults and larvae (Parrish et al. 1989). Sardines are notably absent in the western Atlantic, even though the temperate zones of the northwest and southwest Atlantic appear to be suitable for sardines, and both regions host populations of anchovies.

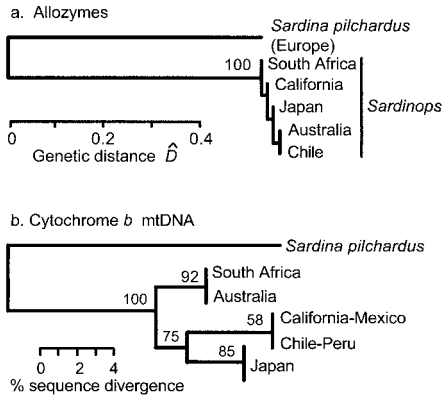

Figure 2. Majority-rule bootstrap of neighbor-joining trees representing phylogenetic relationships among taxa of sardines (*Sardina,* and *Sardinops*). Percentage bootstrap (over loci for allozymes, over nucleotide sites for sequences) support indicated at nodes of trees. **(a)** Nei's unbiased genetic distances based on 34 protein-coding loci (Grant and Leslie 1996). **(b)** Sequence divergences based on a 220 bp sequence in the cytochrome *b* gene of mitochondrial DNA (Grant et al., unpublished data).

The proposal that current Indian–Pacific sardine populations are ephemeral or have become established only recently is based on the observation that present-day populations of *Sardinops* are shallow twigs at the termini of an ancient lineage extending back to the Miocene. In an analysis of 34 allozyme loci, Grant and Leslie (1996) reported a Nei's genetic distance of $D = 1.04$ (± 0.24 SE) (Figure 2a) between the Atlantic–Mediterranean (*Sardina*) and Indian–Pacific (*Sardinops*) forms. An approximate time frame for this separation can be calibrated with divergences between fish populations separated by the rise of the Isthmus of Panama about 3 million years ago (Grant 1987; Keigwin 1978, 1982; Vawter et al. 1980) and by dispersal through the Bering Strait, also about 3 millions years ago, prior to the late Pliocene cooling of the Arctic Ocean (Grant 1984; Grant and Ståhl 1988; Grant et al. 1984). The resulting clock ($D = 1.0$ about 19 million years) yields an estimate of the divergence time between *Sardina* and *Sardinops* of about 19 million years BP (15–24 million years). This time frame coincides closely with the collision of the African plate against southern Europe (Steininger et al. 1985), a vicariant event which divided the Tethys Sea into Atlantic and Indian-Pacific components. An alternative scenario, postulated by Okazaki et al. (1996), is that the initial split between ancestral sardine populations occurred via the Isthmus of Panama. However, the magnitudes of the allozyme genetic distance between *Sardina* and *Sardinops* and sequence divergence between cytochrome *b* sequences (Figure 2) contradict this recent separation.

Although both allozyme and mtDNA data point to a deep evolutionary history for *Sardinops,* divergence among present-day populations reflects only a shallow history reaching back less than half a million years (Bowen and Grant 1997; Grant et al., in press; Grant and Leslie 1996). This shallow time frame and the low levels of allozyme and morphological diversity indicate that present sardine populations have expanded only recently around the rim of the Indian– Pacific Ocean. At least two legacies of this colonization process are apparent in the genetic data. One is a significant excess of low-frequency allozyme alleles over that expected with drift-mutation equilibrium in datasets for Indian–Pacific sardines (Grant and Leslie 1996), for California sardines (Hedgecock et al. 1989), and for South African sardines (Grant 1985). Such an excess is usually attributed to the retention of new mutations during population growth or expansion (Watterson 1984). Another indication that Indian–Pacific sardines have recently expanded is a Poisson-like distribution of the number of nucleotide differences observed in comparisons of cytochrome *b* sequences (Grant et al., in press). This distribution is attributed in other species to mutation-drift disequilibrium caused by explosive population growth (Rogers and Harpending 1992).

Phylogenetic relationships among regional populations are not resolved with

Table 1. mtDNA haplotype and nucleotide diversities and allozyme diversities in sardines (*Sardina, Sardinops*)

Region	Control region[a]			Cytochrome *b*[b]			Allozymes[c]	
	h	π	*n*	*h*	π	*n*	*H*	*n*
Sardina								
Europe				0.36	0.002	5	0.024	26
Sardinops								
South Africa	1.00	0.02	15	0.62	0.004	15	0.036	46
Australia	1.00	0.02	15	0.62	0.004	15	0.045	50
Chile	1.00	0.03	18	0.76	0.006	15	0.037	30
California	1.00	0.03	15	0.76	0.007	15	0.036	30
							0.010	149[d]
Japan	0.96	0.01	18	0.67	0.005	14	0.022	50

[a] Bowen and Grant 1997.
[b] Grant et al., in press.
[c] Grant and Leslie 1996.
[d] Hedgecock et al. 1989.

the allozyme data of Grant and Leslie (1996) because of the recency of divergence (Figure 2a); estimates of allozyme gene diversities ranged from 0.045 in Australian sardines to 0.022 in Japanese sardines (Table 1). Hedgecock et al. (1989) reported an estimate of $H = 0.010$ for California sardines and concluded that an ancient population bottleneck or founder effect may have reduced genetic diversity. These diversity values are low relative to those reported for other marine fishes (Ward et al. 1994) and much lower than diversities in other clupeiform fishes (see Table 8 in Hedgecock et al. 1989). In contrast, polymorphisms in the mtDNA control region and cytochrome *b* are relatively abundant, presumably due to the elevated mutation rate in mitochondrial DNA relative to nuclear protein-coding loci. The mtDNA gene trees, consisting of a network of minimal mutational distances between haplotypes for both the control region (Bowen and Grant 1997) and cytochrome *b* (Grant et al., in press), indicate a probable dispersal pathway around the rim of the Indian–Pacific Ocean connecting South Africa and Australia, with Chile, California, and Japan (Figure 3a,b).

Shallow divergences among these regional populations may be explained by two alternative models of population persistence and dispersal. First, *Sardinops* may have inhabited a limited area for most of the last 20 million years before expanding to the temperate corners of the Indian and Pacific Oceans in the last few hundred thousand years. Alternatively, regional *Sardinops* populations may have been extinguished repeatedly and recolonized by transoceanic or transequatorial migrants. Genetic analyses of present-day populations alone may not be able to resolve these alternative scenarios. While expected gene genealogical patterns are quite different under the two models, they may have converged in present-day populations due to regional extinctions that erased evidence of previous population histories (Figure 4). Fortunately, paleoclimate and fossil records may eventually offer a resolution of these two scenarios. In a study of marine Pleistocene and Pliocene sediments from coastal California, Fitch (1969) reported a conspicuous absence of sardine hard parts but a continuous record of other common species [hake (*Merluccius*), mackerel (*Trachurus*), and anchovy (*Engraulis*)]. Sardines also were not detected in elevated marine deposits dating from about 100,000 to 3 millions years BP, but were present in Native American middens about 7,000 years BP (Casteel 1975). Although temporal resolution in elevated marine deposits is not precise, these studies yield an approximate time frame for the arrival of the present *Sardinops* population in the California Current. It is not yet clear, however, whether this was the initial colonization or the most recent event in an extinction/recolonization cycle; a fossil record extending back 5–20 million years is needed to resolve this issue. Nonetheless, these results are consistent with the genetic data in indicating that shallow gene genealogies in *Sardinops* populations are due (at least in part) to a late Pleistocene dispersal around the rim of the Pacific Ocean.

Anchovies (*Engraulis*)

Anchovies are active plankton feeders found in the same temperate boundary currents as sardines, but additionally occur in less productive areas off Argentina–Brazil and in the western North Atlantic (Figure 1b). Regional populations of anchovies belong to a single genus, *Engraulis,* but the level of morphological differentiation between Old World and New World species indicates that a separate genus for Old World species may be warranted (Hubbs 1952; Whitehead 1973). The taxonomy of anchovies is further confused by the inclusion of three tropical species (genus *Cetengraulis*) within the morphologically based phylogenetic tree of *Engraulis* (Nelson 1984). Molecular data reinforce the arguments for revision of anchovy taxonomy, but we will refer to regional populations by traditional species names: *E. encrasicolus* (Europe), *E. capensis* (southern Africa), *E. australis* (Australia), *E. japonicus* (Japan), *E. mordax* (California–Mexico), *E. ringens* (Chile–Peru), *E. anchoita* (Argentina–Brazil), and *E. eurystole* (Atlantic U.S.–Canada).

Genetic partitions in anchovies are markedly different from those in sardines. The analyses of 31 allozyme loci (Figure 5a) and 521 bp of cytochrome *b* (Figure 5b) indicate that anchovies are divided into four relatively deep lineages corresponding to the three New World species (*E. anchoita, E. ringens, E. mordax*), and a lineage consisting of all Old World species combined: *E. japonicus, E. australis, E. capensis, E. encrasicolus* (and presumably West Atlantic *E. eurystole,* which was not assayed but which is morphologically very similar to the European anchovy *E. encrasicolus*). Large genetic distances in the allozyme survey and levels of mtDNA sequence divergence indicate that the four primary lineages have been isolated for 6–10 million years. Shallow genetic distances among the Old World species, however, indicate dispersal events within the last few hundreds of thousands of years and possibly more recently in some cases (Table 2, Figure 6).

While the Old World anchovies are closely related, three of the four (excepting the southern African population *E. capensis*) contain high levels of intraregional genetic diversity relative to the shallow separations between species. For example, two deep mtDNA lineages occur in European anchovies, the apparent result of isolation between Black and Mediterranean Sea populations during glacial maxima in the early Pleistocene (Magoulas et al. 1996). An average sequence divergence of $d = 2.2\%$ between haplotypes in these two lineages (Grant WS and Bowen BW, unpublished data) is consistent with this time frame. These lineages are in apparent secondary contact and are codistributed throughout the Mediterranean Sea and ad-

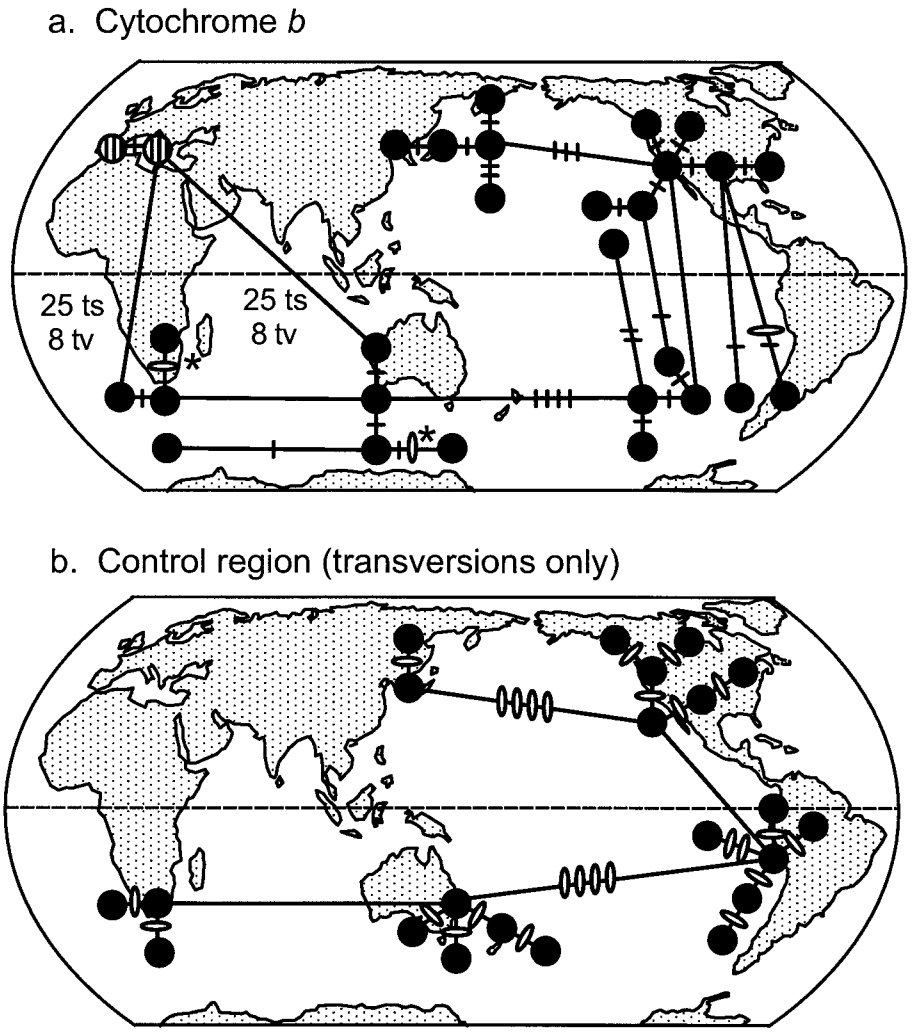

Figure 3. Parsimony network of mtDNA haplotypes in sardines (*Sardina, Sardinops*). **(a)** Cytochrome-*b.* Cross bars represent transitions and ovals represent transversions between haplotypes. Asterisks indicate amino acid replacements. Haplotypes in *Sardina* based on a 220 bp sequence; those in *Sardinops* based on a 258 bp sequence (Grant et al., in press). **(b)** Control region. Transversion haplotypes based on a 500 bp fragment (Bowen and Grant 1997).

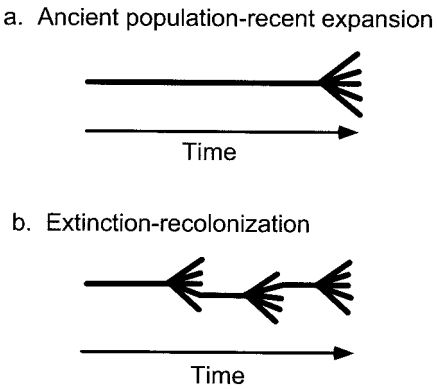

Figure 4. Models of sardine evolution. **(a)** Ancient population with a recent geographic expansion. **(b)** Population histories of extinctions and recolonizations.

jacent Atlantic Ocean. Since the average sequence divergence between Japanese and European haplotypes is only marginally larger, $d = 2.9\%$, the colonization of anchovies into Mediterranean waters appears to have occurred in the late Pliocene or early Pleistocene, possibly facilitated by a global cooling trend. Because continental configurations during this interval were essentially the same as they are now, and because a route of colonization across northern Eurasia was infeasible due to ice accumulation, the only dispersal pathway between Japan and Europe was around the tip of southern Africa and northward to the Mediterranean (see Figure 6). The intermediate position of some Australian haplotypes in the parsimony network is consistent with this route. However, the haplotypes in present-day populations of southern African anchovies are not intermediate between European and Australian anchovies, but are embedded in the network of European haplotypes. This feature of the parsimony network indicates that a previous southern African population has become extinct and has been recolonized from Europe within the last few tens of thousands of years. Notably the reintroduced anchovies in southern Africa contain both of the European mtDNA lineages, implying a colonization event after the reassociation of the Black Sea and Mediterranean forms.

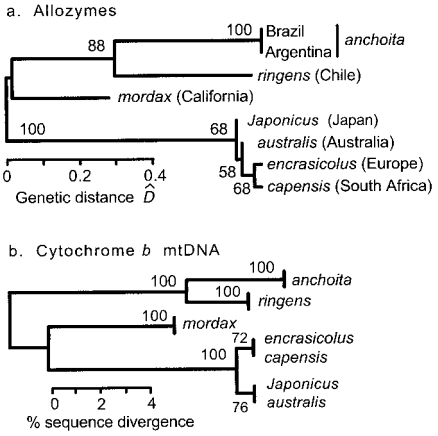

Figure 5. Majority rule, neighbor-joining trees representing phylogenetic relationships among taxa of anchovies (*Engraulis*). Percentage bootstrap support indicated at the nodes of trees. **(a)** Nei's (1978) unbiased genetic distances based on 31 protein-coding loci (Grant et al., unpublished data). **(b)** Sequence divergences based on a 521 bp sequence in the cytochrome *b* gene of mitochondrial DNA (Grant et al., unpublished data).

Table 2. mtDNA haplotype and nucleotide diversities and allozyme diversities in anchovies (*Engraulis*)

	mtDNA[a]			Allozymes[b]	
Species	*h*	π	*n*	*H*	*n*
anchoita	0.44	0.001	19	0.137	60
ringens	0.41	0.001	17	0.087	30
mordax	0.88	0.007	14	0.063	30
				0.075	432
japonicus	0.91	0.010	20	0.044	30
				0.067	30[c]
australis	0.90	0.009	16	0.105	51
capensis	0.21	0.004	18	0.091	60
				0.115	3,019[d]
encrasicolus	0.94	0.015	16	0.060	25
	0.88	0.016	140[e]	0.055	634[f]
	0.75	0.017	749[g]		

[a] 521X bp sequence of cytochrome *b*; from Grant WS and Bowen BW, unpublished data, except where noted.

[b] 31 loci; from Grant WS and Leslie RW, unpublished data, except where noted.

[c] 22 loci; Fujio and Kato 1979.

[d] 31 loci; Grant 1985.

[e] RFLP analysis of 2.5 kb PCR fragment of ND5/6 genes of NADH dehydrogenase complex; Bembo et al. 1995.

[f] 24 loci; Bembo et al. 1996.

[g] RFLP analysis of entire mtDNA molecule; Magoulas et al. 1996.

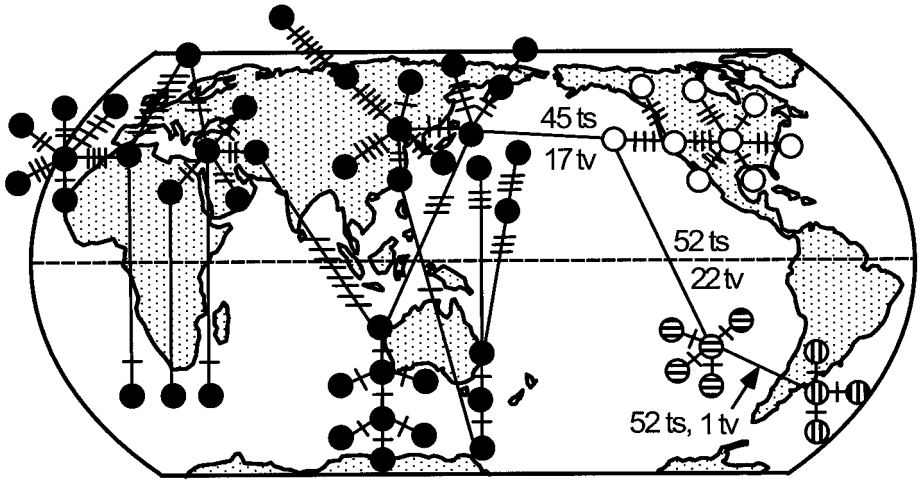

Figure 6. Parsimony network of 58 cytochrome *b* haplotypes in anchovies (*Engraulis*). Haplotype crossbars represent nucleotide substitutions between haplotypes based on a 521 bp sequence (Grant et al., unpublished data).

A similar scenario, invoking the possibility of extinction and recolonization, is apparent in the relationship between Japanese and Australian anchovies. While some of the Australian haplotypes are intermediate between Japan and European lineages, recent recurring contact between Australia and Japan is also strongly implicated. Australian samples include representatives from at least two deep branches of the Japanese network, and Japanese samples include haplotypes that are more closely related to endemic Australian haplotypes than to other Japanese haplotypes. The latter observation strongly implies (but does not prove) a back-dispersal from Australia to Japan after the most recent colonization of Australian waters.

In contrast to the case for Old World anchovies, genetic signatures of extinctions and recolonization are not apparent among the three species of New World anchovies: *E. mordax* off the west coast of North America, *E. anchoita* off Argentina and Brazil, and *E. ringens* off Chile and Peru. The deep levels of mtDNA sequence divergence between these species indicate that regional forms have been isolated for at least 6 million years. Despite these ancient origins, these three species also are characterized by low-to-moderate levels of nucleotide diversity (Table 2) and star-shaped phylogenies consisting of a central abundant haplotype with a few "satellite" haplotypes distinguished by one or two mutations (especially *E. anchoita* and *E. ringens,* see Figure 6). As noted for the sardines, these characteristics may be evidence of recent expansion from a small number of ancestors. Since low mtDNA diversity within these species cannot be readily attributed to recent colonization or founding events, within-region population dynamics are clearly implicated, including severe population fluctuations, strong natural selection on haplotypes, or extinctions and recolonizations on a local scale (within-region metapopulation structure) (see Lluch- Belda et al. 1989). Paradoxically, *E. anchoita* and *E. ringens* have the highest allozyme heterozygosities among the anchovies, providing another reminder that population processes may differentially affect mtDNA and allozyme diversity (Grant and Leslie 1992), and that caution is indicated when inferring population processes from any single class of genetic loci (Bernatchez and Osinov 1995; Karl and Avise 1992; Karl et al. 1992; Palumbi and Baker 1994).

Shallow Genetic Architectures in Sardines and Anchovies

The findings outlined above lead to several conclusions about the genetic architectures of clupeoid fishes inhabiting the world's temperate boundary currents. First, the processes shaping the genetic architectures of regional populations of globally distributed species can be understood only in light of metapopulation dynamics on a planetary scale. For example, we observe low genetic diversity in most of the surveyed sardine populations, but analyses of within-region diversity will not reveal whether this is due to recent origin (founder event) or to large fluctuations in abundance (bottleneck). The consequences of these two processes in terms of extant genetic diversity can be nearly identical (Figure 4). However, a rangewide comparison of sister forms can distinguish between these explanations. The shallow divergences within Indian–Pacific populations of sardines and some populations of anchovies (especially the southern African form) are attributed to recent founder events, because these regional types are closely related to sister taxa. The shallow divergences observed in Argentine–Brazilian and Chilean–Peruvian anchovies are attributed to within-region processes because these lineages are distantly related to sister species (on a scale of 6–10 million years). Both within- and between-region comparisons are necessary to demonstrate that at least two processes (founder events and bottlenecks) are responsible for the shallow genetic architecture of anchovy and sardine populations.

Second, mechanisms influencing the genetic architectures of regional sardine and anchovy populations are probably linked with global trends (or oscillations) in oceanography and climate. In recent decades the size of regional sardine and anchovy stocks could be estimated by the magnitudes of commercial catches and research surveys, and attempts were made to correlate abundances with cyclic warming events such as El Niños (Moser et al. 1987; Smith and Moser 1988). The southern oscillations that produce rapid and regionwide changes in sea surface temperatures and upwelling intensities will directly influence zooplankton abundance in larval nursery areas, and hence regulate the abundances of spawning biomass. Roemmich and McGowan (1995) and Hayward et al. (1996) note an order of magnitude reduction in zooplankton abundance in the California Current in recent decades. Our terrestrial perspective is apparent when a decline in sardines during the same period is deemed a mystery. A comparable decline in faunal biomass of a terrestrial ecosystem would be obvious, as would the reason for corresponding declines of primary consumers. Notably this major decline in sardines occurred during a relatively gentle fluctuation in comparison to the magnitudes of climatic cycles in the last 250,000 years (Dansgaard et al. 1993; GRIP Members 1993).

Third, we observe considerable variability in the magnitudes of genetic divergences between regional forms. On the shallowest scale, sardines and anchovies of southern Africa share haplotypes with fish in Australia and Europe, respectively. On the deepest scale, we observe sequence divergences of 17% between anchovies from California–Mexico and Peru–Chile. Taken as a whole, we see a broad range of genetic separations from the very

Table 3. Nei's (1972, 1978) genetic distances (*D*) between populations (based on allozyme frequencies), geographic range of samples, and genetic distance from sister species for species of marine fishes

Species	*D* between samples	Geographic range	*D* with sister species	Reference
Anglerfish				
Lophius vomerinus	0.0007	SE Atlantic	0.45	Leslie and Grant 1990; Grant and Leslie 1993
Anchovy				
Engraulis spp.	0.047	Old World	0.93	Grant et al., unpublished data
E. anchoita	0.003	Argentina-Brazil	0.75	Grant et al., unpublished data
E. mordax	0.002	California	0.85	Hedgecock et al. 1989; Grant et al., unpublished data
Cod				
Gadus morhua	0.0037	North Atlantic	0.42	Grant and Ståhl 1988; Mork et al. 1985
G. macrocephalus	0.025	North Pacific	0.42	Grant et al. 1987b; Grant and Ståhl 1988
Bigeye				
Heteropriacanthus cruentatus	<0.01	Central Pacific	0.69	Rosenblatt and Waples 1986
Hake				
Merluccius capensis	0.0006	SE Atlantic	0.23	Grant et al. 1987a; Grant, unpublished data
M. paradoxus	0.0007	SE Atlantic	0.48	Grant et al. 1987a; Grant, unpublished data
Halibut				
Hippoglossus stenolepis	0.0002	NW Pacific	0.16	Grant et al. 1984
H. hippoglossus	0.001	North Atlantic	0.16	Fevolden and Haug 1988; Grant et al. 1984
Herring				
Clupea harengus	0.001	North Atlantic	0.27	Grant 1984, 1986
	0.0005			Ryman et al. 1984
C. pallasi	0.039[a]	North Pacific	0.27	Grant and Utter 1984; Grant 1986
Milkfish				
Chanos chanos	0.002	Central Pacific	>1.0[b]	Winans 1980
Mullet				
Mugil cephalus	0.03	Central Pacific	0.62	Rosenblatt and Waples 1986
Sardine				
Sardinops sagax	0.005	Indian-Pacific	1.04	Grant and Leslie 1996
Pufferfish				
Spotted green puffer				
Arothron hispidus	<0.01	Central Pacific	0.56	Rosenblatt and Waples 1986
Guinaefowl puffer				
A. meleagris	0.03	Central Pacific	0.56	Rosenblatt and Waples 1986

[a] Average distance between major east-west subdivision in North Pacific. Nei's distance within each group averages 0.0004.

[b] Monotypic genus; sister taxon uncertain.

young to the very old, probably reflecting the diversity of outcomes that can affect species in fluctuating habitats.

Finally, we observed some discordance between the levels of diversity in nuclear and mitochondrial assays: Indian–Pacific sardines had high haplotype diversity but low allozyme diversity, while two New World anchovies had low haplotype diversities but high allozyme diversities. Sex-specific differences in dispersal or strongly skewed sex ratios can explain such disparities in other species, but there is no evidence that these factors operate in clupeoid fishes. A more likely explanation invokes the relative rate of evolution and the inheritance dynamics of mitochondrial versus protein-coding nuclear loci. During population declines, the loss of genetic diversity will be accelerated in mtDNA relative to nuclear DNA due to the lower effective population size of this maternally inherited genome. During population growth the mitochondrial genome will accumulate mutations more rapidly than protein-coding nuclear loci due to a higher rate of sequence evolution. Hence allozyme diversity might be higher shortly after population crashes and mtDNA diversity might be higher during a recovery phase with high levels of population growth. Given the climate-associated processes outlined above, we may expect to see both conditions in sardines and anchovies. In the next section we explore the general significance of shallow genealogies for understanding the evolution and population biology of marine fishes.

Inferences About Population History From Genetic Diversity

Shallow genetic separations within species, relative to large divergence between sister species, are characteristic of many marine fishes that have been examined with allozymes and mtDNA sequences. Two results are notable in allozyme surveys (Table 3). One is that sister species of many marine fishes have been isolated for a few to several million years, based on genetic distances calibrated with well-dated geologic events. Second, the level of differentiation between populations within many species is an order of magnitude less than the level between sister species. In these cases, the similarity of allele frequencies between populations may be attributed to mixing of eggs, larvae, and adults on extended temporal and spatial scales (Waples 1987). However, surveys of microsatellite DNA, which has a much higher mutation rate, may reveal mixing on time scales of decades and centuries (Bentzen et al. 1996).

The analysis of mtDNA sequences allows marine fishes (Table 4) to be categorized into four classifications (Table 5) based on different combinations of small and large values for haplotype diversity (*h,* a measure of the frequencies and numbers of haplotypes among individuals, varying between 0–1.0) and nucleotide diversity (π, average weighted sequence divergence between haplotypes, varying between 0 for no divergence to over 10% for very deep divergences). Ideally, comparisons of gene genealogies between species should be made with homologous segments of DNA, but the scientific literature on marine fishes is not yet rich enough to allow a review based on a single segment. Table 4 contains examples from restriction fragment analyses of the whole mtDNA molecule as well as direct sequencing of particular mtDNA genes (cytochrome *b,* ND4/5, and cytochrome oxidase). Mutation rates are certain to vary somewhat among these different sequence assays (see Irwin et al. 1991; Saccone et al. 1987; Walker et al. 1995), but are probably not radically different for RFLP and mitochondrial coding regions (Birt et al. 1995; Lamb et al. 1994). Direct comparisons among the different mtDNA assays are justified here because the focus is on the pattern

Table 4. Haplotype and nucleotide diversities, geographic range of samples, and percentage sequence divergence from sister taxon for species of marine fishes

Species	Haplotype diversity (h)	Nucleotide diversity (π %)	Geographic range	Sequence divergence from sister species (%)	Reference
Category 1					
Cod, Atlantic	0.30	0.13[c]	North Atlantic		Carr et al. 1995
	0.36	0.18	NW Atlantic		Carr and Marshall 1991; Zwanenburg et al. 1992
	0.30		NW Atlantic		Pepin and Carr 1993
Beaugregory damselfish	0.41[a,b]	0.30	Caribbean		Shulman and Bermingham 1995
Bluefish	0.11	0.07	Australia		Graves et al. 1992a
Hoki	0.28	0.08	SW Pacific, SE Atlantic		Baker et al. 1995
Red snapper	0.13[a]	0.13	Gulf of Mexico		Camper et al. 1993
Red grouper	0.42[a]	0.08	Gulf of Mexico		Richardson and Gold 1993
Weakfish	0.13	0.13	NW Atlantic		Graves et al. 1992b
Category 2					
Blue marlin	0.84[a]	0.54	Atlantic–Indo-Pacific		Graves and McDowell 1995
	0.74	0.33	Atlantic	3.5	Finnerty and Block 1992
	0.60	0.16	Pacific	3.5	Finnerty and Block 1992
Sailfish	0.80[a]	0.32	Atlantic–Indo-Pacific	3.5	Graves and McDowell 1995; Finnerty and Block 1992
White/striped marlin	0.82	0.29	Pacific		Graves and McDowell 1995
			Atlantic–Pacific	3.9	Finnerty and Block 1992
Shortfin mako	0.76[a]	0.35	Worldwide		Heist et al. 1996
Orange roughy	0.37[a]	0.19	SW Pacific, SE Atlantic		Smolenski et al. 1993
	0.74	0.59	SW Pacific, SE Atlantic		Baker et al. 1995
French grunt	0.78[a,b]	0.62	Caribbean		Shulman and Bermingham 1995
Goldspost goby	0.98[a,b]	0.68	Caribbean		Shulman and Bermingham 1995
Longjaw squirrelfish	0.94[a,b]	0.62	Caribbean		Shulman and Bermingham 1995
Slippery dick	0.78[a,b]	0.62	Caribbean		Shulman and Bermingham 1995
Sergeant major	0.79[a,b]	0.49	Caribbean	4.50	Shulman and Bermingham 1995
					Bermingham et al. 1997
Bluehead	0.55[a,b]	0.48	Caribbean		Shulman and Bermingham 1995
Greater amberjack	0.90	0.34	Gulf of Mexico		Richardson and Gold 1993
Haddock	0.87	0.59	NW Atlantic		Zwanenburg et al. 1992
Cape hake	0.90[a]	0.57	SE Atlantic		Becker et al. 1988
Deepwater hake	0.68[a]	0.55	SE Atlantic		Becker et al. 1988
Capelin	0.81[a]	0.42	NW Atlantic	3.42[a]	Dodson et al. 1991
	0.98[a]	0.51	NE Atlantic	3.42[a]	Dodson et al. 1991
Atlantic herring	0.91[a]	0.55	NW Atlantic		Kornfield and Bogdanowicz 1987
Pacific herring	0.90[a]	0.49	NE Pacific		Schweigert and Withler 1990
Spanish sardine	0.83	0.53	W Atlantic		Tringali and Wilson 1993
Red Drum	0.95[a]	0.58	Gulf of Mexico		Gold et al. 1993
	0.90[a]	0.56	NW Atlantic		Gold et al. 1993
Stickleback	0.93	0.71	N Atlantic–Pacific		Orti et al. 1994
Category 4					
Bluefish	0.70	1.23	NW Atlantic		Graves et al. 1992a
Atlantic menhaden	1.00[a]	3.20	NW Atlantic		Bowen and Avise 1990
Gulf menhaden	1.00[a]	1.00	Gulf of Mexico		Bowen and Avise 1990
Redlip blenny	1.00[a,b]	1.09	Caribbean	12.4	Shulman and Bermingham 1995; Bermingham et al. 1997

[a] Based on restriction enzyme analysis of whole mtDNA.

[b] Average within population h.

[c] Average percentage sequence divergence among haplotypes.

of genetic diversity rather than the absolute magnitudes.

The first category includes species with small values of both ($h < 0.5$ and $\pi < 0.5\%$). One example is the anchovy of southern Africa ($h = 0.21$, $\pi = 0.40\%$), which, as we have shown, may represent a recent recolonization from Europe. Another example is Atlantic cod ($h = 0.32$, $\pi = 0.15\%$), which show little genetic divergence across the North Atlantic (Mork et al. 1985). Since ongoing gene flow between the northeast and northwest Atlantic is unlikely based on distribution and life history, the lack of differentiation (in conjunction with biogeographic evidence) points to a regional extinction during Pleistocene glaciation, followed by a postglacial range expansion (Carr et al. 1995; Pogson et al. 1995). While such founder events are probably an important factor, these events cannot explain all the species in category one. Anchovies off Chile– Peru ($h = 0.41$, $\pi = 0.10\%$) and off Argentina–

Table 5. Interpreting haplotype and nucleotide diversities for marine fishes

	h	
π	Small	Large
Small	1. Recent population bottleneck or founder event by single or a few mtDNA lineages.	2. Population bottleneck followed by rapid population growth and accumulation of mutations.
Large	3. Divergence between geographically subdivided populations.	4. Large stable population with long evolutionary history or secondary contact between differentiated lineages.

Brazil (h = 0.44, π = 0.10%) also have low haplotype and nucleotide diversities, but the ancient origin of these forms precludes an explanation based on recent colonization. Other mechanisms such as periodic regionwide bottlenecks or metapopulation structure within regions must be invoked to produce the observed low levels of diversity. Other examples in category 1 include Beaugregory damselfish (h = 0.41, π = 0.30%), Australian bluefish (h = 0.11, π = 0.07%), hoki (h = 0.28, π = 0.08%), red snapper (h = 0.13, π = 0.13%), and weakfish (h = 0.13, π = 0.13%). Although little is known about the evolutionary histories of these fishes, their genetic architectures uniformly indicate periods of low effective population size within recent thousands or tens of thousands of years.

The second category consists of populations with high h and low π. This condition is attributed to expansion after a period of low effective population size; rapid population growth enhances the retention of new mutations (Avise et al. 1984; Rogers and Harpending 1987). Examples are typically drawn from large populations or entire species which contain one or two prevalent haplotypes embedded in a cluster of "twigs" that are one or a few mutations removed from the central haplotypes. This second category includes several of the billfishes (h = 0.68–0.85, π = 0.29–0.54%), shortfin mako (h = 0.76, π = 0.35%), as well as northwest Atlantic capelin, northeast Atlantic capelin, goldspot goby, French grunt, slippery dick, longjaw squirrelfish, greater amberjack, haddock, Cape hake, northwest Atlantic and northeast Pacific herring, red drum, and west Atlantic Spanish sardine (h = 0.79–0.98, π = 0.29–0.68%). Many of these species are believed to have originated in the Pliocene or early Pleistocene, but their mtDNA genealogies coalesce on a more recent scale, perhaps the last few hundred thousand years.

A third category, low h and high π, characterizes populations with a few highly divergent haplotypes. This condition may result from secondary contact between isolated populations or by a strong bottleneck in a formerly large, stable population. Secondary reassociation of formerly isolated populations is certain to occur in the marine realm (see Veron 1995), and reticulation of isolated lineages may be relatively common, but this must be coupled with low effective population sizes (to maintain low h) in order to fit the criteria of category 3. Coastal and oceanic fishes are usually not subdivided into small isolated populations, so it may be that few open-ocean fish fit into this category. Such conditions may be more applicable to inshore fauna (Burton 1986; Planes and Doherty 1997) and freshwater organisms (Bermingham and Avise 1986).

The fourth category consists of species with large values of both h and π. The high level of divergence between haplotypes may be attributed to secondary contact between previously differentiated allopatric lineages (as in category 3) or to a long evolutionary history in a large stable population. Examples of the first condition may include the European anchovy (h = 0.86, π = 1.6%) and Atlantic menhaden (h = 1.0, π = 3.20%), both of which contain a pair of divergent and twiggy mtDNA lineages which (based on geographic considerations) probably arose in isolation. Possible examples of the second condition include the Japanese anchovy (h = 0.91, π = 1.0%), Atlantic bluefish (h = 0.70, π = 1.23%), Caribbean blenny (h = 1.0, π = 1.09%), and Gulf menhaden (h = 1.0, π = 1.0%), for which extended geographic isolation is unlikely because of the configuration of the open coastline where they occur (Japanese anchovy and Gulf menhaden) or because of strong dispersal capabilities (bluefish). It is notable that even in category 4 the levels of divergences between lineages are typically an order of magnitude less than the divergence between sister taxa.

Shallow Genetic Architectures in Marine Fishes

These four categories are defined by demographic events that alter the likelihood of mtDNA lineage survival and the time to ancestral coalescence of lineages. Most of the species in Table 4 fit the first or second categories, which include populations with a recent coalescence of mtDNA lineages and shallow histories. It is clear that shifts in climate or oceanographic conditions can be responsible for this condition. What additional factors contribute to this trend? Using recursive simulations, Avise et al. (1984) showed that in a stable population there is a high probability that all haplotypes in the population can be traced to a single female after 4N generations, where N is the female effective population size. Hence the loss of female lineages will accelerate in declining populations or during fluctuations in abundance, and the expected time to coalescence of extant lineages will be correspondingly shorter. A second factor known to produce shallow coalescence of extant lineages is a large variance in reproductive success, which can decrease the genetic effective size of a population without actually reducing population size (Hedgecock 1994; Hedgecock et al. 1994). Marine fishes tend to have very large reproductive potentials (although exceptions exist, especially among the cartilaginous fishes), but propitious combinations of biological and physical conditions are required for larvae to survive and recruit into the adult population. Under conditions of high variance in reproductive success, an entire year class may be the product of relatively few matings. Evidence for such sweepstakes recruitment in marine fishes comes from the observation of genetic differences among individual schools of California anchovies (Hedgecock 1994), Black Sea anchovies (Altukhov 1990), south African anchovies (Grant 1985), Norwegian sprat (*Sprattus sprattus*; Nævdal 1968), and redfish (*Sebastes mentella*; Altukhov 1990). In these cases the effective population size for maternally inherited genes may be one or two orders of magnitude smaller than the census size (see Bowen and Avise 1990), leading to higher rates of lineage extinction than in populations of the same size with many successful spawners.

On the other hand, life-history patterns producing strong population subdivisions may increase the time to coalescence, but numerous allozyme studies indicate that marine fishes do not have strong population partitions relative to freshwater and anadromous fishes (see Ward et al. 1994). Lower levels of differentiation between marine fish populations are attributed to higher dispersal potential during planktonic egg, larval, or adult life-history stages, coupled with an absence of physical barriers to movement between ocean basins or adjacent continental margins. In

contrast, strong population subdivisions (and corresponding barriers) for freshwater fishes may serve to retain divergent lineages (see Bermingham and Avise 1986; Mayden 1993). The physical factors which buffer freshwater fish lineages against extinctions are notably absent from the marine realm.

Conclusion—Conservation Lessons

Marine fishes are generally regarded as resistant to extinction because of large diffuse populations and because marine waters are often viewed as boundless habitats. As a result, few species of marine fish are considered to be strong conservation concerns (Vincent and Hall 1996). However, several factors promoting lineage turnover and shallow population structure in several time scales may make marine fishes vulnerable to overharvesting and climate change. Lineage sorting from sweepstakes recruitment takes place on a scale of generations and is proportional to the magnitude of the reproductive variance in the population. Major population fluctuations, at least in sardines and anchovies, take place on a scale of decades and centuries. Regional extinctions, dispersal events, and recolonizations take place on a scale of thousands to millions of years. The relative importance of these factors may differ between tropical and temperate zones, and between species with diverse life histories. Nonetheless, they probably all contribute to the observed trend of shallow genetic architecture in marine fishes.

What are the implications of shallow mtDNA population structure and low genetic diversity for the conservation of marine fishes? First, it is apparent that this is a widespread phenomenon among marine fishes, and therefore only exacerbated in recent decades by deteriorating coastal and pelagic habitats (Sherman 1994) and fishing activities. If natural conditions commonly result in low mtDNA diversity in marine fishes, then such findings do not invariably signal inbreeding depression or other genetic health problems. However, evolutionarily rapid drops in genetic diversity due to fishing (Smith et al. 1991), and the loss of low-frequency alleles (not usually detected by estimates of heterozygosity) may be of special concern to the genetic health of marine species and to the maintenance of their evolutionary potential (Ryman et al. 1991).

Second, even very large populations can be susceptible to regional extinction. The passenger pigeon analogy may be appropriate for coastal marine fishes, especially those in upwelling zones and other fluctuating but productive habitats. Most of the demographic indices of healthy marine fish populations are ratcheted downward by overharvesting, and in many cases the majority of the biomass in heavily fished populations consists of young fish. Under these circumstances, recruitment failures over 3 or 4 years could lead not only to commercial extinction but to the total extinction of a regional population or species. At least for sardines and anchovies, genetic imprints indicate that regional collapses occur without the added burden of intense harvesting. Therefore, management strategies for sardine and anchovy fisheries, which are among the most productive harvests on the planet, must include allowances for the fragility of populations in unstable habitats. Depleted stocks will not invariably recover.

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Corresponding Editor: Fred W. Allendorf