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CHAPTER 25

Climate Change and Overexploitation

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Introduction

The complex evolutionary and biogeographic history of the California marine fish fauna has been amply demonstrated in the preceding chapters. In this concluding chapter our purposes are to summarize concisely the historical origins of the fauna, its present status, and the future of the fauna under a scenario of ongoing and perhaps accelerated climate change. This increased rate of change is most likely to be seen as increasing ocean temperatures in the northeastern Pacific into the foreseeable future. Over the last three decades the understanding of climate change has grown dramatically in both finer resolution on different spatial and temporal scales and on greater predictability of its impacts on the distribution and abundance of coastal fish faunas and other biotic elements. Major geological events and associated climatic upheavals have been central to the development of the California fish fauna with its signatures of varied origins and high diversity. Smaller scale events and episodes in recent millennia, centuries, and decades increasingly mix with anthropogenic influences of the past 150 years to complicate the picture of faunal dynamics as seen at the present time. Predicting the future conditions of the California fish fauna, then, must somehow take into account both the anticipated impacts of climate change and the entangling influences of human activities, especially overexploitation.

Deep History: Pangaea to the Miocene

The distant origins of the California fish fauna might reasonably begin with the major plate tectonic events that occurred in the middle to late Mesozoic as summarized by Brown and Lomolino (1998). The formation of the supercontinent Pangaea and the world ocean Panthalassa in the early Triassic, about 250 million years ago, and its subsequent breakup starting in the late Triassic and extending through the Cretaceous had profound consequences for global climate and biogeographic patterns of both terrestrial and marine biotas. Landmasses drifted northward, and marine basins formed and became isolated to differing degrees. Pangaea split, forming Laurasia to the north and Gondwanaland to the south, and each of these large landmasses fragmented leading to the continental positions and configurations seen today. By the end of the Cretaceous, shallow seas had broadly transgressed onto and then receded from the land, and the Tethys Sea, an equatorial seaway, had opened. With increased longitudinal and latitudinal separation of ocean basins the opportunity for the evolution of distinct coastal marine biotas emerged.

Several events occurred in the Cenozoic era that had lasting effects on coastal biotas in the Pacific including, ultimately, the development of the California fish fauna. Separation of Antarctica from Australia by the early Oligocene epoch established the cold circum-antarctic current and, in turn, the global latitudinal temperature gradient, resulting in climatic change and extinction of a variety of tropical organisms (Stanley, 1987). A mid-Miocene warming event in low latitudes then may have led to the antitropical distributions known among several groups of New World marine fishes, including the silversides (Atherinidae; now Atherinopsidae, see below) and anchovies (Engraulidae), according to evidence assembled by White (1986). His climatic vicariance hypothesis for the diversification of the silversides also involves emergence and disappearance of an early (Paleocene) Central American land barrier as well as emergence of the more well-known and existing Central American isthmus in the Pliocene about 50 million years later (fig. 25-1). White (1986) asserted that a result of this series of geological and climatic events was the antitropical distribution of the Atherinopsinae with members in both North America and South America. The more recent systematic treatment of the New World silversides (Atherinopsidae) by Dyer (1998) does not reject White's vicariant hypothesis nor does the analysis of genetic divergence of a similarly distributed fish group, the myxodin clinids, by Stepien (1992). On the other hand, the widely differing patterns of genetic divergence among antitropical chub mackerels (*Scomber*), jack mackerels (*Trachurus*) and hakes (*Merluccius*) show that such distributions are not all of similar origin, and these patterns led Stepien and Rosenblatt (1996) to propose that antitropical distributions in the eastern Pacific are best understood based on varying dispersal abilities and temperature tolerances. The complex origins and distribution patterns of California marine fishes again become evident.

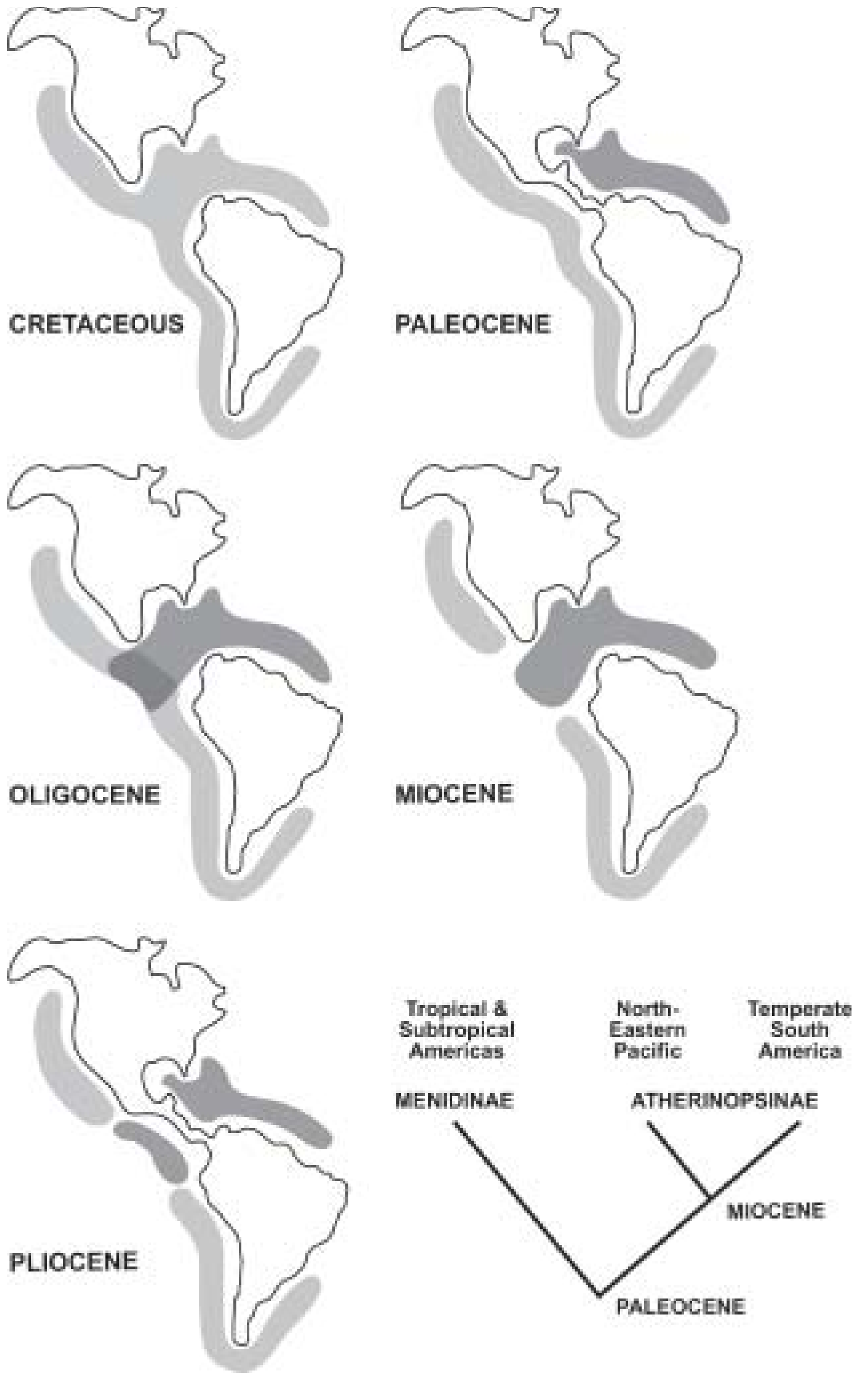

FIGURE 25-1 Biogeographic history and phylogenetic relationships of New World silversides (Atherinopsidae) from the Cretaceous period to the Pliocene epoch. Significant vicariant events in evolution of the family indicated on area cladogram at lower right: divergence of the Atherinopsinae and Mediniinae followed emergence of early Cenozoic isthmian link; divergence of modern tribes of Atherinopsinae followed climatic disruption in Miocene (after White, 1986).

The strictly marine North American atherinopsines not only provide an example of how a portion of the California fish fauna may have developed but also of species with disjunct populations or sister taxa in the upper Gulf of California and temperate northeastern Pacific including California. Six species in four genera compose the monophyletic atherinopsine group (Dyer, 1998). Three species are restricted to the upper Gulf of California. These taxa are the false grunion (*Colpichthys regis* and *C. hubbsi*) and the Gulf grunion (*Leuresthes sardina*), which is sister to the California grunion (*Leuresthes tenuis*) that occurs on the Pacific coast of California and Baja California. Topsmelt (*Atherinops affinis*) and jacksmelt (*Atherinopsis californiensis*) are distributed widely in the northeastern Pacific, but only the topsmelt has a disjunct population in the upper Gulf.

These disjunct distributions among the atherinopsine fishes signal another set of geological processes that has fundamentally affected California fish biogeography beginning in the middle Miocene. At this time, about 15 MY ago, the peninsula that was to become Baja California began to separate from mainland Mexico and by the end of the Miocene, about 5 MY, had reached its current configuration, thus forming the Gulf of California in the process (Helenes and Carreno, 1999; see chapter 2). At least 19 species of coastal fishes representing 14 families and a wide range of ecological groups have unequivocally disjunct populations in the northern

Gulf of California and Pacific coastal waters of California and Baja California (chapter 2). The number of disjunct taxa is likely to increase as molecular techniques continue to be applied to assessing the degree of genetic divergence between the isolated populations in the two regions within a framework of dispersal/vicariance hypotheses. According to Dawson and co-authors (chapter 2), the 12 species with disjunct distributions that have been subjected to molecular analysis show either indistinct Gulf and Pacific populations (4 species), suggesting high levels of gene flow, or distinct Gulf and Pacific clades (8 species), indicating vicariant events. Of the latter group, divergence times range from as recently as 0.2–0.4 MY in the bluebanded goby (*Lythrypnus dalli*) to 0.4–3.0 MY for California grunion and Gulf grunion. Whether disjunction of populations occurred via dispersal around the peninsula during episodes of Pleistocene glacial cooling or after passage through a seaway in the southern or the northern part of the peninsula remains uncertain, but, overall, generally similar historical conditions molded the population structure of these divided species (Bernardi et al., 2003).

The absence of populations of these disjunct species in the southern part of the Gulf apparently cannot be explained by warmer temperatures alone but requires lack of suitable habitat and perhaps other features of the southern Gulf to exclude these species (see chapter 2). What does seem clear from the study of these disjunctions is that biogeographic provinces are the products of both evolutionary processes and ecological conditions. As an example in the same part of the world, Hastings (2000) showed that chaenopsid fishes in rocky shore habitats are isolated from one another by long stretches of soft-bottom habitat separating the Cortez and Mexican provinces and the Mexican and Panamic provinces from one another. The latitudinal temperature gradient that had developed by the Oligocene combined with this type of habitat isolation seems to have promoted speciation, produced coincident range end points, and led to recognition of faunal provinces and regions.

Shallow History: Pliocene and Pleistocene Epochs

Effects of Glacial and Interglacial Periods

The foregoing discussion has presaged the importance of the climatic cooling that began in the Pliocene (5.0–1.8 MY) and culminated in the glaciation cycles of the Pleistocene (1.8 MY ago—Recent) for influencing the distribution patterns of California coastal fishes. Colder temperatures during the Pleistocene realigned northeastern Pacific coastal provinces to the south (fig. 25-2) and pushed California fish species southward, allowing some populations to traverse the existing Baja California peninsula, as mentioned above, either by dispersing around the end or migrating through seaways that subsequently closed. With recession of the glaciers and warming of ocean temperatures during interglacial periods, cool-water species returned northward including into the northern Gulf of California where they became disjunct populations.

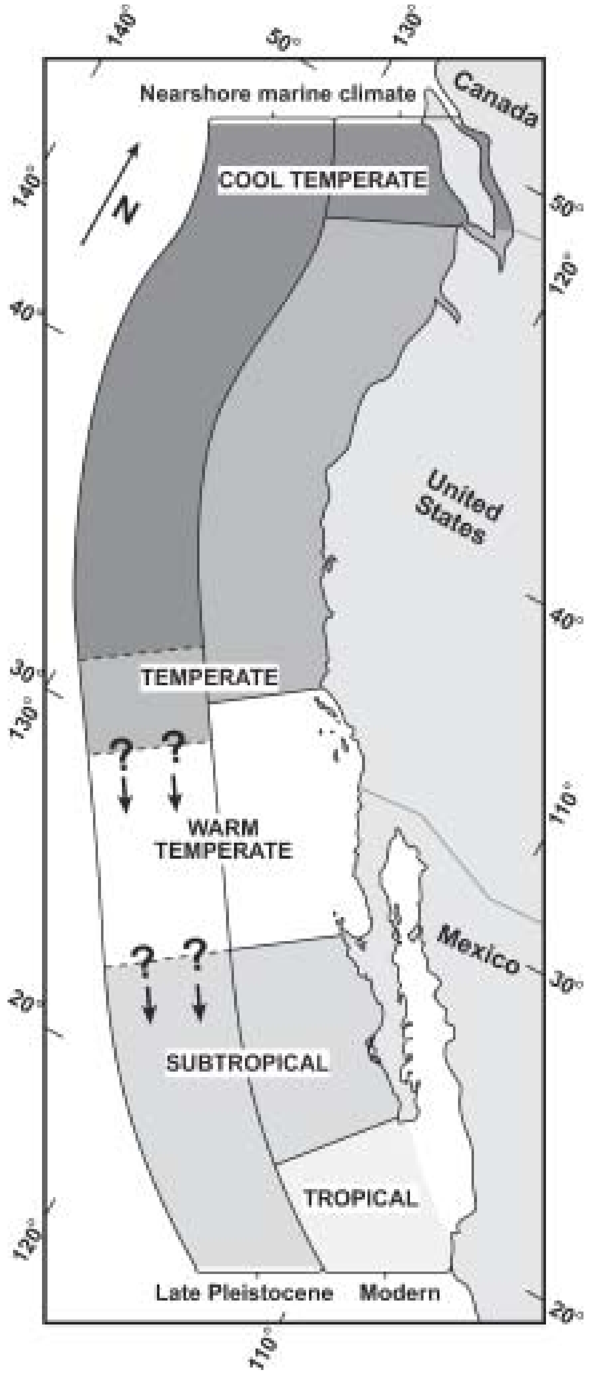

FIGURE 25-2 Shifts in marine biogeographic provinces along the west coast of North America between 18,000 BP (late Pleistocene) and modern times. According to Fields et al. (1993), provinces in the waters off southern California and northern Baja California may have remained relatively stable while those in other regions varied more during the same period. More recent data on coastal foraminiferan assemblages, however, suggest that temperatures were cooler in southern California waters during the last glaciation (18,000 BP) and that the northern boundary of the warm temperate region was pushed farther south along the coast of Baja California (after Kennett and Venz, 1995).

Another effect of the Pleistocene glaciations was to lower sea levels and thus to lessen the distances between the California mainland and neighboring Channel Islands as well as among the islands, especially the northern group (Anacapa, Santa Cruz, Santa Rosa, and San Miguel islands). The islands formed about 5 MY ago and as a result of uplift have generally increased in area since that time (Vedder and Howell, 1980; Sorlien, 1994). These increased sizes and reduced distances stemming from glacial and tectonic activities are reflected in the population genetic structure of the few coastal fish species that have been studied. For example, Dawson and co-authors (chapter 2) showed that populations of black perch (*Embiotoca jacksoni*) around the northern Channel Islands are genetically similar to one another and, collectively, to fish at the mainland area closest to the islands. Moreover, black perch populations from the southern Channel Islands (San Nicolas, Santa Catalina, and San Clemente) are more similar to those from the northern islands than to the closest mainland populations. The authors of chapter 2 emphasize the importance of deep-water barriers in reducing gene flow and of the direction of prevailing current patterns in maintaining genetic similarity.

We have focused attention above on the glacial periods and their effects, but, of course, they alternated with interglacial periods that produced opposing impacts. Overall, highly fluctuating climatic conditions dominated the coastal environment during the Pleistocene epoch. In a highly integrated analysis incorporating paleoclimatology, coastal geomorphology, paleoceanography, and archaeology, Graham et al. (2003) argued that the late Quaternary (Pleistocene + Holocene or Recent) sea-level rise of the last 18,500 years caused a major ecological shift in the Southern California Bight from highly productive rocky reefs to less productive sandy habitats, each supporting very different benthic communities. These authors argue that, until recent centuries or perhaps millennia, the southern California coastal zone alternated between long periods of rocky reef-kelp forest dominated habitats and shorter periods of sandy infaunal ecosystems at a frequency of about 100,000 years, all driven by climatic fluctuation and sea-level change. The kelp forest habitat should have been inhabited by expansive populations of seaweeds, large fishes such as giant sea bass (*Stereolepis gigas*), California sheephead (*Semicossyphus pulcher*), lingcod (*Ophiodon elongatus*) and numerous species of rockfishes (*Sebastes* spp.), rocky-reef invertebrates such as abalones, sea urchins and mussels, and the predatory sea otter (*Enhydra lutris*). Rocky intertidal zones in southern California might have resembled the rich and diverse rocky shore habitats now found only north of the Southern California Bight. As the climate warmed and sea level rose, productivity declined, infaunal invertebrates became prominent, and, overall, less food was available to American Indians who appeared in the southern California region at least as early as 12,000–13,000 BP. The food habits of these indigenous peoples appear to have tracked the changing marine resources although these early Americans may have influenced the ecosystems of which they were a part through selective predation but in a pattern of exploitation sustained over millennia (e.g., Erlandson, 1994).

Population Histories of Anchovies and Sardines

A final observation on the temporal scale of the Pleistocene, i.e., shallow histories ranging from thousands to millions of years, offers potential insights for current problems of marine fish exploitation and for future designs on maintaining sustainable populations. Grant and Bowen (1998) point out that our increasing knowledge of past climates reveals that periodic climate changes are accompanied by strong regime shifts in the global ocean and that these changes in surface temperatures, current pathways, upwelling patterns, and retention eddies can result in severe population swings or even regional extinctions. Their molecular genetic analyses of anchovies (*Engraulis*) and sardines (*Sardina, Sardinops*) demonstrate that populations of these two clupeoid taxa, renowned for their marked fluctuations in temperate-zone boundary currents around the world (Schwartzlose et al., 1999), are subject to periodic extinctions and recolonizations and that mtDNA genealogies for *Sardinops* at least coalesce backward in less than 0.5 MY. Grant and Bowen reason that such climate-driven population changes may explain the low levels of genetic diversity and the shallow coalescence of mtDNA genealogies. The value of their analysis for halting the present-day upward spiral of exploitation is that even the most abundant marine fish populations are potentially at risk of extinction on both ecological and evolutionary time scales.

Recent History—Millennial Scale

Anchovies and Sardines

On a time scale of the Holocene or Recent epoch (i.e., thousands of years) we can continue with an examination of population fluctuations of anchovies and sardines in southern California that links backward to the Pleistocene patterns described above and forward to the fluctuations over the last century. Soutar and Isaacs (1969, 1974) published the first accounts of historical fluctuations of California fish populations by identifying and counting fish scales from anaerobic deposits off southern California and Baja California. Their data extended from 1810 to 1970 and included scales of northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), Pacific hake (*Merluccius productus*), Pacific saury (*Cololabis saira*), and Pacific chub mackerel (*Scomber japonicus*). Reconstruction of northern anchovy and Pacific sardine populations over the past two millennia by Baumgartner et al. (1992) using fish-scale-deposition rates in the Santa Barbara Basin revealed that these two species tend to vary over a period of about sixty years with northern anchovy also fluctuating over a period of 100 years (fig. 25-3). Anchovies and sardines show moderate correlation of population changes on time scales of centuries but not over shorter time periods. The scale-deposition record indicates nine major recoveries (increases from less than one to more than four million metric tons in biomass) and subsequent collapses of the sardine population during a 1,700-year span with an average recovery time of 30 years.

Sockeye Salmon

In contrast, the abundance patterns of sockeye salmon (*Oncorhynchus nerka*) in Alaska based on sediment records were out of phase with those of anchovies and sardines in southern California over the past two millennia (Finney et al., 2002; fig. 25-4). Multi-century shifts of inferred sockeye abundance at about 2,100 BP and 1,200–800 BP correspond to intervals of major change in atmosphere-ocean circulation in the northeastern Pacific. At 2,100 BP sockeye abundance dropped sharply in synchrony with warming of marine waters in the Santa Barbara basin, whereas after 1,200 BP increased salmon numbers correspond to a time of glacial advances in southern Alaska and the Canadian Rockies. Both northern anchovies and Pacific sardines were more abundant from about 1,700 to 800 BP when sockeye salmon were low in numbers, whereas the reverse trend is apparent for the last 800 years. The abundances of other fishes depicted over the 2,200-year time span varied out of sequence with both the salmon and the anchovies and sardines (fig. 25-4). An important contribution of Finney

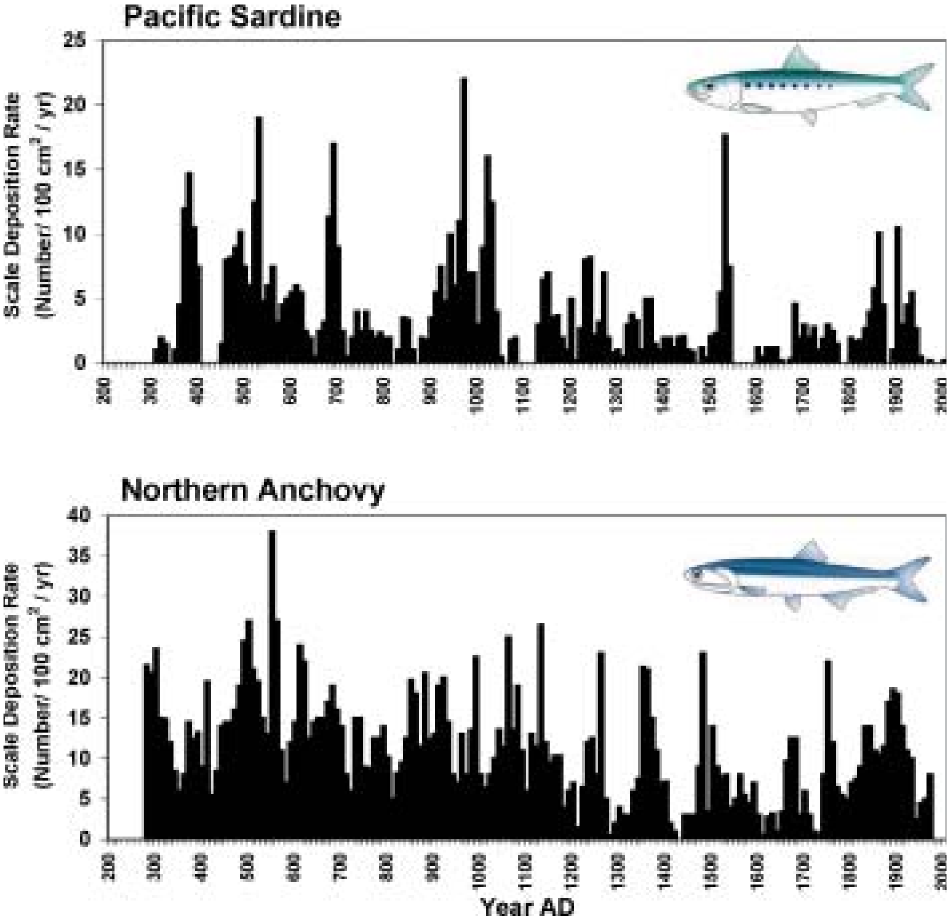

FIGURE 25-3 Composite time series of northern anchovy and Pacific sardine scale-deposition rates in the Santa Barbara Basin over the last ~1700 years (after Baumgartner et al., 1992).

and co-workers is that their reconstructions of sockeye salmon abundances show that a shift to a regime of very low productivity, lasting centuries, can occur without the impacts of fisheries or other human influences. These results emphasize the need to understand the connections between ocean ecosystems and climate change now that fish species are seriously impacted by the additional stresses of commercial fishing, habitat deterioration, and global warming.

Historical Overfishing

The analysis by Jackson et al. (2001) provides an effective transition from the millennial scale to the immediate past of the last 150 years and current conditions (see below) of coastal ecosystems in that they assess the impacts of historical overfishing from about 125,000 years ago to the present time. Their analysis of paleoecological, archaeological, and historical data provides a suggestion that overfishing of large vertebrates and shelled invertebrates has been the first and most important human disturbance to affect the coastal ecosystems that these authors examined. In historical times, overfishing would have been the only major impact of indigenous peoples on coastal resources. They expand preindustrial environmental effects to industrial societies and hypothesize a similar pattern (fig. 25-5). The sequence of other disturbances may vary, and the lag time between the onset of fishing and consequent alterations in coastal ecosystems may take decades to centuries. They conclude that overfishing precedes all other types of disturbances but that such excessive exploitation also may often create the necessary conditions for eutrophication, disease outbreaks, and species introductions to occur. Moreover, their assessment places human-driven climate change as a now compounding force in but not the original cause of microbe population explosions, disease outbreaks, and species invasions in general. Jackson and colleagues argue that massive ecological extinctions of predators (e.g., sharks, sea otters), grazers (e.g., sea turtles, manatees), and suspension feeders (e.g., oysters) are bound to leave coastal ecosystems more vulnerable to invasion.

The most relevant part of the Jackson et al. (2001) analysis for the California fish fauna is their focus on kelp forests in the northeastern Pacific (Alaska and California) as compared to those in the northwestern Atlantic (Gulf of Maine). The relatively diverse food web in southern California kelp forests historically included California sheephead as well as spiny lobsters and sea otters as predators of sea urchins and several species of abalone as competitors of sea urchins. Although sea otters were extirpated by the early 1800s, kelp forests in southern California did not begin to decline on a large scale until the 1950s when increased exploitation led to the ecological extinction of the sheephead, lobsters, and abalone. Information on these ecological extinctions is sparse, and certainly recent data show little evidence of either sheephead or spiny lobster decline in the Palos Verdes kelp forest over this period even with the loss of kelp (Stephens et al. 1984). The loss of the

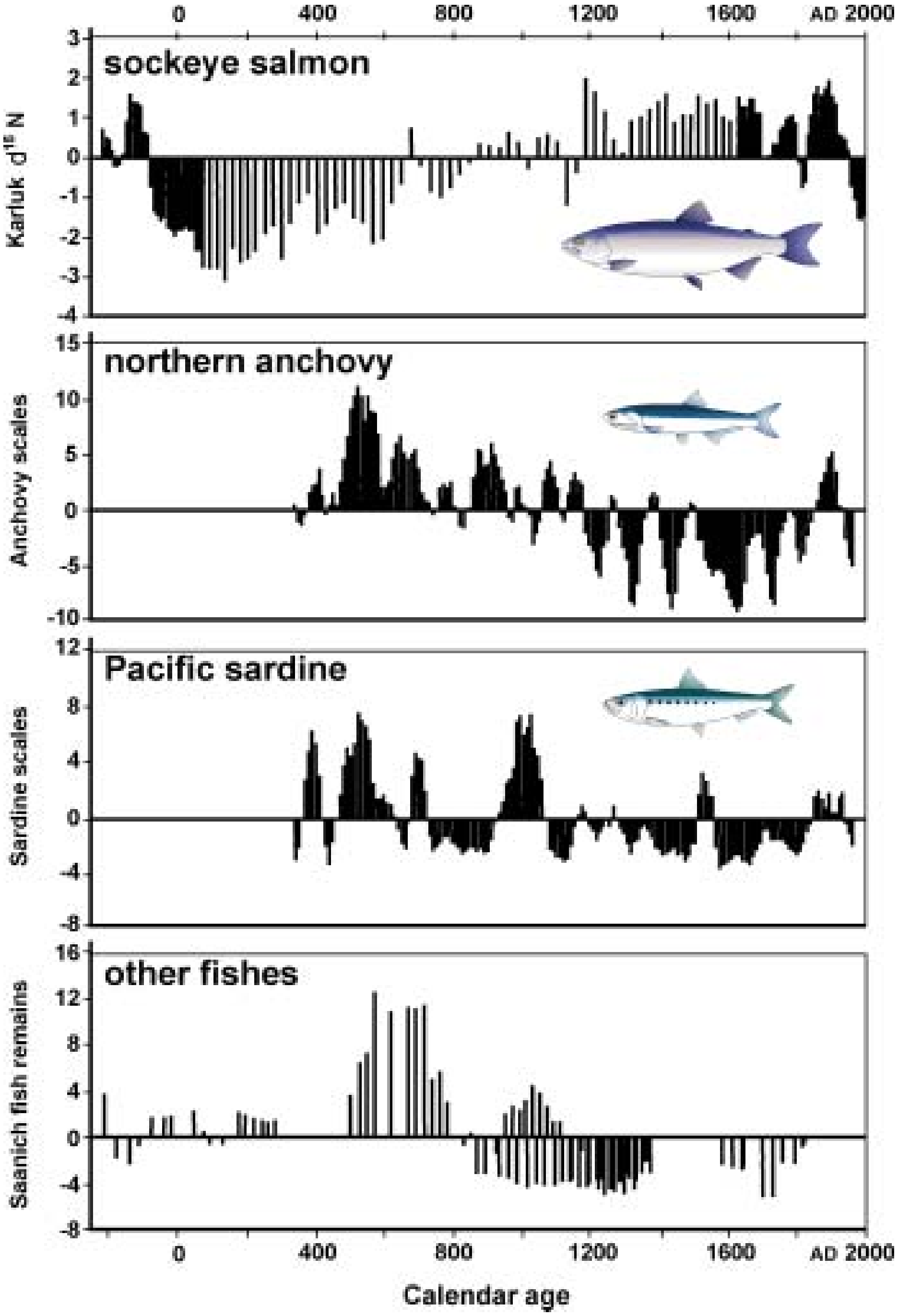

FIGURE 25-4 Reconstruction of fish abundances in the northeastern Pacific Ocean over the past ~2,200 years. Each series is plotted as the difference from the series mean calculated over this time period. Sockeye salmon abundances in Alaska are represented by the Karluk lake δ^{15}N profile (0/00). Northern anchovy and Pacific sardine abundances are represented by scale-deposition rates (no. of scales per 1,000 cm^2 per year) from the Santa Barbara Basin, California (Baumgartner et al., 1992). A 50-year running average was applied to highlight long-term trends. Abundances of other fishes, including Pacific herring, Pacific hake, and cartilaginous fish, are represented by fish remains per 100 cm^3 recovered from Saanich Inlet, British Columbia (Tunicliffe et al., 2001); data from two overlapping cores are presented (after Finney et al., 2002).

abalone reflects both overfishing and withering foot disease. Ironically, commercial exploitation of the largest sea urchin species in the 1970s and 1980s resulted in recovery of some of the kelp forests, but these systems now lacked substantial populations of consumers (Tegner and Dayton, 2000; see below).

Immediate Past History: Last 150 Years to the Present Day

Over the past century and a half, commercial exploitation, habitat degradation, and climate change have become increasingly serious problems for the existence and health of the California fish fauna. These major concerns have been

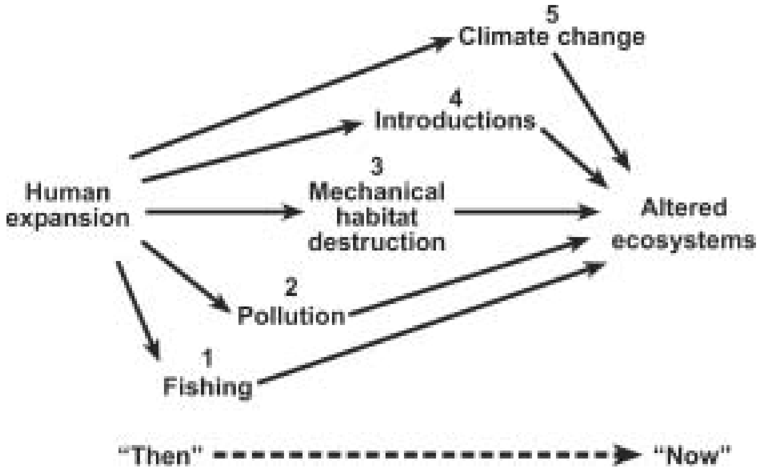

FIGURE 25-5 Historical sequence of human disturbances affecting coastal ecosystems. Fishing (step 1) always preceded other human disturbance in all cases examined. This sequence is the basis for the authors' hypothesis of the primacy of overfishing in the deterioration of coastal ecosystems worldwide. Subsequent steps 2 through 5 have not been observed in every case and may vary in order (after Jackson et al., 2001 with permission from the American Association for the Advancement of Science).

discussed for the contemporary situation in earlier chapters of the book: biogeography of California coastal fishes by Horn, L. G. Allen and Lea in chapter 1; subsistence, commercial and recreational fisheries by Love in chapter 22, and pollution and habitat alteration by M. J. Allen and Pondella in chapter 23. In this section, we first summarize the changes in kelp forest ecosystems during the last 150 years. We then focus our attention on climate change but within a perspective that includes overexploitation and its pervasive importance as already described in the previous section. Overall, our rationale for an emphasis on climate change stems from our belief that the impacts of climate shifts ultimately will be greater and harder to manage than those resulting from overfishing, pollution, and other forms of habitat degradation.

Phase Shifts in Kelp Forest Ecosystems

In their analysis of the past, present, and projected future of kelp forest ecosystems, Steneck et al. (2002) provide details of changes in these systems in southern California over the past few centuries and mainly the last 150 years that effectively links the Jackson et al. (2001) study of historical overfishing to present-day conditions that include increased attention to the effects of climate change. In the Southern California Bight, American Indians formed one of the densest concentrations of indigenous peoples in the world starting at least 12,000–13,000 BP, and they depended heavily on animals associated with kelp forests such as sheephead, abalone, and marine mammals, especially sea otters. Based on analysis of middens on San Clemente Island, increased fishing activity by maritime Indians appears to have caused a decline in sheephead size leading to a subsequent increase in purple sea urchin populations (Salls, 1991, 1995). Although Indians may have created local sea urchin barrens by hunting sea urchin predators such as sheephead and sea otters, any such effects were short-lived because Indian fishing activities essentially ended upon European contact as old world diseases and colonial oppression devastated American Indian societies (Erlandson et al., 2004). The 150-year lag between sea otter extinction in the early 1800s and the phase shift in kelp forests during the mid-twentieth century induced by sea urchin overgrazing (fig. 25-6) may have resulted from the countering effects of alternate competitors, herbivores, and predators of sea urchins (Cowan, 1983; Tegner and Levin, 1983; Schmitt, 1987). By the 1950s and 1960s, excessive harvesting of abalone, lobster, and sheephead may have greatly reduced these strong interactors in the kelp forest food web. These reductions freed urchins to overgraze kelp forests, and, along with a series of El Niño events, led to the virtual absence of kelp during the mid-twentieth century (fig. 25-6). The commercial harvesting of urchins that began in the 1970s reduced the urchin stocks and facilitated a shift back to a forested state (Tegner and Dayton, 1991; Steneck et al., 2002). Sheephead harvesting, however, accelerated again in the late 1980s with the development of a live fish market, reducing the importance of this predator in the system (Tegner and Dayton, 2000). Even though the relatively high diversity of southern California kelp forests probably has been important in maintaining the presence of these ecosystems in the region as currently recognized, kelp forests nevertheless have been subjected to "serial trophic-level dysfunction" (Steneck et al., 2002).

Climate Change, Fishing Pressure, and the Accelerating Dynamics of Coastal Fish Populations

Both climate change and overexploitation have contributed in recent decades to an increasingly dynamic fish fauna in California coastal waters and to an extremely challenging set of problems threatening the continued health of marine ecosystems in the northeastern Pacific. Knowledge of climate change accelerated during the twentieth century such that, by the dawn of the present century, we have become much more adept at identifying and predicting shifts in climate over a wide range of spatial and temporal scales. Recent climate change can now be placed in a more global and longer-term perspective, and different types of climatic conditions, occurring over varying geographic expanses and time intervals, can be recognized. The importance of climate change now has global attention with an international scientific committee providing advice to stakeholders (Pittock, 2002). Present situations are being assessed and future conditions predicted for many marine ecosystems and their fish populations (e.g., Beamish and Noakes, 2002; McFarlane et al., 2002; Scavia et al., 2002; Wang and Schimel, 2003). Together, climate change and overexploitation have the potential to act synergistically to shift production areas and alter community composition and dominance (Verity et al., 2003) and most likely to multiply the problems each creates for the sustainability of marine ecosystems.

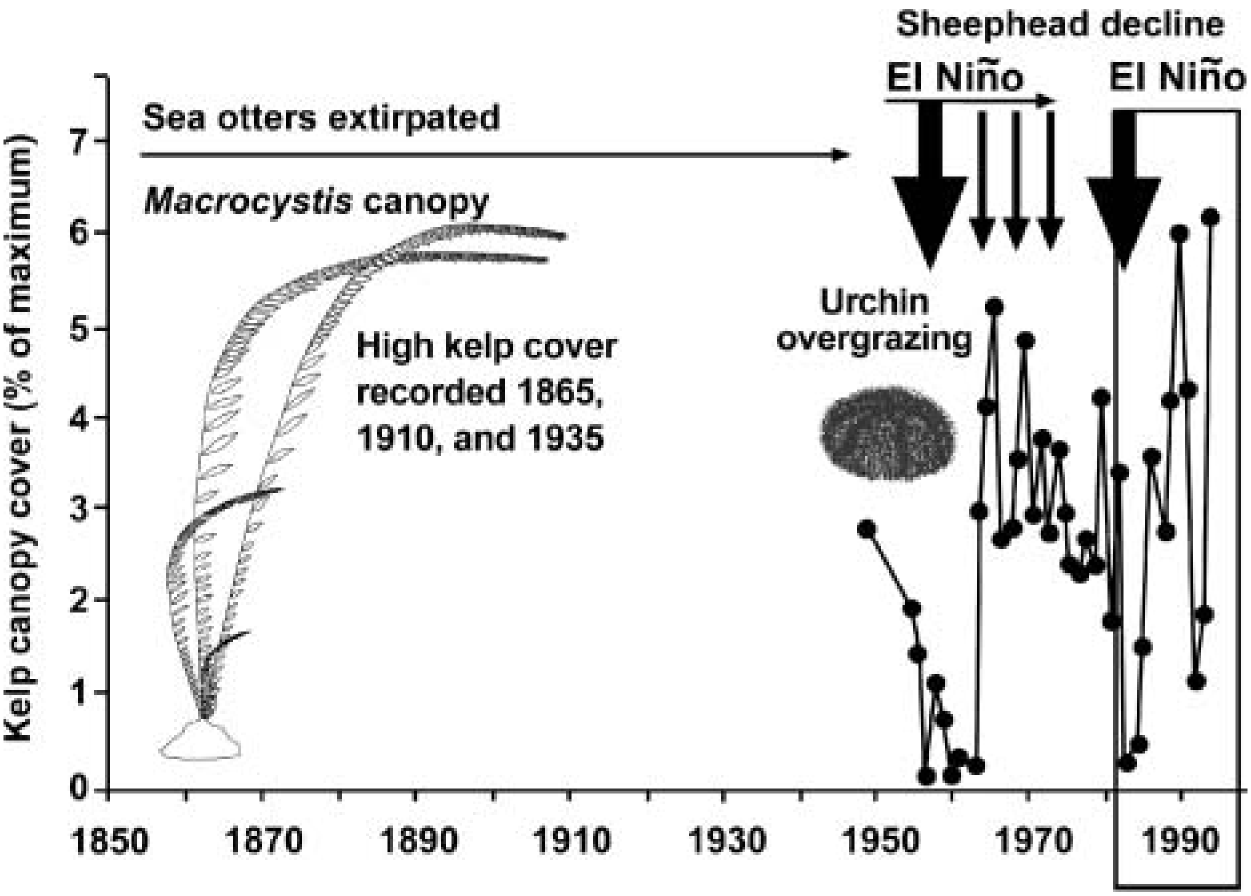

FIGURE 25-6 Temporal trends in kelp forests at Point Loma near San Diego in southern California. Width of arrows represents the magnitude of the impact of the forcing function. The boxed area on the right of the figure indicates a period of high resolution subtidal data (after Steneck et al., 2002).

Types of Climatic Change Affecting the California Marine Fish Fauna

At least three major kinds of climatic events influence the distribution and abundance of California marine fish species: 1) El Niño Southern Oscillation (ENSO) episodes, 2) Pacific Decadal Oscillations (PDO), and 3) global warming (see next section), in order of increasing spatial and temporal scales.

EL NIÑO SOUTHERN OSCILLATION (ENSO)

ENSOs comprise alternating warm El Niño and cool La Niña intervals. As described in chapter 1, El Niño events clearly affect fish distributions in the northeastern Pacific. Radovich (1961) documented the change in the fish fauna related to coastal warming in 1957–1959 (now recognized as a large ENSO event, and Mearns (1988) described unusual geographic occurrences of certain fish species along the Pacific coast. Lea and Rosenblatt (2000) documented the appearance of numerous warmer-water, Panamic species in the Southern California Bight during the 1997–1998 El Niño event, and Horn and co-authors (chapter 1) list 20 species, mostly of southern affinities, that have been added to the California fauna over the last 25 years. The majority of these added species appeared in California waters during this most recent El Niño episode. The alternating La Niña events are often of shorter duration (Kousky and Bell, 2000) and can cause reduced abundance among species of warm-water affinities (e.g., reef finspot, *Paraclinus integripinnis*) or increased abundance of even a transitional species such as the woolly sculpin (*Clinocottus analis*) in the same rocky intertidal habitat (Davis, 2000; chapter 8). Species of ichthyoplankton also showed predictable changes in abundance as well as in latitudinal distribution during the ENSO periods of the last half century based on analysis of CalCOFI samples (Moser and Watson, chapter 11). Among commercially important species, the cool-temperate chinook salmon (*Oncorhynchus tshawytscha*) was caught in much smaller numbers during the strong 1982–1983 El Niño event, whereas several warm-water species including yellowtail (*Seriola lalandi*) and skipjack tuna (*Katsuwonus pelamis)* were landed in much greater numbers (McGowan, 1985; Tegner and Dayton, 1987). Early juvenile Pacific hake (*Merluccius productus*), a member of the cool temperate and polar family Merlucciidae, responded to the 1997–1998 El Niño event in central California waters by broadening their zooplankton diet in response to low zooplankton biomass and then suffering poor growth and lowered survival rates in the face of the reduced food supply (Grover et al., 2002).

PACIFIC DECADAL OSCILLATION (PDO): CLIMATE AND OCEANOGRAPHY

Like an ENSO event, the PDO comprises a warm and a cool interval, but the PDO regimes are each 20–30 years in duration (Mantua et al., 1997; Hare et al., 1999; Hare and Mantua, 2000; Chavez et al., 2003; Levin, 2003). Major ecological

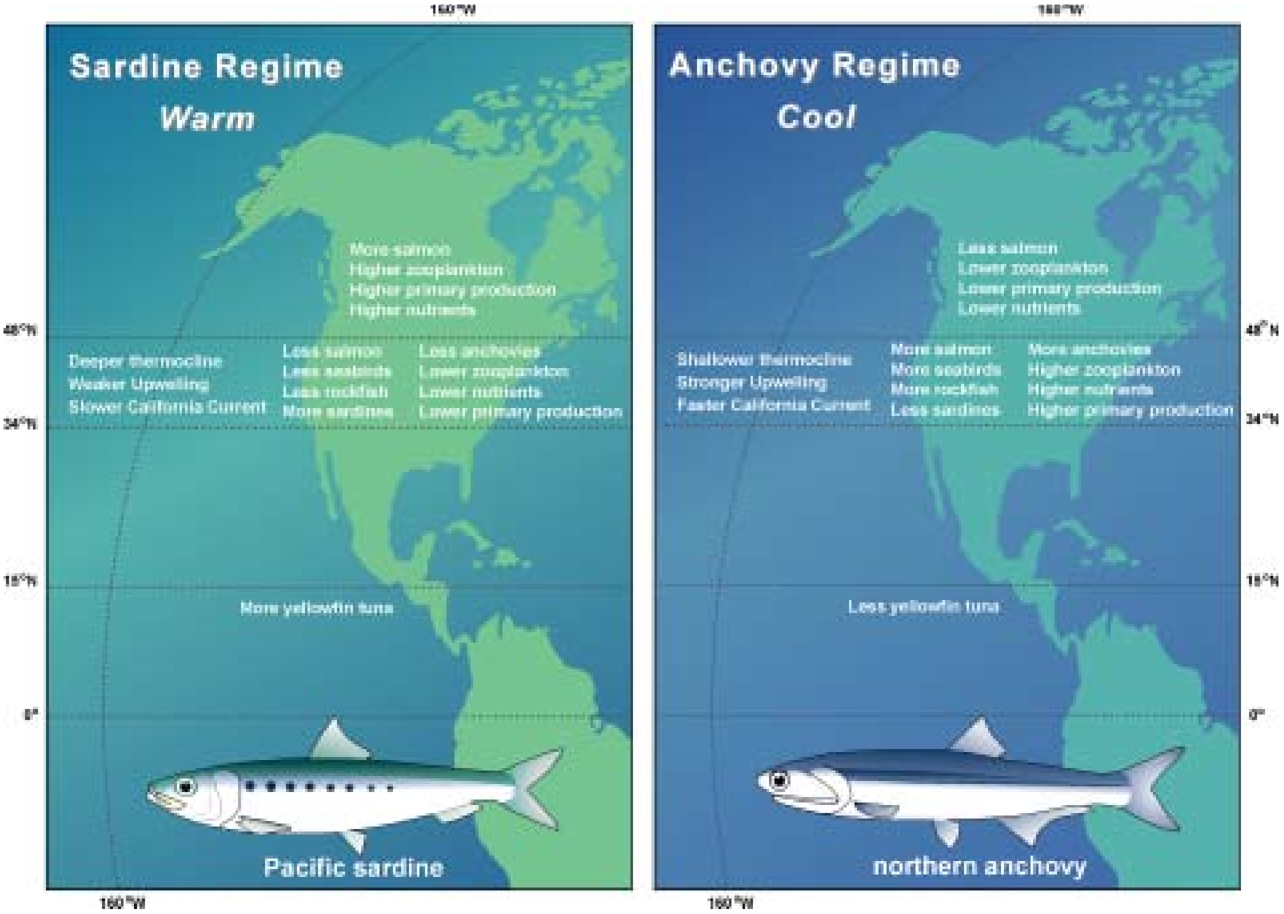

FIGURE 25-7 Condensed synthesis of oceanographic and biological conditions in the northeastern Pacific during sardine (warm) and anchovy (cool) regimes (after from Chavez et al., 2003).

events occur on the decadal scale and in response to a shift from one regime to another (McGowan et al., 2003). The warm regime is characterized by above average sea-surface temperatures (SSTs) along the coasts of the Americas and in the tropics, cooler than average SSTs in the central North Pacific, anomalously low atmospheric pressure at sea level over the north Pacific and eastern Tropical Pacific, and high pressure anomalies in the western tropical Pacific centered over northern Australia. These conditions are basically reversed during the cool regime. Over the past century, two cool ocean regimes (1900–1924 and 1947–1976) and two warm regimes (1925–1946 and 1977–1999) have been generated by PDOs. The regime shift of 1976–1977 in the California Current was characterized by an abrupt rise in upper-ocean temperature associated with an intensified Aleutian Low-pressure system and a large, decadal decline in zooplankton biomass (McGowan et al., 2003).

PDO: EFFECTS ON ANCHOVIES AND SARDINES

The multidecadal shifts in northern anchovy and Pacific sardine populations in boundary currents around the Pacific Ocean basin over the last century are now better understood with the discovery of the biological regime shifts associated with PDO events. Chavez et al. (2003) summarized these anchovy and sardine fluctuations in the context of cyclic changes in atmospheric and oceanographic conditions in the Pacific basin (fig. 25-7) and in doing so provided a more comprehensive explanation for the population variations than does fishing pressure alone (cf. Murphy, 1966). The discovery of these biological regime shifts occurring about every 25 years preceded the description of the underlying physical processes and led to the suggestion (Hare and Mantua, 2000) that regime shifts may be better detected by monitoring marine organisms rather than climate. Synchrony exists among air and ocean temperatures, atmospheric carbon dioxide levels, coastal and open-ocean productivity, and anchovy and sardine landings as shown by Chavez et al. (2003), particularly for the southwestern tropical Pacific off Peru. Their extension of the analysis to the northeastern Pacific shows that the cool-water northern anchovy increases in abundance during a cool regime lasting about 25 years followed by a shift to a warm regime during which the warm-water Pacific sardine becomes relatively more abundant. The strength of these associations is demonstrated by Chavez and co-workers identifying these periods as an anchovy regime and a sardine regime, respectively. The commercial landings of northern anchovy and Pacific sardine in California over the better part of the twentieth century reflect these regime shifts reasonably well (fig. 25-8).

PDO: EFFECTS ON OTHER SPECIES

The conditions that prevail during anchovy and sardine regimes affect more than just these two taxa (Chavez et al., 2003) as both commercial and non-commercial species are affected. During an anchovy regime at latitudes encompassing California, Oregon, and Washington, there are, relatively

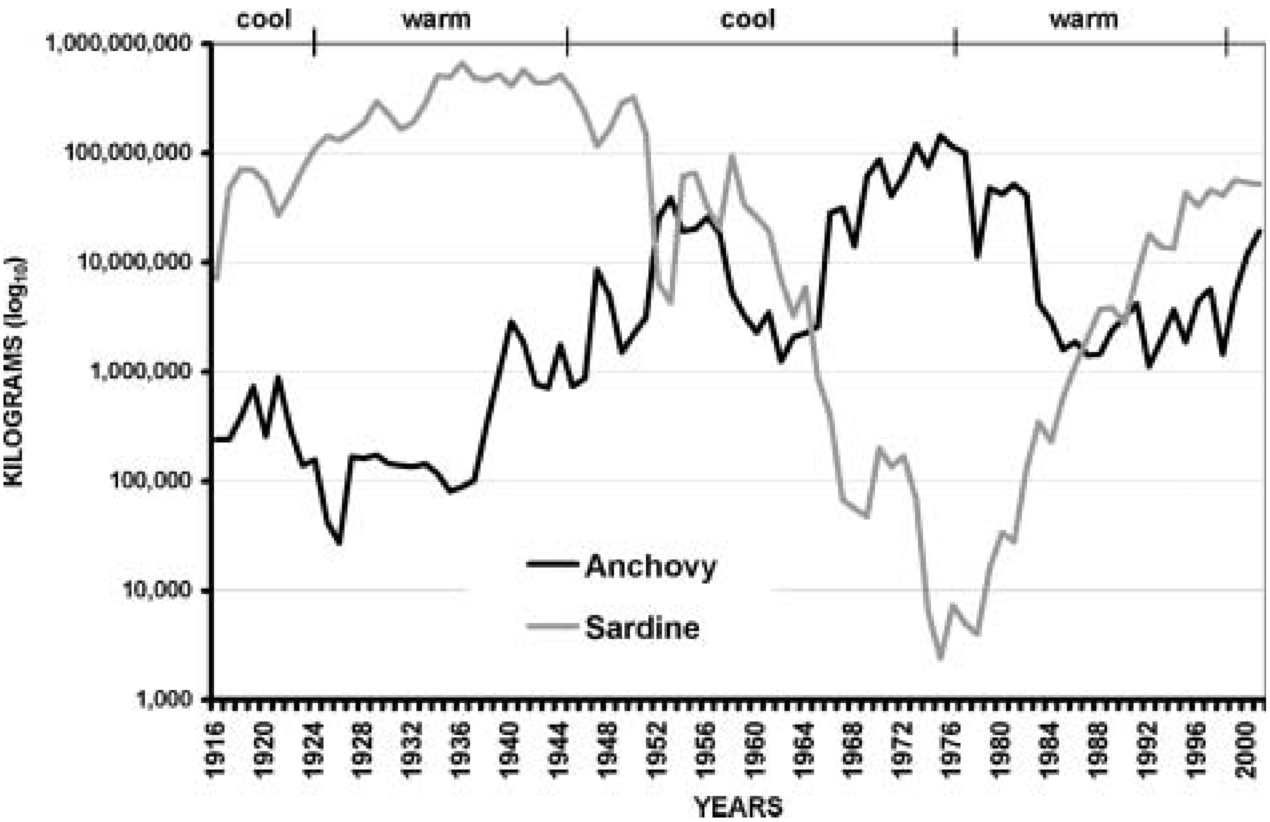

FIGURE 25-8 Commercial landings ($\log_{10}$ kg) of northern anchovy and Pacific sardine in California from 1916–2001 with cool and warm regimes superimposed on this time period. Landings data for 1916–1999 obtained from Leet et al. (2001) and updated to 2001 from the California Department of Fish and Game website (www.dfg.ca.gov).

speaking, fewer sardines, higher nutrients, primary production, and zooplankton levels, and more salmon, rockfish, and seabirds; in contrast, during a sardine regime, the opposite conditions predominate (fig. 25-7). Although these alternating situations describe the big picture for each regime, a closer examination reveals greater complexity and variability. For example, larvae of mesopelagic fishes of southern offshore species responded to the regime shift of 1976–1977 by increasing markedly in the Southern California Bight after 1977, whereas no consistent response was detected in larval abundance of Subarctic-Transitional mesopelagic species or nearshore taxa (Smith and Moser, 2003). Moreover, chinook salmon populations showed differences in productivity in response to the 1976–1977 regime shift even among three adjacent regions: Snake River, upper Columbia River, and middle Columbia River (Levin, 2003).

In addition, long-term studies (1974–1993 and continuing to the present) on subtidal reef fishes at two mainland sites in southern California, King Harbor and Palos Verdes, further demonstrate the effects of the 1976–1977 regime shift on fish populations (Stephens and Zerba, 1981; Stephens et al., 1994; Holbrook et al., 1997; fig. 25-9). Abundances of northern (cool-temperate) species declined abruptly with the onset of the warming event then remained relatively constant for 12 years before declining further in the 1990s. In contrast, abundances of southern species increased over the first 10–12 years of the study then declined sharply starting in the mid-1980s. Finally, so-called Bight species increased sharply in abundance at the outset of the warm regime then declined followed by stable abundances over the next 16 years. Species richness declined by 15–25%, and, by 1993, 95% of the fish species had fallen in abundance by an average of nearly 70% because of drastic recruitment failure over the two decades. Ecosystem effects were similar over a study period of 1982–1995 at Santa Cruz Island, an island site to the north, where the surfperch (Embiotocidae) populations, their crustacean prey, and understory macroalgae all declined by about 80% (Holbrook et al., 1997). At King Harbor, recruitment and larval abundance have been at a low level since the late 1980s (Pondella and Stephens, 2002; Stephens and Pondella, 2002). At Palos Verdes, fish density appears to increase, sometimes sharply, during each El Niño event and then to recover to more long-term averages (J. S. Stephens, Jr., unpubl. data), an indication of the confounding effects of ENSO episodes when they overlay decadal regime conditions.

Long-term studies of rocky intertidal fish assemblages are scarce in southern California compared to somewhat more extensive data available for central California shores. At Palos Verdes, Stephens (unpubl. data) noticed an increased abundance of zebraperch (*Hermosilla azurea*) following the 1976–1977 shift to a warm regime, an observation that matches the overall increased occurrence of the species in the Southern California Bight during the sustained warm period from 1977 to 1999 (Sturm and Horn, 2001). Shorter-term effects of ENSO periods on the structure and habitat use by rocky intertidal fish assemblages near San Diego also have been documented (Davis, 2000; see chapter 8). On the central California coast near Piedras Blancas, a tidepool removal study that began in 1978 and spanned the 1982–1983 El Niño episode and a discontinuous 23-year period showed virtually no detectable

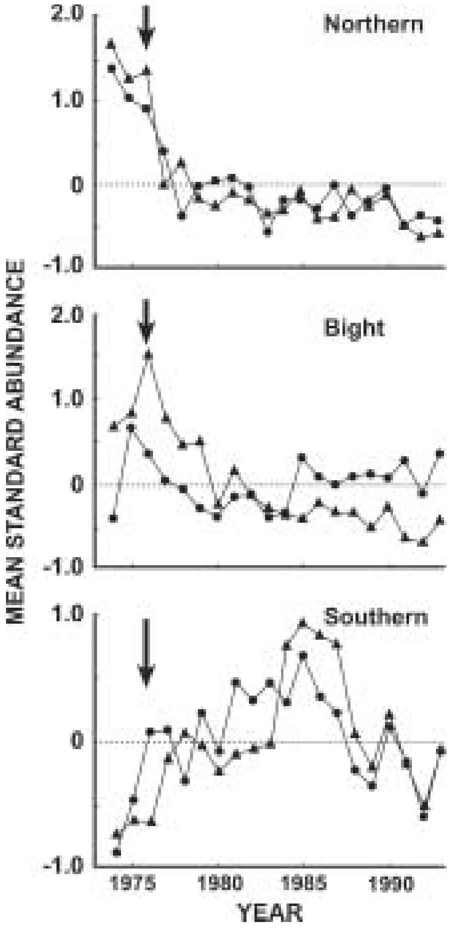

FIGURE 25-9 Temporal patterns in the mean standardized abundances of temperate reef fishes at King Harbor (dots) and Palos Verdes (triangles) in southern California for species belonging to the Northern, Bight, and Southern geographical range groups. The dashed line at 0 represents the 20-yr mean abundance of all species. Arrows indicate the 1976–1977 climatic shift from a cool regime to a warm regime (after Holbrook et al., 1997 with permission from the Ecological Society of America).

response either to the El Niño condition or to the presumed shift to a cool regime in 1999 (Horn, Allen and Boyle, unpubl. data).

Trawl studies of near shore fish assemblages in the Southern California Bight (see chapters 4 and 6) that began in the 1960s as part of monitoring programs associated with ocean sewage outfalls and hot-water effluent from coastal power plants also show changes in fish populations that may, in retrospect, be related to the 1976–1977 regime shift. A significant drop in total number of fish caught per trawl occurred between 1976 and 1980 as well as reduction or loss of some dominant species such as halfbanded rockfish (*Sebastes semicinctus*), stripetail rockfish (*S. saxicola*), shiner perch (*Cymatogaster aggregata*), and speckled sanddab (*Citharichthys stigmaeus*) (Mearns et al., 1980; Stephens et al., 1983). Both shiner perch and sanddab disappeared from the shallow sand substratum at King Harbor during this time period and have not returned in large numbers. In a study conducted during the strong El Niño/La Niña episode of 1982–1984, Love et al. (1986) documented reduced recruitment in 10 southern California coastal species including the dominant sciaenids, queenfish (*Seriphus politus*) and white croaker (*Genyonemus lineatus*), as well as the walleye surfperch (*Hyperprosopon argenteum*), white seaperch (*Phanerodon furcatus*) and speckled sanddab (see chapter 10). The most comprehensive trawl studies of soft-bottom fishes in the Bight since the 1980s have been conducted by the Southern California Coastal Water Research Project (SCCWRP). Their results show that in 1994 and 1998 the number of fish per trawl were still low compared to those obtained in the mid-1970s and that species, including queenfish and white croaker, began disappearing in the 1980s (Allen et al., 2001, 2002; see chapter 6). The most recent SCCWRP survey (2003) documents a return of some species not commonly observed since the regime change in the late 1970s (M. J. Allen, pers. comm.)

PDO: UNANSWERED QUESTIONS

As Chavez et al. (2003) point out, several fundamental questions associated with regime shifts remain to be answered. These questions pertain to the underlying forcing behind these shifts, the mechanisms through which they influence fish populations, the time frame for a regime shift, and their relationship to El Niño and La Niña events. Determining that the late 1970s regime shift occurred took more than a decade, but these investigators assert that verification of the late 1990s shift will occur much sooner. Chavez and colleagues appeared confident of the 1999 shift citing the changes in fish abundance off Peru (fig. 25-7) as probably the strongest evidence for a long-term, late 1990s regime shift. They also mention declining sardine abundance off California (fig. 25-8) and Japan as further evidence. Still other signs of a recent shift to a cool regime include increasing anchovy abundance (fig. 25-8), recruitment failure of all three species of *Paralabrax* (kelp bass, *P. clathratus*; barred sand bass, *P. nebulifer*; and spotted sand bass, *P. maculatofasciatus*) during the last two years, and heavy recruitment of several species of cool-temperate fishes, including olive rockfish (*Sebastes serranoides*), vermilion rockfish (*S. miniatus*), cabezon (*Scorpaenichthys marmoratus*), and lingcod (*Ophidion elongatus*), based on diving and fishing observations at 10–30 m depth in the vicinity of Los Angeles Harbor (L. G. Allen, pers. comm.). ENSO episodes complicate the matter, as mentioned above, because although cool conditons prevailed all through 1999, 2000, and early 2001, warm or neutral conditions prevailed for the rest of 2001 and 2002 (data from the Climate Prediction Center, Camp Springs, Maryland, www.cpc.ncep.noaa.gov). Only more time and further studies will verify or refute the existence of a regime shift in the late 1990s.

Future Status: Next 100 Years

Overexploitation

The twenty-first century has begun with fishery decline representing a major problem in the northeastern Pacific and other ocean regions and climate change looming as a crisis of uncertain magnitude for marine ecosystems. Quantitative assessments of fishery catch data have demonstrated that intense, size-selective fishing mortality over the last 50 years has resulted in a decline in the mean trophic level of exploited fish groups (Pauly et al., 1998, 2000; Sala et al., 2004). This “fishing down the food web” means that the world fish catch has shifted gradually from primarily long-lived, high trophic-level

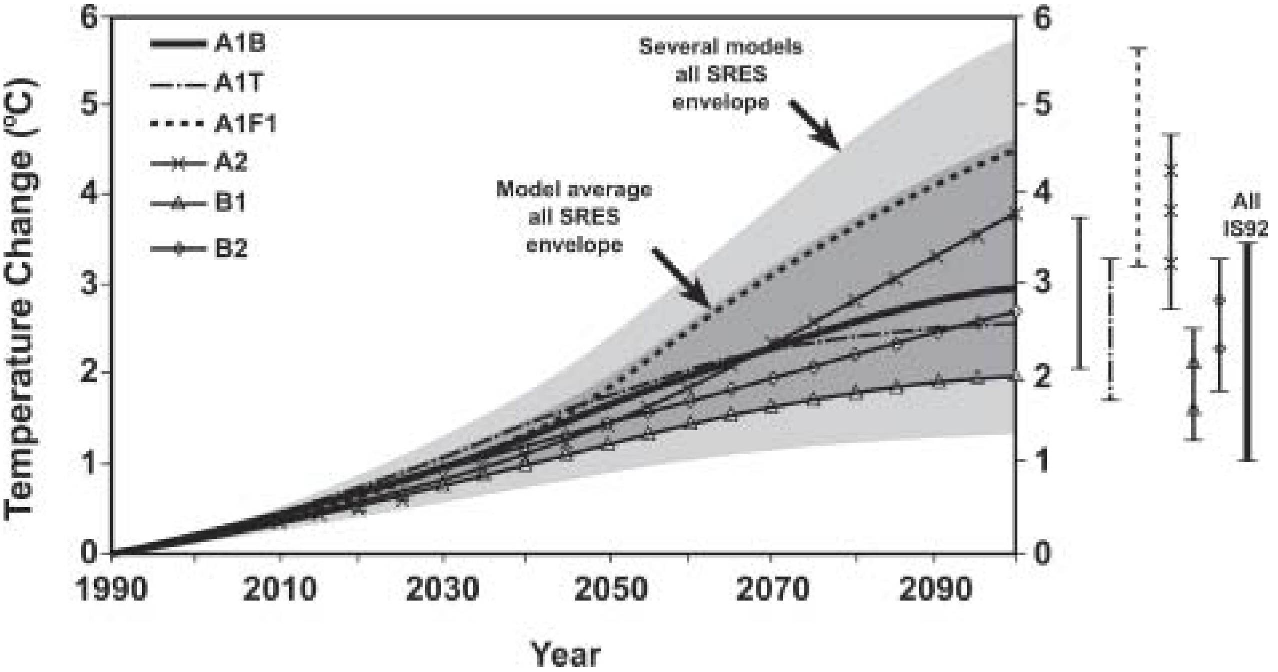

FIGURE 25-10 Global mean temperature projections from 1990 to 2100 for the six illustrative scenarios generated in the Special Report on Emissions Scenarios (SRES) based on a simple climate model tuned to a number of complex models with a range of climate sensitivities. The darker shading represents the envelope of the set of 35 scenarios employed to force climate models, using the average of the simple model results (mean climate sensitivity is 2.8° C). The lighter shading is the envelope based on all seven model projections (with climate sensitivity in the range of 1.7 to 4.2° C). The bars show, for each of the six illustrative SRES scenarios, the range of simple model results in 2100 for the seven model tunings. For comparison, the IS92 range of warmings in 2100 generated by the International Panel on Climate Change also is shown (after Pittock, 2002, as adapted from Houghton et al., 2001 with permission of Springer Science & Business Medic B.V.).

species to short-lived, low trophic level species. The evidence is staggering in its magnitude. Recent assessments report world declines in biomass of large predatory fishes of 90% from pre-industrial levels in the last 40 or so years (Myers and Worm, 2003), precipitous declines in large shark abundance (Baum and Myers, 2003; Baum et al., 2004), and collapse in abundance (median reduction of 83%) of principal fishery species groups from known historic levels with slow, even improbable, prospects for recovery (Hutchings and Reynolds, 2004). In the northeastern Pacific, recent assessments indicate that the biomass of at least seven species of rockfishes (*Sebastes* spp.) are at or below 25% of that estimated in the 1970s, and one of these species, bocaccio (*S. paucispinis*), has fallen in biomass by about 98% from its 1969 level (Love et al., 2002). Interestingly, the decline of northeastern Pacific rockfish species is coupled to the change in PDO, which clearly affected recruitment of cool-water species. This lack of adequate recruitment without compensatory reductions in fishing effort is overexploitation because of poor management and the lack of adequate fishery data. Worldwide, more than 80 fish stocks have recently been recognized as at risk of extinction (Musick et al., 2000). Although reduction in fishing pressure is clearly necessary, persistence and recovery also are influenced by life history features, habitat alteration, changes in food webs, genetic responses to exploitation, and declines in population growth as a result of the Allee effect (Hutchings and Reynolds, 2004). These authors emphasize that effective recovery strategies require greater understanding of how fish behavior, habitat, ecology, and evolution impact population growth at low abundance. A case in point is a recent study of the Atlantic cod (*Gadus morhua*), which shows that, up until the population collapse and fishing moratorium on this species in eastern Canada, the species gradually shifted toward maturation at earlier ages and smaller sizes, suggesting predictable fishery-induced evolution of maturation patterns (Olsen et al., 2004). The existence of multiple factors compounding the effects of overexploitation seem particularly relevant for the species of Pacific salmon (not included in the Hutchings and Reynolds survey), which use marine, estuarine, and freshwater habitats in their life history and therefore are imperiled by habitat alterations in each of these systems (see chapter 5). In summary, all of these recent revelations indicate strongly that fisheries management needs to be spatially explicit (e.g., to protect spawning aggregations) and to regulate according to fishing effort (Sala et al., 2004). No-take zones and networks of marine reserves are seen as necessary parts of management strategies (Murray et al., 1999; Sala et al., 2002), as are the rebuilding and restoring of depleted marine ecosystems (Pitcher, 2001).

Global Warming

Evidence for global warming over the last 100 years is widespread, including melting of glaciers, elevated sea level, earlier onset of growing seasons, and distributional shifts in both terrestrial and marine organisms (e.g., Walther et al., 2002; Root et al., 2003). Uncertainty still exists on the amount of human contribution to this warming trend although anthropogenic factors appear to have become increasingly important compared to natural forcings in recent decades (Stott et al., 2000). The climate models for the next century predict accelerated warming within a range of scenarios (fig. 25-10). Overall warming in the twentieth century was about 0.6° C, a rate much faster than the average warming at the end of the last glaciation (Pittock, 2002). In contrast, projections made by the Intergovernmental Panel on Climate Change for surface warming by the end of the present century (2100) range from 1.4 to 5.8° C, or about 2–10x that of the last century (Pittock, 2002; fig. 25-10). Warming in the Pacific Northwest during the 20th century has been estimated at 0.7–0.9° C, higher than the global average, and with the highest warming rates occurring in the maritime zone of the region (Mote, 2003).

Global warming casts a shadow of uncertain magnitude over the shorter-term and more regional ENSO and PDO conditions. Clearly, ENSO events and PDO regimes affect the distribution and abundance of fish populations, and they may act in conflict or in consort with each other. Nevertheless, the global warming occurring at the present time and predicted to increase over the next century promises to be the most important influence on the California marine fish fauna in the future. Overexploitation and various types of habitat alteration including nitrogen loading, sediment accumulation, and heavy metal contamination seem tractable and manageable on a regional basis given appropriate application of scientific information and sufficient public pressure and political will. In California, legislation to curtail overfishing and to establish marine reserves are tangible efforts that have begun to be implemented. Global warming, on the other hand, is so pervasive, so difficult to predict on a region by region basis, and still often ignored or suppressed, that it must be regarded as the major environmental problem for the future. Combined with continued overexploitation and habitat deterioration, worldwide warming presents a crisis-level threat to the coastal zone and marine environment in general.

Predictions

A prognosis for the California fish fauna over the next century almost certainly needs to include marked changes in the species composition and dominance of fish communities in most coastal habitats. Continued warming of California waters will be accompanied by a shift of warm- and cool-temperate fish species northward with replacement by tropical and warm temperate species depending upon the particular degree of latitude. The ability of organisms to survive in a changing thermal environment depends upon their ability to extract sufficient oxygen from the reduced oxygen levels of heated waters and to effect growth and reproduction using thermally sensitive metabolic pathways (Fields et al., 1993). The rockfish (*Sebastes* spp.) fishery in southern California can be expected to fail (if it, in fact, recovers from its current low ebb) because of the inability of rockfish larval stages to survive in warm surface waters. Surfperches (Embiotocidae) also will be restricted to more northerly sites, probably only northward of Point Conception, while families with tropical affinities such as Labridae, Pomacentridae, Kyphosidae, Haemulidae, perhaps Serranidae, and some species of Sciaenidae will dominate the expanded warm-temperate zone in coastal waters. Of interest here is the notion first offered by Hobson (1994) that relates the success of rockfishes and surfperches north of Point Conception to their development of viviparity as a successful adaptation to offshore larval dispersal in areas of intense upwelling. Assuming that climate change will not affect the level of upwelling, then Point Conception may limit the northward expansion of species in the Southern California Bight even if conditions warm. Transitional mesopelagic communities will be diminished or become dominated by eastern tropical Pacific species. Benthic species on the continental slope also may collapse as a community because of low survival of their larvae in the warmer surface layers. Pacific sardines may increase in abundance throughout California waters while northern anchovies retreat northward even during a cool regime.

Tropical and subtropical pelagic species may flourish in the warmer waters, especially in the Southern California Bight, and also occur with increasing abundance in more northerly waters. Anadromous salmonids are likely to disappear from waters south of Point Conception or even San Francisco Bay. Persistent warm periods, as in a warm-regime PDO, appear to diminish salmon abundance in the Pacific Northwest (Mote et al., 2004), an effect that will likely extend into California and that could be exacerbated by long-term global warming. In summary, the Southern California Bight looks to become primarily a marginal Panamic and Mexican fauna of conspicuous warm-water affinities with the marine regions of central and northern California increasingly warm-temperate in character. The disjunct temperate populations of the northern Gulf of California, although tolerant of wide temperature fluctuations, may become ecologically extinct or entirely extinct as separate taxa and replaced by more southerly Gulf elements.

Some cause for optimism emerges with regard to overexploitation and habitat deterioration in California marine waters given that these mounting problems have been met somewhat by deeper understanding, fresh approaches, and new techniques aimed at solving or ameliorating the developing crises. If equal or greater attention and ingenuity can be applied to climate change issues, the threats posed by global warming perhaps can be anticipated and managed. In this regard, long-term monitoring of marine fish populations certainly needs to be continued and expanded, and comparative and experimental studies initiated to predict and meet the looming challenges.

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