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CHAPTER 1

Biogeography

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Introduction

Environment of the Northeastern Pacific Ocean

The marine environment of the northeastern Pacific is a complex and dynamic system that offers a daunting challenge for any distributional analysis of its fish fauna, either of the entire region or a portion, such as the waters along the approximately 10° of latitude (32°–42°N) that border the state of California and that form the focus of this chapter. The narrow continental shelf of northern and central California gives way to a broader continental borderland off southern California that is etched with several deep-sea basins and marked with a series of islands of varying size and distance from the mainland and each other. These borderland features add to the complexity and sheer size of the California marine environment. The region provides a wide variety of habitats for fishes and undergoes changes that lead to shifts in distribution and abundance of the coastal fish fauna. The southward-flowing California Current and inshore countercurrents transport young stages of fishes and influence the movements of larger individuals. Water masses of northern, western, and southern origin impart their own character to the offshore fish fauna and converge to create a large transition zone in waters bordering the southern half of California (fig. 1-1). Upwelling events proceed seasonally from south to north along the coast resulting in sections of nearshore waters that are periodically cooler and more productive and, thus, contain more concentrated food resources.

Biogeographic Regions and Provinces

On a continental scale, two distinctive fish faunas meet and intermingle in California, a warm-temperate, southern element and a cool-temperate, northern component (Briggs, 1974; Horn and Allen, 1978). The well-known biogeographic boundary largely separating these two faunas has long been recognized to occur in the vicinity of Point Conception at about 34.5°N on the south central California coast. This boundary is perceived mainly as a temperature discontinuity, and studies of distributional patterns of fishes (Horn and Allen, 1978), molluscs (Valentine, 1966) and macrophytes (Murray and Littler, 1981) show that these patterns are strongly related to temperature regimes governed by oceanographic processes. Hayden and Dolan (1976) recognized the value of faunal distributions and range end points as indicators of abiotic zones and discontinuities. The traditional biogeographic regions and provinces of the eastern North Pacific have been described with some minor variations in a number of publications (McGowan, 1971; SCCWRP, 1973; Briggs, 1974; Horn and Allen, 1978; Brusca and Wallerstein, 1979; Allen and Smith, 1988; Hastings 2000; fig. 1-1). The politically demarcated latitudinal expanse of California contains parts of two biogeographic regions and subordinate provinces. To the north of Point Conception, the Oregonian Province extends to the Washington–British Columbia or British Columbia–Alaska border before giving way to the Aleutian Province; both provinces are contained within the Boreal Eastern Pacific Region. To the south of Point Conception, the San Diegan Province extends to the temperate-tropical boundary at Bahia Magdalena, Baja California Sur, Mexico. This province coupled with the Cortez Province, which extends from Bahia Magdalena and includes the entire Gulf of California upper Gulf, completes the Warm-Temperate California Region. To the south, the subtropical/tropical Mexican Province extends through Central America and is replaced to the south by the Panamic Province. The Panamic Province extends to northern Peru as part of the Tropical Eastern Pacific Region. This region also includes the Galapagos Province, which is described as all of the oceanic islands from the Galapagos in the south to Islas Revillagigedo off the tip of Baja California Sur to the north. For rocky shore fishes, Hastings (2000) has described the significance of stretches of soft bottom habitat that form gaps in the rocky coastline between the Cortez and Mexican provinces and between the Mexican and Panamic provinces. These subtropical/tropical faunas are bounded to the north and south by thermal transitions. Taken together, these regions and provinces and their boundaries provide useful structure and organization for studying faunal associations and distributional changes in the northeastern Pacific. They convey, however, a certain static picture that belies the complex and shifting interrelationships of the California fish fauna (Hubbs, 1974), which are driven in large part by

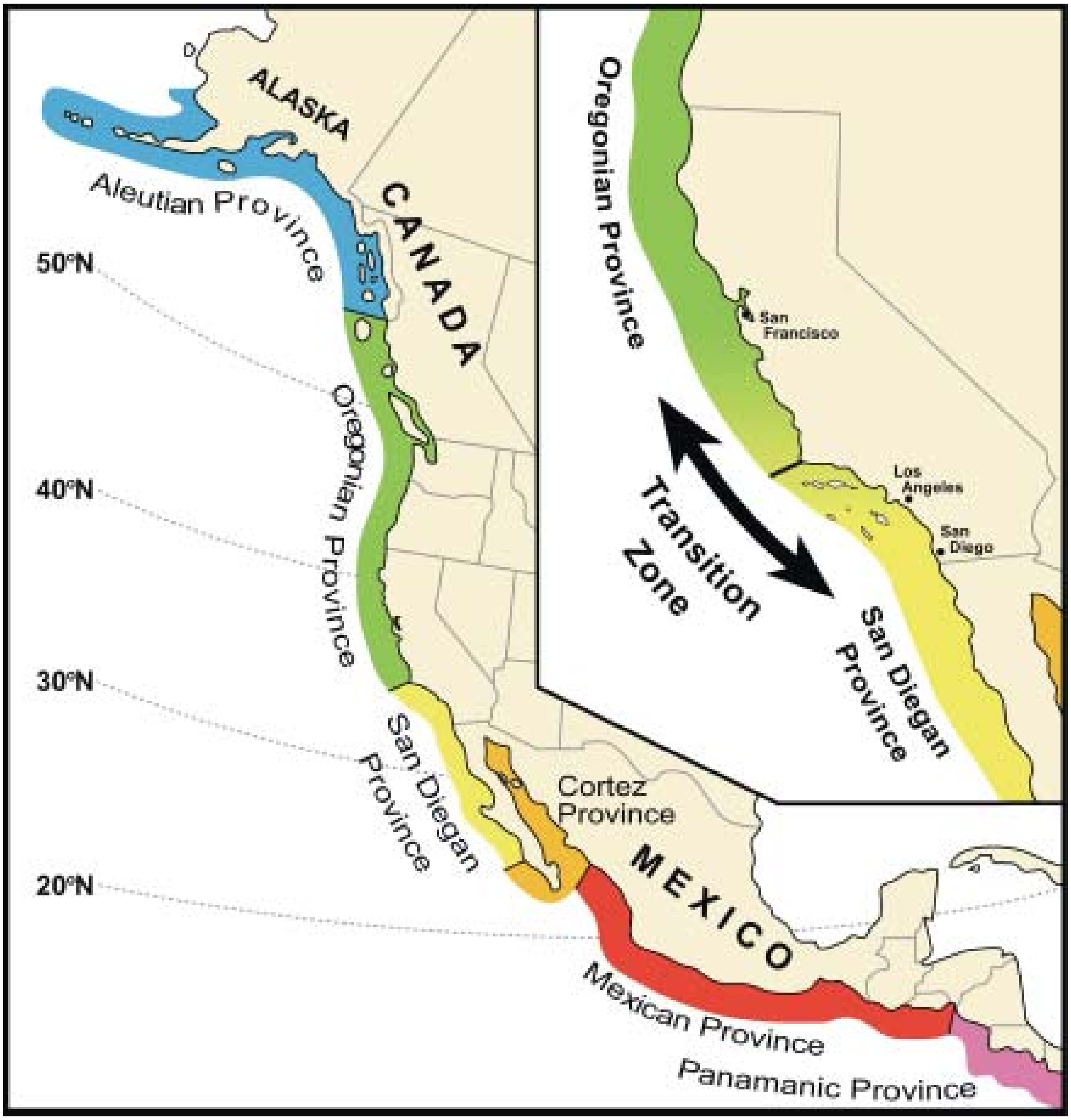

FIGURE 1-1 Zoogeographical provinces of the Pacific coast of North America (after Briggs, 1974).

short- and long-term variability in climate. Consistent with this dynamic picture and with our increasingly detailed knowledge of fish distributions, the generality and validity of Point Conception as a biogeographic boundary for fishes and marine invertebrates has been challenged recently based on phylogeographic analyses (see below).

Climatic Variability

The dynamic nature of the climate in the northeastern Pacific overlays an already complex marine environment in California coastal waters and strains the reliance on fixed boundaries and provinces for understanding the distributional patterns of the fish fauna. Both short- and long-term fluctuations in atmospheric and oceanographic conditions characterize the climate of the region. El Niño–Southern Oscillation (ENSO) events occur naturally as intervals of alternating warm and cool oceanographic conditions in the eastern tropical Pacific but affect regions far beyond, including the California marine environment (Kousky and Bell, 2000). El Niño events represent the warm extremes of the cycle and result in higher sea surface temperatures, weaker upwelling, and reduced nutrient levels in the water column. These events tend to occur every 4 to 5 years, last 12–15 months, and emerge strongest every 10–15 years (e.g., the powerful El Niño conditions of 1982–1983 and 1997–1998). El Niño events, detectable back to the 1700s in climate records and as a long ago as 5000 years in paleoclimatic signals, can now be predicted 9 to 12 months in advance. La Niña and more neutral conditions alternate in an irregular pattern with El Niño events in the ENSO cycle. La Niña conditions represent the cool extremes of the cycle and result in lower sea surface temperatures, stronger, deeper upwelling, increased nutrient levels, and heightened productivity in coastal waters. These events may last 1 to 3 years; for example, the recent La Niña event characterized by rapid onset in 1998 and persistence at least into early 2001 (Durazo et al., 2001). Although a shift to a cold-water regime has been suggested (Bograd et al., 2000) for the California Current system that may be associated with a Pacific Decadal Oscillation (Mantua et al., 1997), monitored features of the system do not yet indicate a climate regime shift (Durazo et al., 2001), although Chavez et al. (2003) present evidence that the shift has indeed occurred. Thus, the dynamics of the California marine environment create regional complexities beneath, so to speak, the recognized (e.g., Houghton, 2002) overall trend of global warming. The California Transition Zone provides an excellent 'natural' experiment for studying this process.

Continued Interest in Fish Distribution Patterns

Since the last distributional analysis of California coastal fishes was published more than 25 years ago (Horn and Allen, 1978), several events and developments have occurred in the intervening years to sustain and increase the scientific interest in the biogeography of California marine organisms including fishes. As alluded to above, most prominent among these occurrences has been climate change, particularly the warming of ocean surface waters, especially in the Southern California Bight, from the mid-1970s up through the strong El Niño conditions of 1997–1998, followed then by a rapid change to cooler temperatures and La Niña conditions from late 1998 to early 2001 (Smith, 1995; Bograd et al., 2000; Durazo et al., 2001). The intensified focus on this warming phenomenon has revealed that the ecosystem changes can be relatively slow and pervasive as in zooplankton declines occurring over two decades of warming (Roemmich and McGowan, 1995), or rapid and dramatic as in the 1997–1999 El Niño–La Niña cycle (Lynn and Bograd, 2002), with remarkable additions of Panamic fishes to the California fish fauna occurring during this brief period (Lea and Rosenblatt, 2000; Pondella and Allen, 2001). The increased attention to climate change and its effects on biotic distributions has helped provide the impetus for long-term monitoring studies of fish abundances and distributions, which, in turn, has yielded biogeographic information on fishes at local and regional scales (e.g., see Chapter 8, Rocky Reefs and Kelp Beds; Chapter 9, Near Shore Soft Bottoms).

Also important for California fish biogeography during the last quarter century has been the development of two new disciplines in biology—phylogeography and macroecology. Each of these nascent fields has had its champion, who has described the field in detail in book-length treatments. John Avise has led the emergence of phylogeography and recently synthesized the discipline (Avise, 2000). Phylogeography is about the geographic distributions of genealogical lineages particularly within and among closely related species. The discipline has grown out of the burgeoning mitochondrial DNA analyses of lineages and forms a link between microevolution, especially involving population genetics, and macroevolution, in particular the subdisciplines of historical geography and phylogenetics. This rapidly expanding field has infused new life into the analysis of traditional biogeographic boundaries because lineages of natural populations frequently show distinct geographic patterns.

As a subdiscipline of biogeography, phylogeography prompts the question whether the geographic orientation of genetically structured populations matches that of well-known biogeographic boundaries. For example, studies of two California fish species, black perch (*Embiotoca jacksoni*) by Bernardi (2000) and tidewater goby (*Eucyclogobius newberryi*) by Dawson et al. (2001), showed that, for these taxa, phylogeographic structure is not concordant with the biogeographic break at Point Conception. This unexpected finding has given rise to alternative hypotheses about the possibility of biogeographic boundaries at other locations. In a review of the literature describing the distributional patterns of coastal marine taxa in California, Dawson (2001) provided evidence that phylogeographic breaks are concordant with biogeographic patterns but that the boundaries match environmental discontinuities in the vicinity of Los Angeles (33°–34°N) and Monterey Bay (36°–37°N), not Point Conception. He points out that the range termini of fishes actually peak at 33°N in the Horn and Allen (1978) study, which was completed before phylogeographic analyses had begun. Even though Dawson (2001) acknowledges that Point Conception marks the northern limit of some San Diegan species and the southern limit of some Oregonian fishes, he asserts that Point Conception is more appropriately recognized as the center of a California Transition Zone (fig. 1-1). This zone is interpreted by Dawson as a heterogeneous region in which Oregonian and San Diegan faunas are replaced incrementally over several degrees of latitude and in which most species cross Point Conception and end their ranges elsewhere. In light of the Dawson work, we interpret our distributional analyses in this chapter with respect to the California Transition Zone concept as well as to Point Conception as the traditional biogeographic boundary. Phylogeography and the associated topics of genetic variation, population dispersal, and gene flow are discussed in detail in Chapter 2.

The second relevant discipline to emerge in the last two decades is macroecology, a field devoted to identifying and understanding ecological patterns on large spatial scales although the focus is not necessarily restricted to any particular spatial scale (Blackburn and Gaston, 2002). James Brown is the co-founder of macroecology and described the discipline in a book by the same name (Brown, 1995). Macroecology involves interpreting the statistical patterns of abundance, distribution, and diversity and examining the domain where the discipline intersects with ecology, biogeography, and paleontology. The premise of the field is that finding repeated statistical patterns of ecological variables leads to testable hypotheses of underlying mechanistic processes (Brown and Lomolino, 1998). Topics of macroecological interest include the distribution of geographic range sizes and the relationship between body size and species diversity. A recent application of macroecology involved analysis of body size and depth of occurrence of 409 species of eastern North Pacific pelagic fishes occurring at 40° to 50°N latitude and within a depth gradient of 0 to 8000 m (Smith and Brown, 2002). Their analysis did not include the latitudinal ranges of species, but they argue that species richness ought to be driven more by depth than latitude because the vertical temperature gradient in the ocean is so much greater than the horizontal (latitudinal) gradient.

A third recent approach to biogeographic analysis has been termed thermogeography by its proponents, Adey and Steneck (2001). This temperature/time/space model was developed by Adey and Steneck to show conditions under which assemblages of marine benthic algae evolve regional biogeographic patterns in their distribution and abundance. The model generates distribution patterns based on the part of geographic ranges where the taxa studied are most abundant rather than on total ranges that emphasize range end points. According to Steneck and Adey, the core of most of the classic coastal biogeographic regions, including those of the northeastern Pacific, correspond to those derived by the thermogeographic model. Whether the model can be applied successfully to more mobile taxa, such as fishes, remains to be determined, but it is worthy of consideration in the future.

Purposes and Expectations of the Chapter

Our analytical contribution to this chapter consists mainly of an update of the distributional analysis of California coastal fishes completed more than 25 years ago (Horn and Allen 1978). The current analysis incorporates range extensions and recent additions of species to the fauna. Given that surface water temperatures generally have warmed in the northeastern Pacific over the last 25 years, that most of the period (1976–1998) lay within a warm regime cycle, and that three strong El Niño events occurred during the interval, we expected our new analysis to reflect the known additions to the fauna and perhaps to detect some northward range shifts in the fauna as a whole.

The updated analysis largely paralleled that of the earlier work in that we (1) displayed the species richness gradient for California coastal fish species over their geographic ranges as far north as 60°N and to the equator and beyond southward; (2) portrayed richness patterns of principal taxa (family or genus) across California latitudes to emphasize the northern or southern affinities of these faunal elements; (3) examined the relationship of fish distributions, sea surface temperatures, and degrees of latitude; (4) determined the effectiveness of established faunal boundaries, especially Point Conception and more recently identified breaks in part derived from phylogeographic analyses (see Dawson, 2001, and Chapter 2), for bay-occurring and non-bay occurring fish species using cluster analysis; and (5) compared the effectiveness of these same boundaries for coastal species of northern and southern affinities based on principal coordinates analysis and range end-point analysis. Given that our analysis included only the juvenile and adult stages of coastal (primarily continental shelf) fish species, the contributions on ichthyoplankton by Moser and Watson (Chapter 11) and deep-sea fishes by Neighbors and Wilson (Chapter 13) help to provide a relatively complete picture of the distributional patterns of fishes in California waters.

Methods

The basic data for the analysis were derived from a list of 519 fish species known to occur in the coastal waters of California (Appendix 1). The list, with geographic ranges, was obtained from Miller and Lea (1972), with distributional information on certain species also acquired from Hart (1973). Additions to the California fauna since the Horn and Allen (1978) analysis were obtained from several published sources including Lea and Rosenblatt (2001) and are given in table 1-1. Most of the deep midwater and benthic species in the list of Miller and Lea (1972) were not used in the analysis although the distribution patterns of deepwater assemblages are examined, as mentioned, in Chapters 11 and 13 of this volume. Three sets of species and their geographic ranges were used: (1) a set of 519 species referred to as "all coastal species"; (2) a set of 225 species that occur in bays and estuaries (hereafter, "bay" used for "bay and estuary") and correspond to the species in 13 bays used in Horn and Allen (1976) plus two additional sites, Carpinteria Marsh and Mugu Lagoon; and (3) a set of 289 species that do not occur in bays. Species distributions at 1° or 2° intervals of latitude were plotted depending upon the type of analysis performed. A species was considered to occur or end its range at a particular latitude if it had been recorded at any geographic location within that latitudinal interval (e.g., any location from 32.0° to 32.9°N was considered 32°N). A few species now recorded as occurring in California were not included in the analyses because they were added too recently or because of lack of other information. These species include white mullet (*Mugil curema*), Pacific golden-eyed tilefish (*Caulolatilus affinis*), Pacific dog snapper (*Lutjanus novemfasciatus*), armed grunt (*Conodon serrifer*), Cortez grunt (*Haemulon flaviguttatum*), bluestriped chub (*Sectator ocyurus*), Panamic sergeant major (*Abudefduf troschellii*), swallow damselfish (*Azurina hirundo*), silverstripe chromis (*Chromis alta*), threeline prickleback (*Esselenichthys carli*), twoline prickleback (*Esselenichthys laurae*), saddled prickleback (*Lumpenopsis clitella*), deepwater bass (*Serranus aequidens*), and Pacific stargazer (*Astroscopus zephyreus*). References on the distributional information for these species can be obtained from any of the authors of this chapter.

To show the degree of resemblance among bays and degrees of latitude in terms of their fish faunas, cluster analysis was performed. A Pearson product-moment correlation matrix was used to produce linkage distances among the bays or latitudes scaled to a maximum linkage distance of 100%. The principal coordinates analysis used to generate the ordination two-way table of 289 non-bay species by latitude (Appendix 2) was performed according to a procedure described in Smith (1976) and used by Horn and Allen (1978). Ordination in the present study means that the species were ranked on a north-to-south latitudinal axis according to the average axis score of the species at each degree of latitude. For example, the first species in the ranking occurred only at 41° and 42°, the last species at 32°, and the intermediate species at latitudinal intervals that were progressively more southerly in character.

Sea surface temperatures at 2° intervals of latitude were obtained from charts prepared by Eber et al. (1968). Minimum temperatures were derived from monthly means for the 14-year period 1949–1962. Although ocean temperatures increased slightly in the latter half of the century, our fundamental distributional information largely reflects the long-term temperature profile of the warm- to cool-temperate waters of California latitudes. This approach allowed us to emphasize the changes in recent decades in fish distributions as shown in table 1-1 and as related to changes in ocean temperatures as presented in the Discussion (see below).

Results

Species Richness Patterns

The species richness of California non-bay coastal fishes was highest in southern California, peaking at 32°N with 243 species (fig. 1-2). Species richness declined relatively sharply from 33° to 34° and then gradually to the north with 125 species recorded at 42°. The number of fish species was significantly correlated ($r = -0.92$, $p < .0001$) with latitude (32°–42°N), and latitude was significantly correlated ($r = -0.94$, $p < .0001$) with minimum sea surface temperature.

TABLE 1-1

Changes (in Part) in California Marine Fish Fauna Since the Publication of Horn and Allen (1978)

Common Name	*Scientific Name*	*Family*	*Reference or Comment*
Species added to the list in the present study			
Machete	*Elops affinis*	Elopidae	Fitch and Schultz (1978)
Deepwater cornetfish	*Fistularia corneta*	Fistulariidae	Lea and Rosenblatt (2000)
Flag rockfish	*Sebastes rubrivinctus*	Scorpaenidae	inadvertently omitted in Horn and Allen (1978) study
Puget Sound sculpin	*Ruscarius meanyi*	Cottidae	Lea (1974)
Striped sea chub	*Kyphosus analogus*	Kyphosidae	Crooke (1973)
Greater sand perch	*Diplectrum maximum*	Serranidae	Lea and Rosenblatt (2000)
Pink cardinalfish	*Apogon pacificus*	Apogonidae	Lea and Rosenblatt (2000)
Bigeye trevally	*Caranx sexfasciatus*	Carangidae	Lea and Walker (1995)
Cocinero	*Caranx vinctus*	Carangidae	Lea and Rosenblatt (2000)
Mexican lookdown	*Selene brevoortii*	Carangidae	Lea and Walker (1995)
Pacific tripletail	*Lobotes pacificus*	Lobotidae	Rounds and Feeney (1993)
Blackspot wrasse	*Decodon melasma*	Labridae	Lea and Rosenblatt (2000)
Loosetooth parrotfish	*Nicholsina denticulata*	Scaridae	Lea and Rosenblatt (2000)
Sabertooth blenny	*Plagiotremus azuleus*	Blenniidae	Lea and Rosenblatt (2000)
Slender cockscomb	*Anoplarchus insignis*	Stichaeidae	Miller and Lea (1976, Appendix)
Decorated warbonnet	*Chirolophis decoratus*	Stichaeidae	Miller and Lea (1976, Appendix)
Channel Islands clingfish	*Rimicola cabrilloi*	Gobiesocidae	Briggs (2002)
Blacklip dragonet	*Synchiropus atrilabiatus*	Callionymidae	Lea and Rosenblatt (2000)
Mexican barracuda	*Sphyraena ensis*	Sphyraenidae	Lea and Rosenblatt (2000)
Speckletail flounder	*Engyophrys sanctilaurentii*	Bothidae	Lea and Rosenblatt (2000)
Gulf sanddab	*Citharichthys fragilis*	Paralichthyidae	Allen (1976)
Longnose puffer	*Sphoeroides lobatus*	Tetraodontidae	Fitch (1973)
Balloonfish	*Diodon holocanthus*	Diodontidae	Leis (1978)
23 species			
Species deleted from the Horn and Allen (1978) list and not included in the present study			
Smoothtail mobula	*Mobula lucasana*	Mobulidae	California records not this species; only *M. japanica* known from state
Orangemouth corvina	*Cynoscion xanthulus*	Sciaenidae	Introduced into Salton Sea; no coastal records
Scarlet kelpfish 3 species	*Gibbsonia erythra*	Clinidae	Synonym of *Gibbonsia montereyensis*; see Stepien and Rosenblatt (1991)
Replacement names or name changes			
	present study		**Horn and Allen (1978)**
Threadfin bass	*Pronotogrammus multifasciatus*	Serranidae	As *Hemanthias peruanus*
Pacific crevalle jack	*Caranx caninus*	Carangidae	Previously as *Caranx hippos*
Bigscale goatfish	*Pseudupeneus grandisquamis*	Mullidae	As *Mulloidichthys dentatus*; see Lea and Rosenblatt (2000)
Masked prickleback	*Ernogrammus walkeri*	Stichaeidae	As *Askoldia* sp.
Sixspot prickleback	*Kasatkia seigeli*	Stichaeidae	As *Stichaeopsis* sp.
Pacific scabbardfish	*Lepidopus fitchi*	Trichiuridae	As *Lepidopus xantusi*

NOTE: The net 20 species are included among the 519 species used in the overall analysis of the fauna in this chapter. Replacement names and name changes that have occurred since the 1978 study also are listed.

The numbers of species within 14 principal taxonomic groups representing 13 families and one genus (fig. 1-3) account for about 50% of the fish species occurring in California coastal waters. These are plotted at 1° latitudinal intervals in California (32°–41°) and resulted in at least three geographic patterns of richness (fig. 1-4). These three patterns are as follows: (1) six of the families (Carcharhinidae, Sciaenidae, Carangidae, Scombridae, Gobiidae, and Clinidae) showed highest richness in southern California (mainly 32°–33°), reflecting their warm temperate to tropical affinities; (2) three of the families (Zoarcidae, Pholidae, Agonidae,) displayed gradual increases in species richness northward with peak species richness at 40° and 41°, an indication of their cool-temperate affinities in the northeastern Pacific (see Miller and Lea, 1972; Eschmeyer et al., 1983); and (3) the remaining taxa showed highest richness across a broad expanse of latitude either across southern and central California (Embiotocidae, 32°–38°, *Sebastes*, 33°–37°) or central and northern California (Cottidae, Stichaeidae, Pleuronectidae). Note that latitude 34°, encompassing 34.0° to 34.9°, straddles the Point. Conception area at 34.5°. This geographic detail means, for example, that the Cottidae showed relatively high richness in this area with a drop in species richness at 33° and that *Sebastes* exhibited relatively high species richness at both 33° and 34°.

Cluster analysis produced dendrograms for three distributional groupings of coastal fishes that revealed different amounts of faunal resemblance among latitudinal components of the fauna (fig. 1-5a). The cluster of 15 bays showed the greatest distance (mean linkage distance, MLD = 40.0% ± 24.1, $n = 14$) among the three clusters. Linkage distance was greatest (scaled linkage distance, LD = 100%) between three large northern

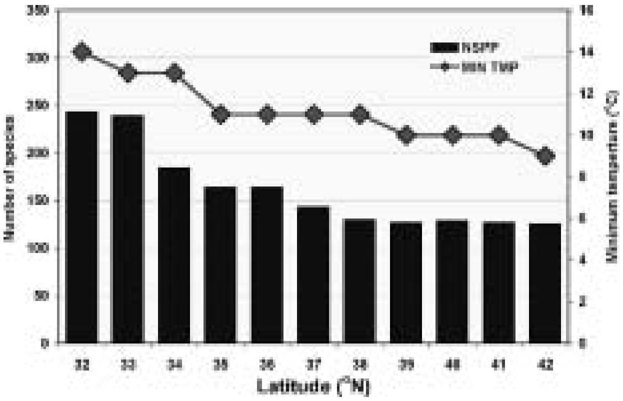

FIGURE 1-2 Numbers of coastal fish species at 1° intervals of latitude encompassing the California coastline. Minimum sea surface temperatures derived from monthly means for the 14-year period 1949–1962 (after Eber et al., 1968).

California bays (Tomales-Bodega Bay, Humboldt Bay, San Francisco Bay) plus Elkhorn Slough on the central coast and the remaining 11 bays both north (Bolinas Lagoon) and south (10 central and southern California bays) of San Francisco Bay. The next largest distance (LD = 60%) separated a cluster consisting of four southern California bays (Mugu Lagoon, Newport Bay, Mission Bay, and San Diego Bay) from a northern California (Bolinas Lagoon), a central California (Morro Bay), and five southern California bays (Alamitos Bay, Anaheim Bay, Carpinteria Marsh, Los Penasquitos Lagoon, and Tijuana Estuary). In turn, Bolinas Lagoon and Morro Bay were separated by an LD of 44% from the five southern California systems. These two more northerly bays were separated by a linkage distance (LD = 35%) almost as great. In southern California, two clusters emerged in the analysis separating Alamitos Bay and Anaheim Bay from the remaining three bays (LD = 29%). This cluster analysis of 15 bays shows that these systems were not related in a strictly linear (i.e., consecutive latitude) arrangement. For example, Elkhorn Slough on the central coast was linked with the three large northern California bays, and Morro Bay, also on the central coast, was linked most closely with Bolinas Lagoon located just north of San Francisco Bay. Moreover, Carpinteria Marsh to the north was linked most closely to Los Penasquitos Lagoon and Tijuana Estuary, two bays near Mission Bay and San Diego Bay. Mugu Lagoon, geographically nearest to Carpinteria Marsh, linked mostly closely (although at LD = 36%) with the three large southern bays (Newport Bay, Mission Bay, and San Diego Bay). Alamitos Bay and Anaheim Bay, however, were closely linked (LD = 17%) and are nearest one another along the southern California coast.

The dendrogram for non-bay species (fig. 1-5b) was entirely linear with respect to latitude and exhibited the lowest mean within-cluster MLD (24.4% ± 31.6, n = 9) although two large breaks occurred. Cluster distance was greatest (LD = 100% scaled linkage distance) between two southern California latitudes (32° and 33°), and the eight other more northerly latitudes, including 34°, which, again, encompasses the Point Conception area. The second largest dichotomy (LD = 48%) occurred between a set of three central California latitudes (34°–36°) and a set of five more northerly latitudes (37°–41°). Latitudes 38° and 39° were closely linked (LD = 1%) as were latitudes 40° and 41° (LD = 3%).

The dendrogram for all coastal species (fig. 1-5c) was entirely linear with respect to latitude, and the cluster analysis produced a mean within-group MLD (27.7% ± 31.8, n = 9) intermediate between that for the bay and the non-bay species. The cluster topology was more similar to that for the non-bay species set than to that for bay species; the greatest separation (LD = 100% scaled linkage distance) was between two southern latitudes (32° and 33°) and the eight more northerly latitudes. The second largest distance (LD = 59%) mirrored that for the non-bay species described above but with slightly deeper dichotomies between 38° and 39° (LD = 4%) and between 40° and 41° (LD = 5%). The 37° interval was distinct from the four more northerly latitudes, at an LD of 24%, and the 34° interval was distinct from the two other central latitudes at LD = 21%.

The distributional pattern derived from the principal coordinates analysis with ordination of the 289 non-bay species (fig. 1-6) depicts several biogeographic features of the California coastal fish fauna. The ordination showed the high degree to which latitude is associated with the distributions of this subset of the fauna. The length and position of each latitudinal line in fig. 1-6 represent the species richness and composition of species at each latitude relative to the ranked list of 289 species represented by the length of the rectangle. The magnitude of the decline in species richness and change in species composition in a south-to-north direction compared to that in a north-to-south direction is proportional to the sizes of the "open areas" in the upper left and lower right sections of the rectangle. The relatively high species richness in southern California was well illustrated, with 83% and 84% of all of the 289 species occurring at 32° and 33°N. The marked decrease in species richness reflects the importance of boundaries in southern California, or in the Point Conception area (see below), as a faunal break for southern species. A total of 95 species (18.3% of all 519 species) occurred exclusively no farther north than 33°, whereas 64 species (12.3%) occur only north of this latitude. Four large discontinuities occurred in proportions of non-bay species represented per degree of latitude. The largest break in proportions occurred between 33° and 34° (83% to 64%), the next largest between 34° and 35° (64% to 57%), then between 36° and 37° (57% to 49%), and, finally, from 37° to 38° (49% to 45%). The ordination showed an overall northward shift in the non-bay fauna compared to the 1978 ordination with each latitude showing at least a 1% increase in proportion of the total species contained and with the latitudes 32°, 33°, and 36° registering a 2% increase in proportions.

Analysis of End Points of Species Ranges

Range end-point analysis (fig. 1-7) showed that California coastal fishes as a group occur over a broad latitudinal expanse but that southern and northern range end points are bimodal in frequency and therefore concentrated at relatively narrow latitudinal intervals. Southern limits of species ranges occurred most frequently off Baja California, southern California, and South America (table 1-2), whereas northern limits occurred most commonly in Alaska, southern California, and central California (table 1-3). Although the distal modes of each bimodal pattern were at latitudes remote from California, the proximal modes were adjacent or clearly overlapped in southern California (32° and 33°). The differing patterns of southern and northern range end points are expressed somewhat further by the degree of correlation between end points and sea surface temperatures (which as shown above are highly correlated with latitude) off California.

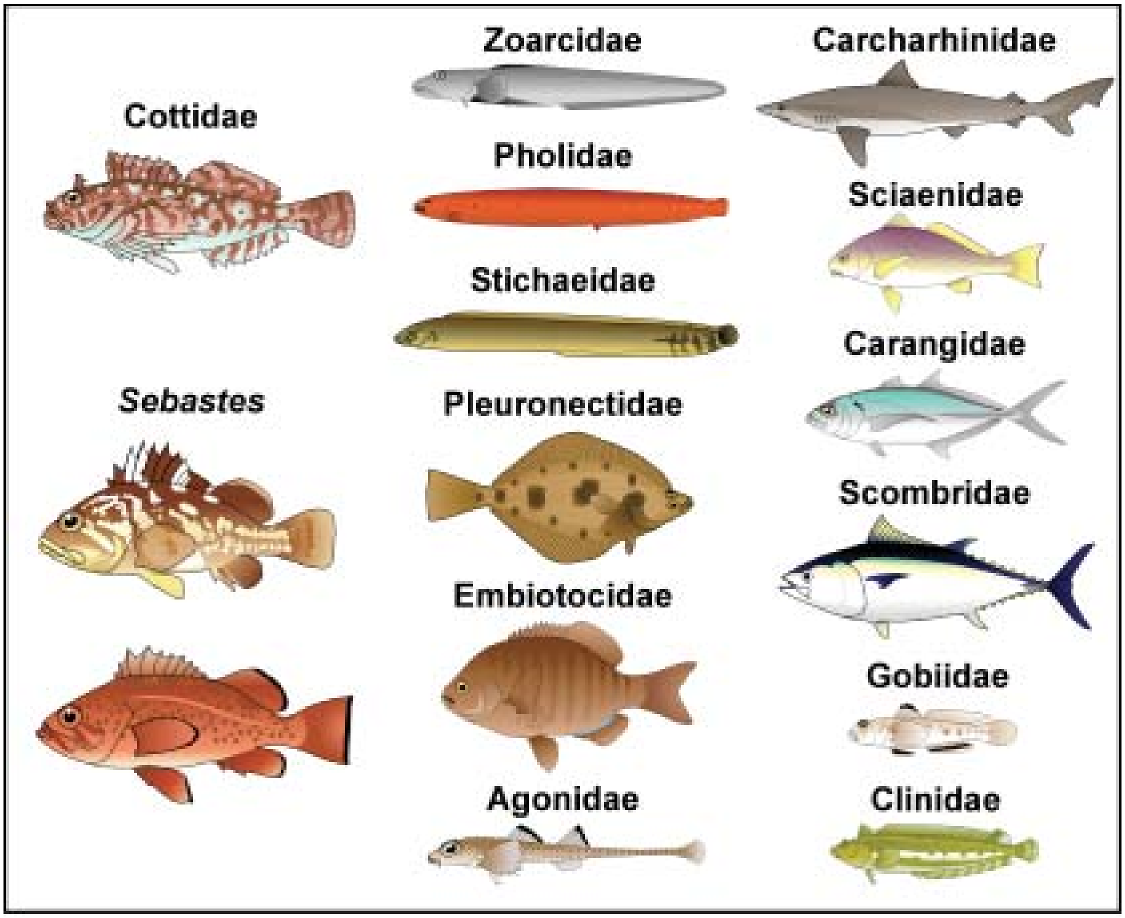

FIGURE 1-3 Illustrations of representative species for 13 families and one genus of fishes occurring in California coastal waters (see fig. 1–4).

The number of southern end points at each degree of latitude in California was significantly correlated ($r = 0.93$, $p < .0001$) with minimum surface temperatures, whereas the number of northern end points was less strongly though still significantly correlated with surface temperatures ($r = 0.62$, $p = .040$). These differing correlation values reflect the patterns that, whereas northern end points peaked sharply at temperatures corresponding to 33°N and then declined irregularly northward, southern end points gradually increased in number southward along the California coast peaking at temperatures corresponding to 32°N (tables 1-2 and 1-3). One must keep in mind that species richness is a function of sampling effort, which is not equal across the range of these fishes.

Discussion

Both similarities and differences are apparent between the distributional analyses published in Horn and Allen (1978) and the present analysis. The broad pattern of geographic ranges of the California fish fauna, as expected, remains largely unchanged. The specific changes, however, that have occurred in coastal fish distributions are notable and can be interpreted in the light of our increased knowledge of climate change, including fluctuations at different spatial and temporal scales. Moreover, the increased resolution that now can be brought to distributional analysis through phylogeographic approaches using molecular genetic techniques has added a new dimension to the study and understanding of California fish biogeography, as can be seen in Chapter 2.

The species-rich fish fauna occurring in California waters is of varied origin and complex distribution, but it is largely a mixture of warm-temperate and subtropical species dominating in southern California and blending with a cool-temperate fauna descending from northerly latitudes. Species richness is clearly greatest in southern California with a sharp decline in richness northward beyond this region and then a more gradual decline farther northward in central and into northern California. This richness pattern is highly correlated with increasing latitude and decreasing minimum surface temperature across California latitudes. To the south of California, the richness of species that occurs in California declines more rapidly than that observed to the north, as demonstrated by range end-point distributions. This marked decline reaches its lowest point in southern Baja California followed by a more gradual decrease in the occurrence of California species southward to central Chile. Overall, this southerly pattern in the distribution of California fish species most likely reflects a combination of changing oceanographic conditions, the presence of a diverse fauna occupying the tropical eastern Pacific biogeographic region (see Hastings, 2000), and less intense and consistent sampling efforts across these lower latitudes.

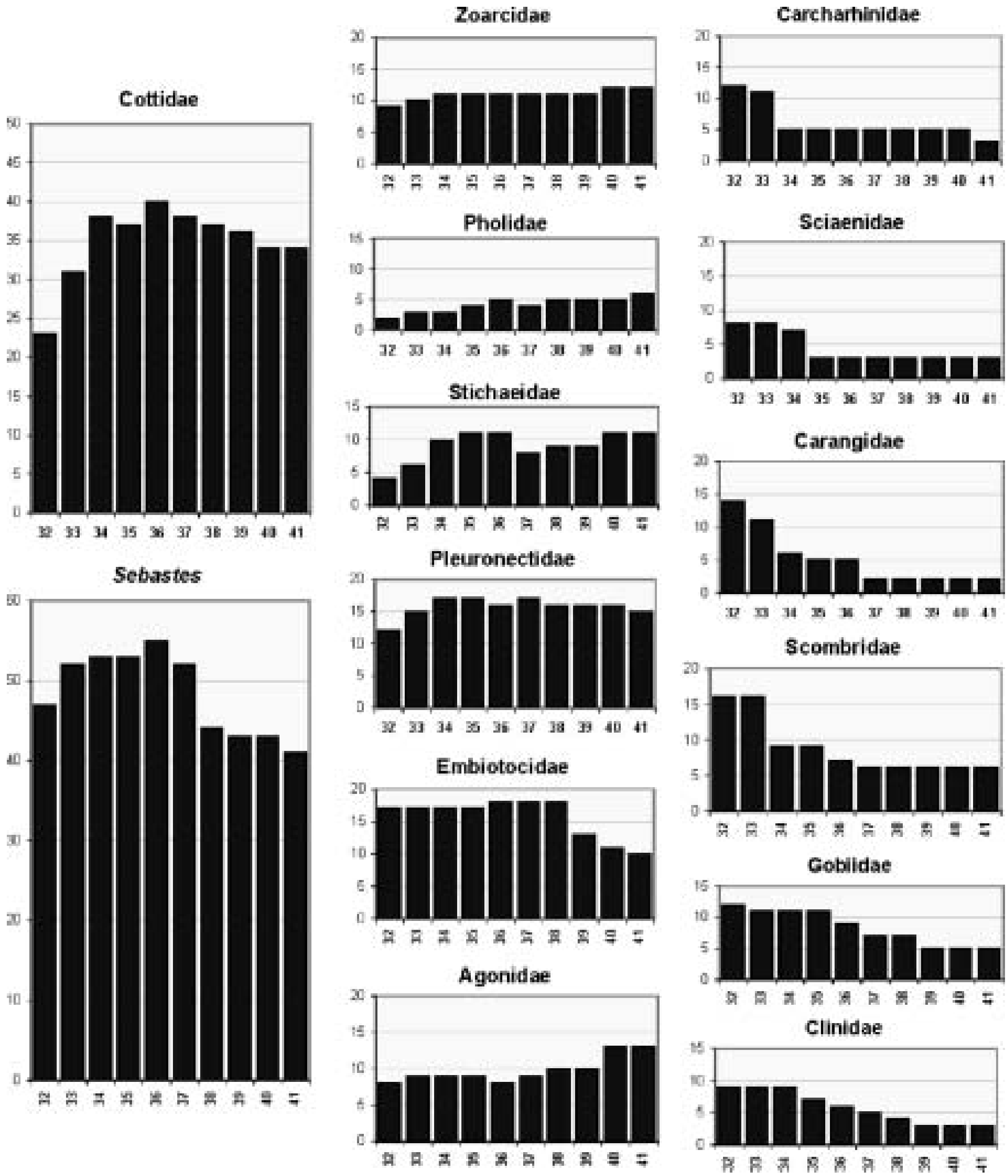

FIGURE 1-4 Species richness patterns in California waters at 1° intervals of latitude for 13 families and one genus of California coastal fishes. (see fig. 1–3).

Latitudinal Patterns of Particular Faunal Elements

Richness patterns for several families and a species-rich genus (*Sebastes*) across California latitudes demonstrate the varied origins and complexity of the marine fauna of the state (fig. 1-4). Some families clearly illustrate the warm-temperate and tropical component of the fauna with highest richness in southern California. Other families represent the cool-water affinities of part of the fauna with highest richness in more northerly latitudes. Still other higher taxa, including the genus *Sebastes*, reach peak species-richness in central California or across a broad expanse of latitudes in southern and central California or central and northern California. The overall species richness patterns observed in these higher taxa in the present analysis are similar to those depicted in the earlier study.

Cluster Analysis of Bay and Non-Bay Species

Like Horn and Allen (1978), we also found that the dendrogram based on bay-occurring species clustered less tightly than that based on non-bay-occurring species arranged by latitude. This difference may be explained by at least two factors. First, bay-occurring fish species, among them California killifish

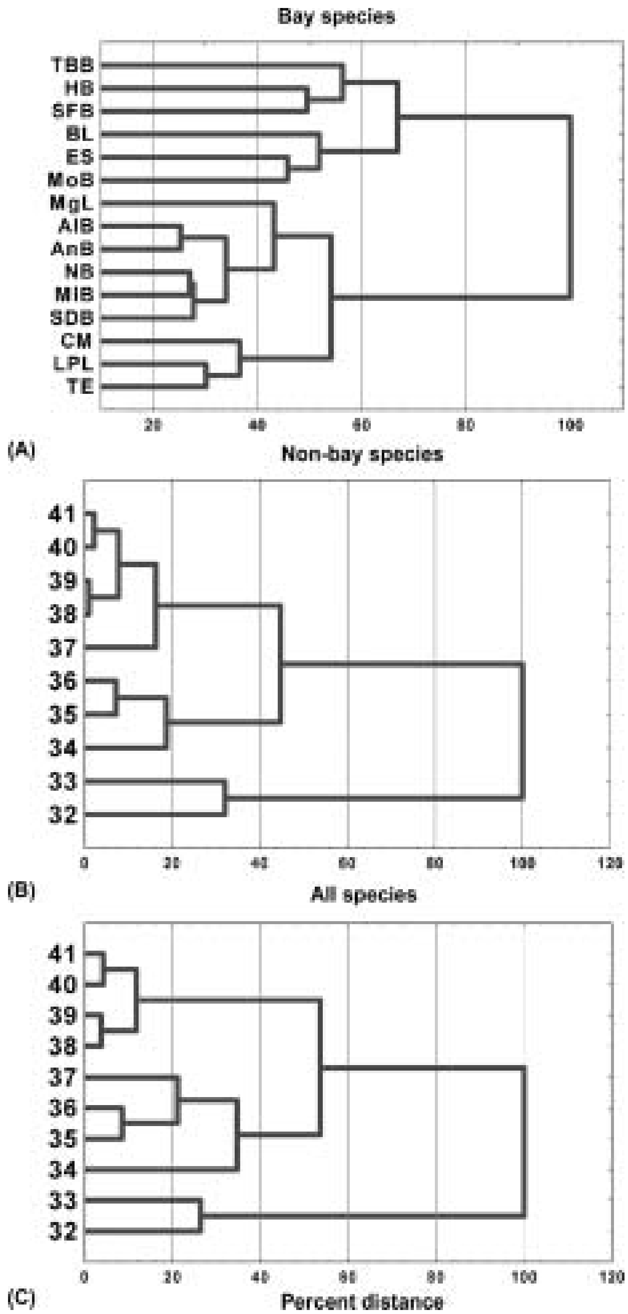

FIGURE 1-5 Dendrograms of the clustering of 1° intervals of latitude or bays at irregular latitudes based on presence/absence of fish species using a Pearson product-moment correlation matrix to produce linkage distances among the bays or latitudes scaled to a maximum linkage distance of 100%. (A) For 225 bay-occurring species where the recorded latitudes are those at the midpoints of the mouths of the 15 bays: HB = Humboldt Bay, TBB = Tomales-Bodega Bay; SFB = San Francisco Bay; ES = Elkhorn Slough MgL = Mugu Lagoon, NB = Newport Bay; MiB = Mission Bay; SDB = San Diego Bay; BL = Bolinas Lagoon; MoB = Morro Bay; AlB = Alamitos Bay; AnB = Anaheim Bay; CM = Carpinteria Marsh; LPL = Los Penasquitos Lagoon, TE = Tijuana Estuary. (B) For 289 non-bay-occurring species. (C) For the total of 519 coastal species.

(*Fundulus parvipinnis*) and certain species of goby, such as arrow goby (*Clevelandia ios*) and longjaw mudsucker (*Gillichthys mirabilis*), tend to be inshore species or even confined to bay habitats and therefore have limited powers of latitudinal dispersal. In contrast, non-bay species, as the name implies, are more offshore taxa with greater opportunities for dispersal across latitudes. Second, the uneven distribution of bays along the California coast promotes greater dissimilarity among the faunas of the more widely separated bays. The third dendrogram, for all coastal fish species, was intermediate in similarity but more similar to the non-bay than to the bay cluster.

An important difference emerged from the bay dendrogram in the present study compared to that in the 1978 publication. In the earlier investigation, the greatest dissimilarity in all three dendrograms was found between latitudes or bays north and south of Point Conception, emphasizing the distinctiveness of the southern California fish fauna compared to that of the rest of the state. These differences were sustained in the present study for the non-bay and all-species clusters but not for the bay cluster. The greatest dissimilarity in the more recent bay dendrogram emerged between three large northern bays (Humboldt Bay, Tomales-Bodega Bay, and San Francisco Bay) plus Elkhorn Slough on the central California coast versus the 11 other bays from various parts of the state (table 1-4: fig. 1-8). A further divergence in the present study was that the next largest break among the bay faunas was that uniting Morro Bay on the central coast and Bolinas Lagoon in northern California with five southern California bays more closely than the latter were to the remaining four southern California bays. At least three factors may have helped to produce this different bay dendrogram. The first two involve differences in the analysis, one about the bays included and the second concerning use of a different clustering index. Two southern California bays, Mugu Lagoon and Carpinteria Marsh, were added to the present analysis, and the Pearson product-moment correlation matrix was used in the current study instead of the Canberra-metric dissimilarity measure of the earlier work. Neither of these differences would be expected a priori to produce the differences found between the current and earlier bay dendrograms. The addition of two southern California bays predictably would enhance the distinctiveness of the southern California bay faunas. Moreover, the two different indexes ought to parallel each other in cluster pattern rather than causing the divergence observed between the two dendrograms. The third factor that may have helped to cause the greater latitudinal mixing among the bay faunas in the present study was the overall increase in coastal surface temperatures that occurred during the 25-year interval between the two distributional analyses. Hubbs (1948, 1960) observed that bays tend to be warmer than deeper, more offshore waters thus enhancing the occupation of central and northern California bays by southern species moving northward with the overall warming of coastal waters.

Ordination Analysis by Latitude

The ordination of non-bay species by principal coordinates analysis shows two important differences in outcome compared to that of a similar analysis presented in the 1978 paper. The first difference is that the faunal discontinuity in southern California between 33° and 34° is the most prominent boundary in California, exceeding that between 34° and 35°, which encompasses Point Conception. The prominence of the southern California discontinuity was present in the 1978 analysis, as pointed out by Dawson (2001), but was deemphasized in favor of the more well-known break in the vicinity of Point Conception. Dawson (2001) also notes that peaks in range end points occur between 33° and 34° N

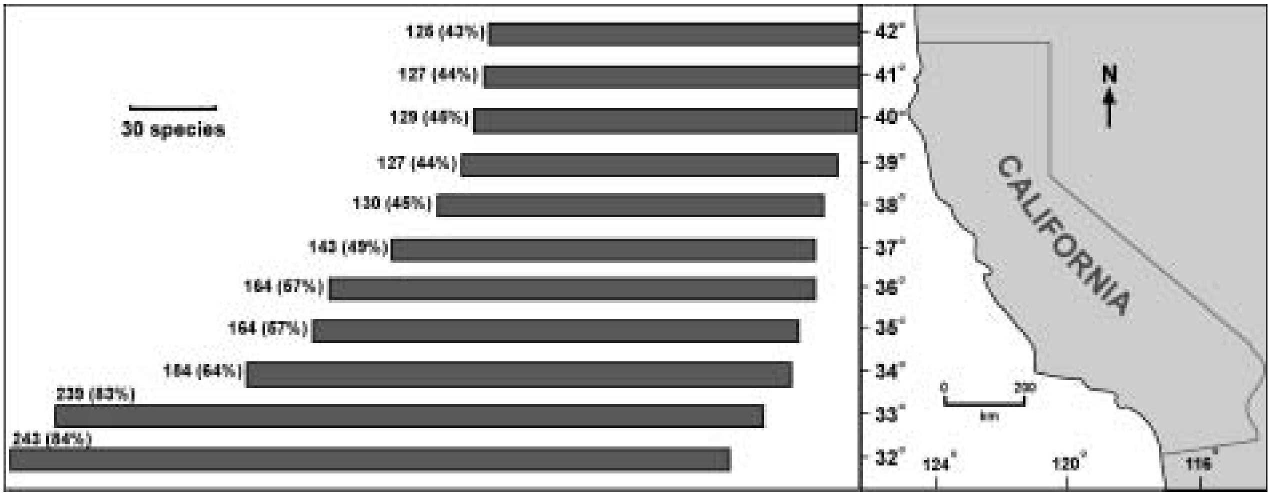

FIGURE 1-6 Number and compositional pattern of fish species occurring at each degree of latitude in California. The data were analyzed by principal coordinates analysis with ordination of species by latitude. The length of the rectangle (to the left of the map) represents the ordered list of 289 non-bay-occurring species (see Appendix 2). The length and position of the bar for each degree of latitude represent the number and composition, respectively, of fish species relative to the ordered list. The numbers at the left end of each bar are the number and percentage of species for that degree of latitude. (Further explanation in the text.)

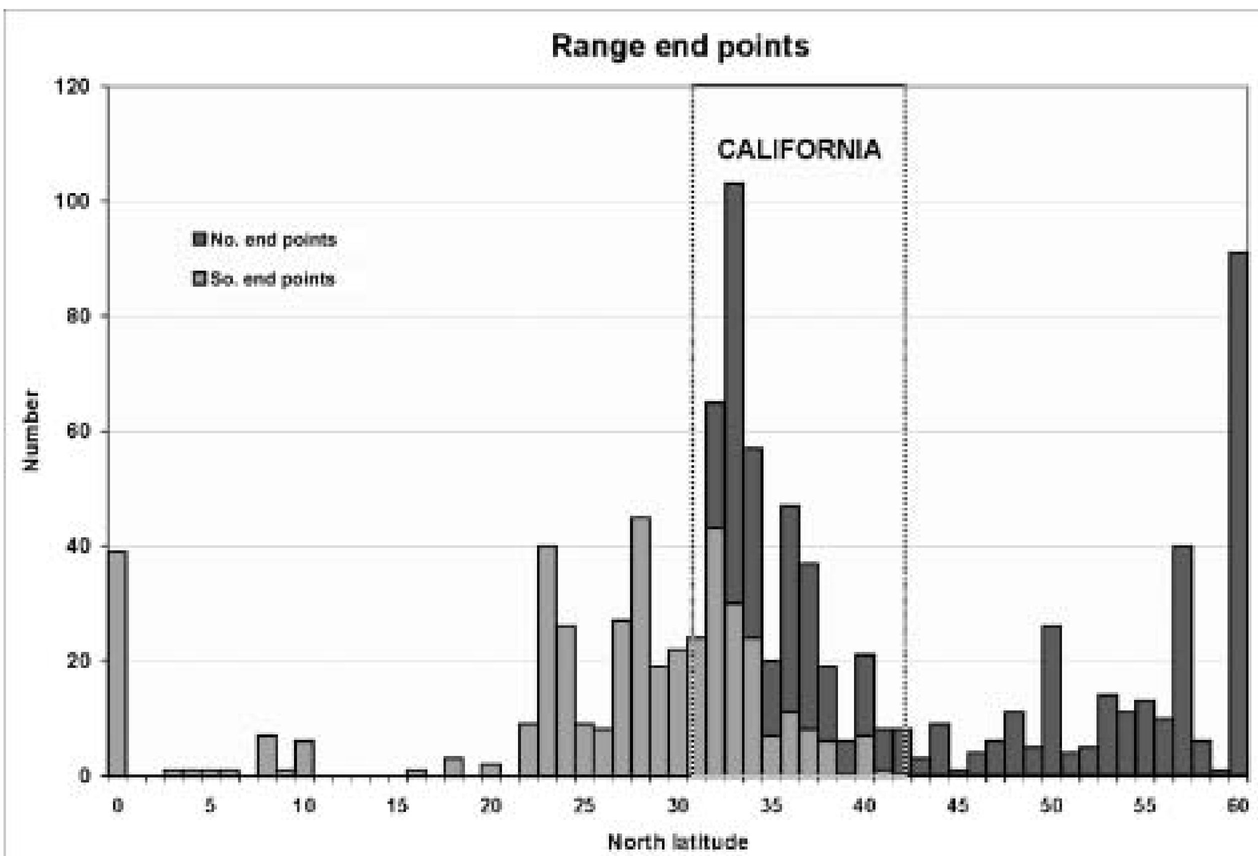

FIGURE 1-7 Frequency of northern and southern end points of geographic ranges of 519 California coastal fish species at each degree of latitude over the total distributional range (0° and south to ≥ 60°N). The bars representing the numbers of northern and southern end points originate at the basal line.

TABLE 1-2

The Top 11 Latitudes for Occurrence of Southern Range End Points

Latitude °S	*Number of Range End Points*	*% of Total*	*Geographic Area*
28	45	8.7	Central Baja California
32	43	8.3	Southern California
23	40	7.7	Southern Baja California
(10)	40	7.7	Peru
0 equator	39	7.5	Ecuador
33	30	5.8	Southern California
27	27	5.2	Central Baja California
(30)	26	5.0	Central Chile
24	26	5.0	Southern Baja California
34	24	4.6	Point Conception (Central California)
31	24	4.6	Northern Baja California
		Total 70.1%	

NOTE: Ranked by the number and percentage of end points at each latitude for California Marine Fish Fauna (519 species).

TABLE 1-3

The Top 10 Latitudes for Occurrence of Northern Range End Points

Latitude °N	*Number of Range End Points*	*% of Total*	*Geographic Area*
≥60	91	17.5	Alaska
33	73	14.1	Southern California
57	40	7.7	Alaska
36	36	6.9	Monterey Bay (central California)
34	33	6.4	Point Conception (central California)
37	29	5.6	Central California
50	26	5.0	Southern British Columbia
32	22	4.2	Southern California
53	14	2.7	Central British Columbia
40	14	2.7	Northern California
		Total 72.8%	

NOTE: Ranked by the number and percentage of end points at each latitude for California Marine Fish Fauna (519 species).

TABLE 1-4

Comparison of Results from Horn and Allen (1978) and the Present Study for three Distributional Analyses

Analysis	*Horn and Allen (1978)*	*Present study*
Clustering of bay-occurring species	Greatest dissimilarity between southern California bays and those to the north	Greatest dissimilarity between southern California bays and those to the north
Ordination of non-bay-occurring species	82% of species at 33°N 81% of species at 34°N 55% of species at 36°N	84% at this latitude 83% at this latitude 57% at this latitude
Range end points	Number of northern end points not correlated significantly with minimum sea surface temperature	Number significantly correlated

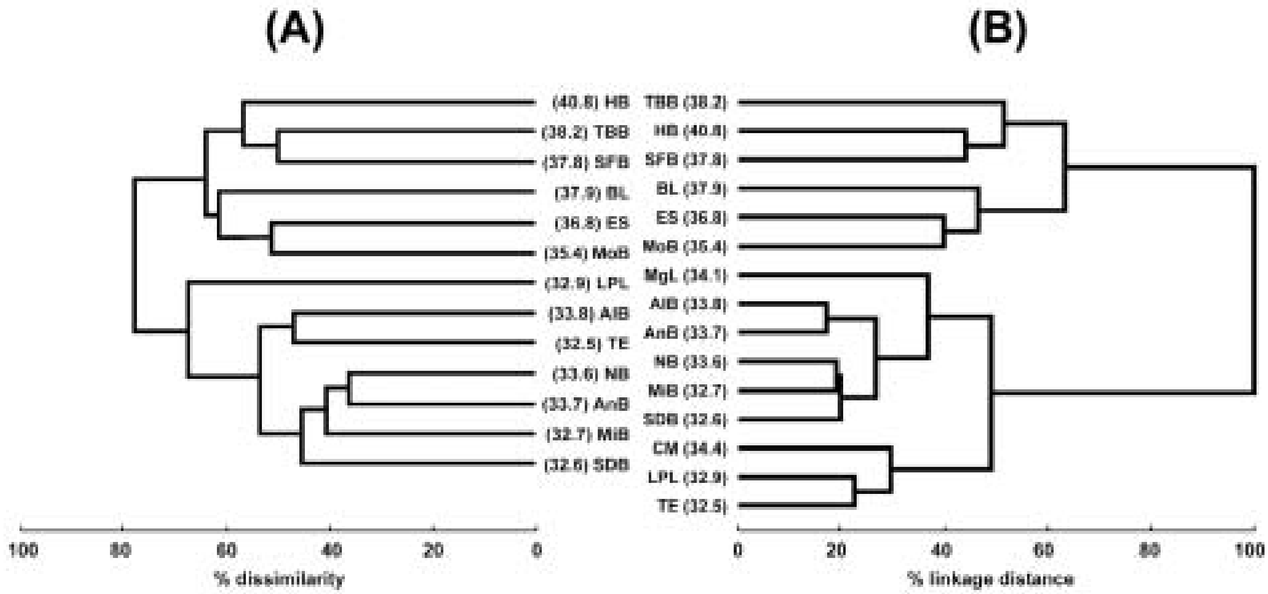

FIGURE 1-8 Visual comparison of the dendrograms for (A) 224 bay-occurring species from 13 bays in the Horn and Allen (1978) analysis and (B) 225 bay-occurring species from 15 bays in the present study. (See fig. 1-5 and the text for details.)

for both mollusks and marine algae and describes the Los Angeles region in this latitudinal interval as marked by several physical discontinuities of probable ancient origin. The second difference is that the current analysis demonstrates an overall northward shift in the fish fauna since the earlier analysis with the largest increase in proportions at two southern (32° and 33°) latitudes and one central (36°) California latitude (table 1-4); the latter is the second latitude of marked discontinuities for the California biota in Dawson's (2001) analysis. These increases appear to reflect mainly the additions to the fish fauna since the earlier study, additions that are composed almost entirely of southern, warmer water species (see table 1-1).

Analysis of Range End Points

The distribution of range end points clearly shows the mixture of southern (warm-water) and northern (cool-water) elements that characterizes the Californian fauna. The narrowly clustered and largely bimodal pattern of southern and northern range end points represents one way to illustrate this faunal mixture. Southern California, the part of the state with the highest species richness, contains about 16% of the total number of northern and southern range end points even though it covers mostly just 2° of latitude (32° and 33°). It is also the most heavily sampled area of our coastline. As Horn and Allen (1978) pointed out in the earlier analysis, numerous species with southern affinities end their ranges northward off southern California and southward off Baja California or much farther south, off South America. Furthermore, the earlier study showed that many species with northern affinities end their ranges northward off Alaska and British Columbia and southward off southern California and Baja California. A noticeable shift in distributional ranges, however, has apparently occurred within the fauna since the 1978 study because in that study, northern end points were not correlated significantly with minimum sea surface, temperature ($r = 0.49$, $p > .05$). In the present study, this relationship was found to be significant ($r = 0.62$, $p = .040$; see Results), indicating some northward shift in the fish fauna since the earlier analysis (table 1-4). Thus, this change based on range end points represents the second part of the current distributional analysis that provides evidence for a northward shift in distributions (table 1-4). As already discussed above, the change in proportions of fish species occurring per degree of latitude in the ordination analysis also appear to reflect the addition of new species to the fauna, mainly of southern, warm-water fishes, and the expansion northward of certain elements of the fauna in a scenario of warming coastal waters.

Summary Based on a Climate Perspective

Distributional patterns are increasingly seen as dynamic entities that shift with climate change occurring at different temporal and spatial scales. Temperature has long been recognized as a major factor influencing the distributions of marine organisms. Collections from both Pleistocene fossil (Fitch, 1967) and Holocene archaeological (Gobalet, 2000) sites support the relationships between distribution and temperature for California coastal fishes as does information from historical times, e.g., the nineteenth and twentieth centuries (Hubbs and Schultz, 1929; Hubbs, 1948, 1960). The northward shifts in distribution of fishes as a result of warm-water intervals off the California coast have been known at least since the 1950s, for example, when Radovich (1961) documented the effects of the increased ocean temperatures of 1957 to 1959 on fish and invertebrate distributions. More recently, as ENSO cycles have become more thoroughly understood and recorded, their impacts on the distributions of California fishes have become increasingly appreciated. For example, the effects of the strong 1997–1998 El Niño condition have been well documented (Lea and Rosenblatt, 2000; Pondella and Allen, 2001) and included some remarkable additions of subtropical fishes to the California fish fauna, including, for example, the loosetooth parrotfish (Lea et al., 2001) and Pacific cornetfish (Curtis and Herbinson, 2001).

Many of these added species are included in the analyses in the present study, as shown in table 1-1. The zebraperch (*Hermosilla azurea*) is an example of a species that temporarily extended its range northward during short-term periods of ocean warming associated with El Niño conditions but increased in abundance and established breeding populations in the Southern California Bight only after the sustained warming trend in the region over the last quarter of the twentieth century (Sturm and Horn, 2001).

Periods of sustained climate conditions are better understood now because of the recognition of intervals intermediate between ENSO cycles of a few years' duration and continued global warming trends. These intermediate-length periods of climatic conditions have been labeled Pacific Decadal Oscillations and are associated with shifts in ecosystem production regimes in cycles of about 50-year duration (Mantua et al., 1997; Zhang et al., 1997). Because these climate regime shifts seem remarkably similar to changes in biological conditions, Hare and Mantua (2000) suggested that a regime shift may best be determined by monitoring marine organisms rather than climate. In this regard, Chavez et al. (2003) labeled the alternating 20–30 year periods of cool then warm periods in the Pacific as "anchovy" and "sardine" regimes, respectively, because the abundance of northern anchovy and Pacific sardine fluctuate in association with large-scale changes in Pacific Ocean temperatures. These authors identified the period of 1976 to about 1998 as a warm or sardine regime and the previous 25-year period (1950–1975) as a cool or an anchovy regime. Thus, the temporal and spatial resolution for associating biological and oceanographic conditions has increased greatly in the last 50 years and has led to finer scale recognition and prediction of the effects of climate change on marine organisms (e.g., Fields at al., 1993; Roemmich and McGowan, 1995; McFarlane et al., 2000; Fiedler, 2002). Our analyses in the present study showing additions to the California fish fauna mainly from the south and suggesting an overall shift northward in the fauna as a whole seem consistent with climatic shifts occurring over different temporal scales but driven largely by an overarching warming trend.

Recommendation for Future Studies

Several types of investigations are needed if we are to deepen our understanding of distributional patterns and to improve our powers to predict the effects of climate change on coastal fish biogeography. New approaches to biogeographic analysis strengthen the prospects for greater resolution and understanding of fish distributions. The variety of techniques and knowledge stores now focused on ocean change on different spatial and temporal scales promises to enhance our assessment and prediction of the effects of climate dynamics on marine ecosystems in general and fish populations in particular. Here are some types of studies that seem worthy of undertaking in the future:

1. Continue ongoing long-term studies of fish distributions in California coastal waters in relation to oceanographic and atmospheric conditions and institute new such studies as appropriate. Investigations could be directed toward key indicator species (e.g., highly responsive species such northern anchovy and Pacific sardine) or the composition and structure of whole communities (e.g., estuaries, kelp beds, coastal soft bottoms). The phylogenetic perspective should be incorporated increasingly into distributional analyses of California fish species as our knowledge of phylogenetic relationships of the faunal elements continues to expand.
2. Combine traditional biogeography with phylogeography and macroecology to form a highly integrated approach to understand more deeply and to predict more accurately the factors controlling shifts in the abundance and distribution of coastal fish species. Applying the thermogeographic method also may become a reality in the future.
3. Analyze fishes in end-point areas to discover the basis for their range terminations, perhaps as related to recruitment patterns or settlement requirements. For example, what are the biotic and abiotic conditions in the Los Angeles and Monterey Bay regions that result in so many species apparently ending their distributions in those locations?
4. Compare distributional shifts of fishes with those of seaweeds and macroinvertebrates to determine the relative importance of different environmental and climatic factors on their ranges and therefore to increase the power of predicting change in entire ecosystems.

Literature Cited

Adey, W.H., and R.S. Steneck. 2001. Thermogeography over time creates biogeographic regions: a temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. J. Phycol. 37:677–698.

Allen, M.J. 1976. Addition of *Citharichthys fragilis* Gilbert to the California fauna. Calif. Fish Game 62:299–303.

Allen, M.J., and G.B. Smith. 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. NOAA Tech. Rept. NMFS 66, Seattle, WA.

Avise, J.C. 2000. Phylogeography, the history and formation of species. Harvard University Press, Cambridge, MA.

Bernardi, G. 2000. Barriers to gene flow in *Embiotoca jacksoni*, a marine fish lacking a pelagic larval stage. Evolution 54:226–237.

Blackburn, T.M., and K.J. Gaston. 2002. Scale in macroecology. Global Ecol. Biogeogr. 11:185–189.

Bograd, S.J., P.M. DiGiacomo, R. Durazo, T.L. Hayward, K.D. Hyrenbach, R.L. Lynn, A.W. Mantyla, F.B. Schwing, W.J. Sydeman, T. Baumgartner, B. Lavaniegos, and C.S. Moore. 2000. The state of the California Current, 1999–2000: forward to a new regime? Calif. Coop. Ocean. Fish. Invest. Rep. 41:26–52.

Briggs, J.C. 1974. Marine zoogeography. McGraw-Hill, New York.

———. 2002. New species of *Rimicola* from California. Copeia 2002:441–444.

Brooks, A.J. 1987. Two species of Kyphosidae seen in King Harbor, Redondo Beach, California. Calif. Fish Game 73(1):49–61.

Brown, J.H. 1995. Macroecology. University of Chicago Press, Chicago, IL.

Brown, J.H., and M.V. Lomolino. 1988. Biogeography. 2d ed. Sinauer, Sunderland, MA.

Brusca, R.C., and B.R. Wallerstein. 1979. Zoogeographic patterns of idoteid isopods in the northeast Pacific, with a review of shallow water zoogeography of the area. Bull. Biol. Soc. Wash. No. 3:67–105.

Chavez, F.P., J. Ryan, S.E. Lluch-Cota, and M. Ñiquen C. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299:217–221.

Crooke S.J. 1973. The first occurrence of *Kyphosus analogus* in California. Calif. Fish Game 59:310–311.

Curtis, M.D., and K.T. Herbinson. 2001. First record of the Pacific cornetfish, *Fistularia corneta* Gilbert and Starks 1904, a new species to the southern California fauna during the 1997–1998 El Niño. Bull. South Calif. Acad. Sci. 100:156–159.

Dawson, M.N. 2001. Phylogeography in coastal marine animals: a solution for California? J. Biogeogr. 28:723–736.

Dawson, M.N., J.L. Staton, and D.K. Jacobs. 2001. Phylogeography of the tidewater goby, *Eucyclogobius newberryi* (Teleostei: Gobiidae), in coastal California. Evolution 55:1167–1179.

Durazo, R., T.R. Baumgartner, S.J. Bograd, C.A. Collins, S. Campa, J. Garcia, G. Gaxiola-Castro, et al. 2001. The state of the California Current, 2000–2001: a third straight La Niña year. Calif. Coop. Ocean. Fish. Invest. Rep. 42:29–60.

Eber, L.E., J.F.T. Sauer, and O.E. Sette. 1968. Monthly mean charts of sea surface temperature, North Pacific Ocean 1949–62. U. S. Fish Wildlife Service Circular 258.

Eschmeyer, W.N., E.S. Harold, and H. Hammann. 1983. A field guide to Pacific Coast fishes of North America from the Gulf of Alaska to Baja California. Houghton Mifflin, Boston, MA.

Fiedler, P.C. 2002. Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. Mar. Ecol. Prog. Ser. 244:265–283.

Fields, P.A., J.B. Graham, R.H. Rosenblatt, and G.N. Somero. 1993. Effects of expected global climate change on marine faunas. Trends Ecol. Evol. 8:361–367.

Fitch, J.E. 1967. The marine fish fauna, based primarily on otoliths, of a lower Pleistocene deposit at San Pedro, California (LACMIP 332, San Pedro Sand). Los Angeles County Mus. Contrib. Sci. 128.

———. 1973. The longnose puffer, *Sphoeroides lobatus* (Steindachner), added to the marine fauna of California. Bull. South Calif. Calif. Acad. Sci. 72:163.

Fitch, J.E., and S.A. Schultz. 1978. Some rare and unusual occurrences of fishes off California and Baja California. Calif. Fish Game 64:74–92.

Gobalet, K.W. 2000. Has Point Conception been a marine zoogeographic boundary throughout the Holocene? Evidence from the archaeological record. Bull. South. Calif. Acad. Sci. 99:32–44.

Hare, S.R., and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. 47:103–145.

Hart, J.L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Bd. Canada 180.

Hastings, P.A. 2000. Biogeography of the Tropical Eastern Pacific: distribution and phylogeny of chaenopsid fishes. Zool. J. Linn. Soc. 128:319–335.

Hayden, B.P., and R. Dolan. 1976. Coastal marine fauna and marine climates of the Americas. J. Biogeogr. 3:71–81.

Horn, M.H., and L.G. Allen. 1976. Number of species and faunal resemblance of marine fishes in California bays and estuaries. Bull. South. Calif. Acad. Sci. 75:159–170.

———. 1978. A distributional analysis of California coastal marine fishes. J. Biogeogr. 5:23–42.

Houghton, J. 2002. An overview of the Intergovernmental Panel on Climate Change (IPCC) and its process of science assessment, pp. 1–20. In: Issues in environmental science and technology 17, Global environmental change, R.E. Hester and R.M. Harrison (eds.). Royal Society of Chemistry, Cambridge, UK.

Hubbs, C.L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. J. Mar. Res. 7:459–482.

———. 1960. The marine vertebrates of the outer coast. Syst. Zool. 9:134–147.

———. 1974. Review, Marine zoogeography by J.C. Briggs. Copeia 1974:1002–1005.

Hubbs, C.L., and L.P. Schultz. 1929. The northward occurrence of southern forms of marine life along the Pacific Coast in 1926. Calif. Fish Game 15:234–241.

Kousky, V.E., and G.D. Bell. 2000. Causes, predictions, and outcomes of El Niño 1997–1998, pp. 28–48. In: El Niño 1997–1998. The climate event of the century, S.A. Changnon (ed.). Oxford University Press, Oxford, UK.

Lea, R.N. 1974. First record of Puget Sound sculpin, *Artedius meanyi*, from California. J. Fish. Res. Bd. Canada 31:1242–1243.

Lea, R.N., E. Erikson, K. Boyle, and R. Given. 2001. Occurrence of the loosetooth parrotfish, *Nicholsina denticulata* (Scaridae), from Santa Catalina Island, California. Bull. South Calif. Acad. Sci. 100: 167–169.

Lea, R.N., and R.H. Rosenblatt. 2000. Observations on fishes associated with the 1997–98 El Niño off California. Calif. Coop. Ocean. Fish. Invest. Rep. 41:117–129.

Lea, R.N., and H.J. Walker, Jr. 1995. Record of the bigeye trevally, *Caranx sexfasciatus*, and Mexican lookdown, *Selene brevoorti*, with notes on other carangids from California. Calif. Fish Game 81:89–95.

Leis, J.M. 1978. Systematics and zoogeography of the porcupinefishes (*Diodon*, Diodontidae, Tetraodontiformes), with comments on egg and larval development. Fish. Bull. 76:535–567.

Lynn, R.J., and S.J. Bograd. 2002. Dynamic evolution of the 1997–1999 El Niño–La Niña cycle in the southern California Current system. Prog. Oceanogr. 54:59–75.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bull. Am. Meteorol. Soc. 78:1069–1079.

McFarlane, G.A., J.R. King., and R.J. Beamish. 2000. Have there been recent changes in climate? Ask the fish. Prog. Oceanogr. 47:147–169.

McGowan, J.A. 1971. Oceanic biogeography of the Pacific, pp. 3–74. In: The micropaleontology of oceans, B.M. Funnell and W.R. Riedel (eds.). Cambridge University Press, Cambridge, UK.

Miller, D.J., and R.N. Lea. 1972. Guide to coastal marine fishes of California. Calif. Dep. Fish Game Fish Bull. 157.

———. 1976. Guide to coastal marine fishes of California. Calif. Dep. Fish Game Fish Bull. 157 (with addendum to 1972 edition).

Murray, S.N., and M.M. Littler. 1981. Biogeographical analysis of intertidal macrophyte floras of southern California. J. Biogeogr. 8: 339–351.

Pondella, D.J. II, and M.J. Allen (eds.). 2001. Proceedings of special symposium: new and rare fish and invertebrate species to California during the 1997–1998 El Niño. Bull. South Calif. Acad. Sci. 100:129–130.

Pondella, Daniel J., II, and M.T. Craig. 2001. First record of the sabertooth blenny, *Plagiotremus azaleus,* in California with notes on its distribution along the Pacific coast of Baja California. Bull. South. Calif. Acad. Sci. 100:144–148.

Radovich, J. 1961. Relationships of some marine organisms of the Northeast Pacific to water temperatures. Calif. Dep. Fish Game Fish Bull. 112.

Roemmich, D., and J.A. McGowan. 1995. Climate warming and the decline of zooplankton in the California Current. Science 267:1324–1326.

Rounds, J.M., and R.F. Feeney. 1993. First record of the tripletail (*Lobotes surinamensis*, family Lobotidae) in California waters. Calif. Fish Game 79:167–168.

Smith, K.F., and J.H. Brown. 2002. Patterns of diversity, depth range and body size among pelagic fishes along a gradient of depth. Global Ecol. Biogeogr. 11:313–322.

Smith, P.E. 1995. A warm decade in the Southern California Bight. Calif. Coop. Ocean. Fish. Invest. Rep. 36:120–126.

Smith, R.W. 1976. Numerical analysis of ecological survey data. Unpubl. Ph.D. Diss. University of Southern California, Los Angeles.

SCCWRP (Southern California Coastal Water Research Project). 1973. The ecology of the Southern California Bight: Implications for water quality management. Tech. Rep. 104, El Segundo, CA.

Stepien, C.A., and R.H. Rosenblatt. 1991. Patterns of gene flow and genetic divergence in the northeastern Pacific Clinidae (Teleostei: Blennioidei), based on allozyme and morphological data. Copeia 1991:863–896.

Sturm, E.A., and M.H. Horn. 2001. Increase in occurrence and abundance of zebraperch (*Hermosilla azurea*) in the Southern California Bight in recent decades. Bull. South. Calif. Acad. Sci. 100:170–174.

Valentine, J.W. 1966. Numerical analysis of marine molluscan ranges on the extratropical northeastern Pacific shelf. Limnol. Oceanogr. 11:198–211.

Zhang, Y., J.M. Wallace, and D. S. Battisti. 1997. ENSO-like interdecadal variability: 1900–93. J. Climate 10:1004–1020.

Appendix 1-1. California coastal fish species

This list of 519 California Coastal fish spercies used in the present study gives their southern and northern latitudinal range limits. See fig. 1-7.

	South Lat.	North Lat.		South Lat.	North Lat.
Pholis laeta	41	60	*Zenopsis nebulosa*	34	37
Agonus acipenserinus	40	64	*Ernogrammus walkeri*	34	36
Asterotheca infraspinata	40	60	*Plagiogrammus hopkinsii*	34	36
Bathygonus nigripinnis	40	60	*Radulinus vinculus*	34	34
Chirolophus decoratus	40	60	*Alopias superciliosus*	33	60
Delolepis gigantea	40	60	*Ammodytes hexapterus*	33	60
Lumpenus sagitta	40	60	*Atheresthes stomias*	33	60
Lyconectes aleutensis	40	60	*Hippoglossus stenolepis*	33	60
Thaleichthys pacificus	38	60	*Hypomesus pretiosus*	33	60
Pallisina barbata	38	58	*Oncorhynchus nerka*	33	60
Sebastes reedi	38	57	*Phytichthys chirus*	33	60
Anoplarchus insignis	38	54	*Psettichthys melanostictus*	33	60
Artedius meanyi	38	50	*Rhamphocottus richardsonii*	33	60
Pholis clemensi	38	50	*Sebastes brevispints*	33	60
Hippoglossoides elassodon	37	60	*Sebastes caurinus*	33	60
Lampetra ayresii	37	60	*Sebastes crameri*	33	60
Liparis rutteri	37	60	*Somniosus pacificus*	33	60
Oncorhynchus clarkii	37	60	*Apodichthys flavidus*	33	57
Spirinchus thaleichthys	37	60	*Chirolophus nugator*	33	57
Trichodon trichodon	37	60	*Oligocottus maculosus*	33	57
Occella verrucosa	37	58	*Hemilepidotus spinosus*	33	56
Ascelichthys rhodorus	37	56	*Radulinus boleoides*	33	54
Liparis pulchellus	36	60	*Oligocottus rimensis*	33	53
Pholis ornata	36	60	*Sebastes melanops*	33	51
Ronquilus jordani	36	60	*Allosmerus elongatus*	33	48
Theragra chalcogramma	36	60	*Xeneretmus leiops*	33	48
Enophrys bison	36	57	*Euprotomicrus bispinatus*	33	40
Erilepis zonifer	36	57	*Oligocottus rubellio*	33	39
Hemilepidotus hemilepidotus	36	57	*Enophrys taurus*	33	37
Sebastes borealis	36	57	*Sebastes phillipsi*	33	37
Zaprora silenus	36	55	*Icelinus fimbriatus*	33	36
Clinocottus acuticeps	36	52	*Rimicola cabrilloi*	33	34
Amphisticus rhodoterus	36	50	*Clupea harengus*	32	65
Pleurogrammus monopterygius	35	60	*Asterotheca pentacantha*	32	60
Scytalina cerdale	35	60	*Bathyraja interrupta*	32	60
Sebastes nigrocinctus	35	60	*Lamna ditropis*	32	60
Bothragonus swanii	35	57	*Lepidopsetta bilineata*	32	60
Liparis fucensis	35	57	*Lycenchelus crotalinus*	32	60
Pholis schultzi	35	49	*Lycodapus fierasfer*	32	60
Blepsias cirrhosus	35	41	*Lycodes diapterus*	32	60
Platichthys stellatus	34	68	*Oncorhynchus gorbuscha*	32	60
Allocyttus folletti	34	60	*Oncorhynchus keta*	32	60
Chlamydoselachus anguineus	34	60	*Oncorhynchus tshawytscha*	32	60
Gadus macrocephalus	34	60	*Poroclinus rothrocki*	32	60
Hexagrammus superciliosus	34	60	*Raja stellulata*	32	60
Isopsetta isolepis	34	60	*Reinhardtius hippoglossoides*	32	60
Liparis florae	34	60	*Sebastes alutus*	32	60
Lycodapus mandibularis	34	60	*Sebastes proriger*	32	60
Sebastes maliger	34	60	*Sebastes ruberrimus*	32	60
Spirinchus starksi	34	58	*Sebastes flavidus*	32	59
Xiphister mucosus	34	58	*Agonopsis vulsa*	32	57
Anoplarchus purpurescens	34	57	*Anarrhichthys ocellatus*	32	57
Artedius harringtoni	34	57	*Icosteus aenigmaticus*	32	57
Clinocottus globiceps	34	57	*Radulinus asprellus*	32	57
Sebastes nebulosus	34	57	*Sebastes helvomaculatus*	32	57
Synchirus gilli	34	56	*Sebastes entomelas*	32	57
Nautichthys oculofasciatus	34	55	*Sebastes wilsoni*	32	57
Artedius fenestralis	34	54	*Icelinus burchami*	32	56
Microgadus proximus	34	54	*Hexagrammus decagrammus*	32	55
Jordania zonope	34	50	*Plectobranchus evides*	32	55

Appendix 1-1. (continued)

	South Lat.	North Lat.		South Lat.	North Lat.
Careproctus melanurus	32	54	*Ophiodon elongatus*	29	57
Icelinus filamentosus	32	54	*Sebastes paucispinis*	29	57
Paricelinus hopliticus	32	54	*Thunnus alalunga*	29	57
Sebastes zacentrus	32	54	*Rhacochilus vacca*	29	56
Melanostigma pammelas	32	53	*Gobiesox maeandricus*	29	55
Sebastes aleutianus	32	53	*Oxylebius pictus*	29	54
Lycodes cortezianus	32	52	*Hyperprosopon ellipticum*	29	50
Sebastes babcocki	32	52	*Liparis mucosus*	29	50
Bothrocara brunneum	32	50	*Xererpes fucorum*	29	49
Icelinus oculatus	32	50	*Stellerina xyosterna*	29	48
Morone saxatilus	32	49	*Hyperprosopon anale*	29	44
Eucyclogobius newberryi	32	48	*Sebastes rufus*	29	42
Neoclinus uninotatus	32	38	*Orthonopias triacis*	29	37
Sebastes lentiginosus	32	33	*Sebastes hopkinsi*	29	37
Acipenser medirostris	31	60	*Sebastes simulator*	29	36
Acipenser transmontanus	31	60	*Gobiesox eugrammus*	29	33
Clinocottus embryum	31	60	*Sebastes diploproa*	28	61
Oncorhynchus mykiss	31	60	*Anoplopoma fimbria*	28	60
Sebastes mystinus	31	60	*Eopsetta jordani*	28	60
Lycodes pacificus	31	58	*Eptatretus deani*	28	60
Brosmophycis marginata	31	57	*Glyptocephalus zachirus*	28	60
Pleuronichthys coenosus	31	57	*Hydrolagus colliei*	28	60
Xipister atropurpureus	31	57	*Pleuronichthys decurrens*	28	60
Embiotoca lateralis	31	56	*Raja binoculata*	28	60
Sebastes pinniger	31	56	*Raja rhina*	28	60
Hexanchus griseus	31	55	*Sebastes elongatus*	28	60
Bothrocara molle	31	53	*Sebastolobus alascanus*	28	60
Gibbonsia montereyensis	31	53	*Odontopyxis trispinosa*	28	57
Zesticelus profundorum	31	53	*Syngnathus leptorhynchus*	28	57
Rimicola muscarum	31	52	*Tetragonurus cuvieri*	28	55
Phanerodon furcatus	31	50	*Icelinus tenuis*	28	53
Rathbunella hypoplecta	31	50	*Torpedo californica*	28	53
Sebastes ovalis	31	42	*Lyopsetta exilus*	28	51
Hypsurus caryi	31	40	*Hyperprosopon argenteum*	28	50
Lethops connectens	31	36	*Lepidogobius lepidus*	28	50
Ulvicola sanctaerosae	31	36	*Seabastes miniatus*	28	50
Anchoa compressa	31	35	*Sebastes aurora*	28	50
Leicottus hirundo	31	34	*Raja inornata*	28	48
Antimora microlepis	30	60	*Seabastes melanostomus*	28	47
Oncorhynchus kisutch	30	60	*Sebastes chlorosticus*	28	47
Sebastes rubrivinctus	30	60	*Atherinopsis californiensis*	28	44
Oligocottus snyderi	30	57	*Sebastes rastrelliger*	28	44
Cymatogaster aggregata	30	56	*Sebastes levis*	28	42
Leptocottus armatus	30	56	*Nezumia stelgidolepis*	28	41
Artedius lateralis	30	55	*Sebastes serranoides*	28	41
Xeneretmus triacanthus	30	52	*Amphisticus argenteus*	28	38
Apristurus brunneus	30	51	*Micrometrus minimus*	28	38
Xenertmus latifrons	30	49	*Oxyjulis californica*	28	38
Artedius corallinus	30	48	*Phanerodon atripes*	28	38
Artedius notospilotus	30	48	*Synodus lucioceps*	28	38
Sebastes jordani	30	48	*Neoclinus blanchardi*	28	37
Seriola lalandi	30	47	*Platyrhinoides triseriatus*	28	37
Lyconema barbatum	30	42	*Sebastes ensifer*	28	37
Cebidichthys violaceus	30	41	*Sebastes eos*	28	37
Gasterosteus aculeatus	30	60	*Sebastes rosenblatti*	28	37
Stereolepis gigas	30	40	*Sebastes serriceps*	28	37
Micrometrus aurora	30	38	*Ophidion scrippsae*	28	34
Sphyrna zygaena	30	37	*Rimicola dimorpha*	28	34
Sebastes gilli	30	36	*Xeneretmus ritteri*	28	34
Cryptotrema corallinum	30	34	*Tenogobius sagittula*	28	32
Lampetra tridentata	29	61	*Eptatretus stoutii*	27	60
Coryphaenoides acrolepis	29	60	*Aulorhynchus flavidus*	27	57
Bathyraja trachura	29	60	*Icichthys lockingtoni*	27	57

Appendix 1-1. (continued)

	South Lat.	North Lat.		South Lat.	North Lat.
Sebastes saxicola	27	57	*Hypsoblennius gilberti*	24	34
Rhinogobiops nicholsii	27	53	*Paraclinus integripinnis*	24	34
Alopias vulpinus	27	50	*Porichthys myriaster*	24	34
Brachyistius frenatus	27	50	*Anchoa delicatissima*	24	33
Gibbonsia metzi	27	50	*Odontaspis ferox*	24	33
Sbastes rosaceus	27	48	*Cetorhinus maximus*	23	60
Chilara taylori	27	45	*Citharichthys sordidus*	23	60
Zaniolepis frenata	27	43	*Citharichthys stigmaeus*	23	60
Zaniolepis latipinnis	27	43	*Lampris guttatus*	23	60
Clinocottus recalvus	27	42	*Microstomus pacificus*	23	60
Sebastes carnatus	27	42	*Parophrys vetulus*	23	60
Sebastes chrysomelas	27	40	*Sardinops sagax*	23	55
Clinocottus analis	27	39	*Sebastolobus altivelis*	23	55
Rhacochilus toxotes	27	39	*Engraulis mordax*	23	53
Sebastes atrovirens	27	38	*Atherinops affinis*	23	50
Zalembius rosaceus	27	38	*Clevelandia ios*	23	50
Sebastes dallii	27	37	*Argentina sialis*	23	44
Sebastes semicinctus	27	37	*Myliobatis californica*	23	44
Chromis punctipinnis	27	36	*Triakis semifasciata*	23	43
Neoclinus stephensae	27	36	*Medialuna californiensis*	23	41
Ruscarius creaseri	27	36	*Lepidopus fitchi*	23	40
Agonopsis sterletus	27	35	*Mustelus californicus*	23	40
Gobiesox rhessodon	27	35	*Mustelus henlei*	23	40
Alloclinus holderi	27	34	*Cosmocampus arctus*	23	38
Squalus acanthias	26	60	*Gillichthys mirabilis*	23	38
Sebastes auriculatus	26	57	*Ilypnus gilberti*	23	38
Scorpaenichthys marmoratus	26	56	*Rhinobatos productus*	23	37
Galeorhinus galeus	26	55	*Hermosilla azurea*	23	36
Amphisticus koelzi	26	48	*Hippoglossina stomata*	23	36
Embiotoca jacksoni	26	39	*Hypsoblennius gentilis*	23	36
Sebastes umbrosus	26	37	*Lythrypnus dalli*	23	36
Rimicola eigenmanni	26	33	*Paralabrax maculatofasciatus*	23	36
Chitonotus pugetensis	25	54	*Parmaturus xaniurus*	23	36
Bathyraja abyssicola	25	54	*Scomberomorus concolor*	23	36
Paralichthys californicus	25	50	*Xystreurys liolepis*	23	36
Peprilus simillimus	25	49	*Quietula y-cauda*	23	35
Seriphus politus	25	44	*Gnathophis cinctus*	23	34
Hypsopsetta guttulata	25	40	*Halichoeres semicinctus*	23	34
Pleuronichthys verticalis	25	37	*Menticirrhus undulatus*	23	34
Pleuronichthys ritteri	25	35	*Roncador stearnsii*	23	34
Typhlogobius californiensis	25	35	*Umbrina roncador*	23	34
Gymnothorax mordax	25	34	*Apogon guadalupensis*	23	33
Merluccius productus	24	60	*Cynoscion parvipinnis*	23	33
Squatina californica	24	60	*Hyporhamphus rosae*	23	33
Atractoscion nobilis	24	58	*Mycteroperca jordani*	23	32
Trachurus symmetricus	24	57	*Porichthys notatus*	22	57
Notorhynchus cepedianus	24	53	*Sphyraena argentea*	22	57
Sebastes goodei	24	51	*Heterostichus rostratus*	22	53
Genyonemus lineatus	24	50	*Cheilopogon pinnatibarbatus*	22	46
Paralabrax clathratus	24	46	*Symphurus atricauda*	22	41
Sebastes constellatus	24	40	*Icelinus quadriseriatus*	22	38
Anisotremus davidsonii	24	34	*Girella nigricans*	22	37
Leuresthes tenuis	24	37	*Semicossyphus pulcher*	22	37
Paralabrax nebulifer	24	37	*Hemianthias signifer*	22	33
Scorpaena guttata	24	37	*Cololabis saira*	20	60
Syngnathus californiensis	24	37	*Chaenopsis alepidota*	20	34
Heterodontus francisci	24	36	*Lythypnus zebra*	18	36
Hypsypops rubicundus	24	36	*Carcharhinus obscurus*	18	33
Icelinus cavifrons	24	36	*Carcharhinus longimanus*	18	32
Sebastes macdonaldi	24	36	*Hypsoblennius jenkinsi*	16	34
Fundulus parvipinnis	24	35	*Bathyraja spinosissima*	10	44
Gibbonsia elegans	24	35	*Citharichthys xanthostigma*	10	36
Cheilotrema saturnum	24	34	*Xanthichthys mento*	10	34

Appendix 1-1. (continued)

	South Lat.	North Lat.		South Lat.	North Lat.
Scorpaenodes xyris	10	33	*Carcharhinus leucas*	−5	33
Uraspis secunda	10	33	*Scomberomorus sierra*	−5	33
Zapteryx exasperata	9	33	*Caranx caballus*	−6	36
Physiculus rastrelliger	8	40	*Chaetodipterus zonatus*	−6	32
Urolobatus halleri	8	40	*Epinephelus niphobles*	−8	35
Albula vulpes	8	37	*Thunnus orientalis*	−10	57
Syngnathus auliscus	8	34	*Caulolatilus princeps*	−10	50
Gobiesox papillifer	8	33	*Katswonus pelamis*	−10	48
Mustelus lunulatus	8	33	*Lepidocybium flavobrunneum*	−10	47
Oligopus diagrammus	8	33	*Thunnus obesus*	−10	47
Hippocampus ingens	6	33	*Prionotus stephanophrys*	−10	46
Bellator xenisma	5	33	*Ophichthus triserialis*	−10	40
Melichthys niger	4	32	*Ophichthus zophochir*	−10	40
Decodon melasma	3	33	*Kathetostoma averruncus*	−10	39
Manta birostris	3	33	*Strongylura exilis*	−10	37
Selene brevoortii	2	32	*Echinorhinus cookei*	−10	36
Nicholsina denticulata	1	33	*Xenistius californiensis*	−10	36
Alepocephalus tenebrosus	0	60	*Elops affinis*	−10	34
Brama japonica	0	60	*Epinephelus analogus*	−10	34
Mola mola	0	55	*Fodiator acutus*	−10	34
Pteroplatytrygon violacea	0	50	*Gymnura marmorata*	−10	34
Pseudopentaceros wheeleri	0	50	*Pristigenys serrula*	−10	34
Lagocephalus lagocephalus	0	39	*Trachinotus rhodopus*	−10	34
Decapterus muroadsi	0	36	*Zalieutes elater*	−10	34
Desmodena lorum	0	36	*Antennarius avalonis*	−10	33
Mugil cephalus	0	36	*Auxis thazard*	−10	33
Naucrates ductor	0	36	*Carcharhinus brachyurus*	−10	33
Ruvettus pretiosus	0	36	*Chaetodon humeralis*	−10	33
Euthynnus lineatus	0	35	*Chloroscrombrus orqueta*	−10	33
Pteraclis aesticola	0	35	*Engyophrys sanctilaurentii*	−10	33
Mobula japanica	0	34	*Fistularia corneta*	−10	33
Lactoria diaphana	0	34	*Galeocerdo cuvier*	−10	33
Allothunnus fallai	0	33	*Lobotes pacificus*	−10	33
Assurger anzac	0	33	*Myrophis vafer*	−10	33
Bagre panamensis	0	33	*Nematistius pectoralis*	−10	33
Prognathodes falcifer	0	33	*Polydactylus opercularis*	−10	33
Chilomycterus reticulatus	0	33	*Rhizoprionodon longurio*	−10	33
Citarichthys fragilis	0	33	*Remora osteochir*	−10	33
Diplectrum maximum	0	33	*Selene peruviana*	−10	33
Echeneis naucrates	0	33	*Seriola rivoliana*	−10	33
Euleptorhamphus longirostris	0	33	*Sphyrna tiburo*	−10	33
Euthynnus affinis	0	33	*Trachinotus paitensis*	−10	33
Hemiramphus saltator	0	33	*Trichiurus nitens*	−10	33
Macroramphosus gracilis	0	33	*Harengula thrissina*	−10	32
Makaira indica	0	33	*Hyporhamphus naos*	−10	32
Makaira mazara	0	33	*Sphoeroides annulatus*	−10	32
Myxine circifrons	0	33	*Eucinostomus dowii*	−11	32
Phtheirichthys lineatus	0	33	*Polydactylus approximans*	−12	36
Plagiotremus azaleus	0	33	*Auxis rochei*	−12	33
Sphyraena ensis	0	33	*Calamus brachysomus*	−12	33
Synchiropus atrilabiatus	0	33	*Eucinostomus currani*	−12	33
Taractichthys steindachneri	0	33	*Kyphosus analogus*	−20	33
Zu cristatus	0	33	*Sphoeroides lobatus*	−20	33
Apogon pacificus	0	32	*Carcharodon carcharias*	−30	60
Caranx caninus	0	32	*Prionace glauca*	−30	60
Caranx vinctus	0	32	*Trachipterus altivelis*	−30	60
Cheilopogon heterurus	0	32	*Sarda chiliensis*	−30	57
Lophotus capellei	0	32	*Scomber japonicus*	−30	57
Rhincodon typus	0	32	*Remora australis*	−30	50
Dormitator latifrons	−2	33	*Coryphaena hippurus*	−30	47
Dasyatis dipterura	−5	50	*Isurus oxyrinchus*	−30	46
Mycteroperca xenarcha	−5	37	*Luvarus imperialis*	−30	44
Cetengraulis mysticetus	−5	34	*Xiphias gladius*	−30	44

Appendix 1-1. (continued)

	South Lat.	North Lat.		South Lat.	North Lat.
Tetrapturus angustirostris	−30	42	*Gempylus serpens*	−30	33
Balistes polylepis	−30	41	*Pseudupeneus grandisquamis*	−30	33
Remora remora	−30	37	*Regalecus glesne*	−30	33
Remora albescens	−30	37	*Trachipterus fukuzakii*	−30	33
Cephaloscyllium ventriosum	−30	36	*Caranx sexfasciatus*	−30	32
Etrumeus teres	−30	36	*Diodon holocanthus*	−30	32
Ranzania laevis	−30	35	*Diodon hystrix*	−30	32
Thunnus albacares	−30	35	*Istiophorus platypterus*	−30	32
Tetrapturus audax	−30	34	*Remora brachyptera*	−30	32

Appendix 1-2. Non-bay-occurring California fish species

This list of 289 non-bay occurring species is ordered by latitude according to principal coordinates analysis. See fig. 1.6 for pattern.

	Latitude (°N)									
	41	40	39	38	37	36	35	34	33	32
Pholis laeta	1									
Agonus acipenserinus	1	1								
Bathyagonus infraspinatus	1	1								
Bathyagonus nigripinnis	1	1								
Delolepis gigantea	1	1								
Lyconectes aleutensis	1	1								
Anoplarchus insignus	1	1	1	1						
Oncorhynchus nerka	1	1	1	1						
Pholis clemensi	1	1	1	1						
Sebastes reedi	1	1	1	1						
Hippoglossoides elassodon	1	1	1	1	1					
Oncorhynchus clarkii	1	1	1	1	1					
Erilepis zonifer	1	1	1	1	1	1				
Pleurogrammus monopterygius	1	1	1	1	1	1				
Ronquilus jordani	1	1	1	1	1	1				
Sebastes borealis	1	1	1	1	1	1				
Theragra chalcogramma	1	1	1	1	1	1				
Zaprora silenus	1	1	1	1	1	1				
Pholis schultzi	1	1	1	1	1	1	1			
Sebastes nigrocinctus	1	1	1	1	1	1	1			
Allocyttus folletti	1	1	1	1	1	1	1	1		
Chlamydoselachus anguineus	1	1	1	1	1	1	1	1		
Clinocottus globiceps	1	1	1	1	1	1	1	1		
Gadus macrocephalus	1	1	1	1	1	1	1	1		
Jordania zonope	1	1	1	1	1	1	1	1		
Lycodapus mandibularis	1	1	1	1	1	1	1	1		
Sebastes maliger	1	1	1	1	1	1	1	1		
Synchirus gilli	1	1	1	1	1	1	1	1		
Alopias superciliosus	1	1	1	1	1	1	1	1	1	
Oligocottus rimensis	1	1	1	1	1	1	1	1	1	
Oncorhynchus keta	1	1	1	1	1	1	1	1	1	
Phytichthys chirus	1	1	1	1	1	1	1	1	1	
Radulinus boleoides	1	1	1	1	1	1	1	1	1	
Rhamphocottus richardsonii	1	1	1	1	1	1	1	1	1	
Sebastes brevispinis	1	1	1	1	1	1	1	1	1	
Sebastes crameri	1	1	1	1	1	1	1	1	1	
Somniosus pacificus	1	1	1	1	1	1	1	1	1	
Xeneretmus leiops	1	1	1	1	1	1	1	1	1	
Agonopsis vulsa	1	1	1	1	1	1	1	1	1	1
Alepocephalus tenebrosus	1	1	1	1	1	1	1	1	1	1
Antimora microlepis	1	1	1	1	1	1	1	1	1	1
Apristurus brunneus	1	1	1	1	1	1	1	1	1	1

Appendix 1-2. (continued)

	Latitude (°N)									
	41	40	39	38	37	36	35	34	33	32
Argentina sialis	1	1	1	1	1	1	1	1	1	1
Artedius corallinus	1	1	1	1	1	1	1	1	1	1
Asterotheca pentacantha	1	1	1	1	1	1	1	1	1	1
Bathyraja interrupta	1	1	1	1	1	1	1	1	1	1
Bathyraja spinosissima	1	1	1	1	1	1	1	1	1	1
Bathyraja abyssicola	1	1	1	1	1	1	1	1	1	1
Bothrocara brunneum	1	1	1	1	1	1	1	1	1	1
Bothrocara molle	1	1	1	1	1	1	1	1	1	1
Brama japonica	1	1	1	1	1	1	1	1	1	1
Carcharodon carcharias	1	1	1	1	1	1	1	1	1	1
Careproctus melanurus	1	1	1	1	1	1	1	1	1	1
Caulolatilus princeps	1	1	1	1	1	1	1	1	1	1
Chitonotus pugetensis	1	1	1	1	1	1	1	1	1	1
Coryphaena hippurus	1	1	1	1	1	1	1	1	1	1
Coryphaenoides acrolepis	1	1	1	1	1	1	1	1	1	1
Cheilopogon pinnatibarbatus	1	1	1	1	1	1	1	1	1	1
Eptatretus deani	1	1	1	1	1	1	1	1	1	1
Euthynnus pelamis	1	1	1	1	1	1	1	1	1	1
Glyptocephalus zachirus	1	1	1	1	1	1	1	1	1	1
Isurus oxyrinchus	1	1	1	1	1	1	1	1	1	1
Lamna ditropis	1	1	1	1	1	1	1	1	1	1
Lampris guttatus	1	1	1	1	1	1	1	1	1	1
Icelinus oculatus	1	1	1	1	1	1	1	1	1	1
Icelinus burchami	1	1	1	1	1	1	1	1	1	1
Icelinus filamentosus	1	1	1	1	1	1	1	1	1	1
Icelinus tenuis	1	1	1	1	1	1	1	1	1	1
Icichthys lockingtoni	1	1	1	1	1	1	1	1	1	1
Icosteus aenigmaticus	1	1	1	1	1	1	1	1	1	1
Lepidocybium flavobrunneum	1	1	1	1	1	1	1	1	1	1
Lepidopsetta bilineata	1	1	1	1	1	1	1	1	1	1
Lycenchelus crotalinus	1	1	1	1	1	1	1	1	1	1
Lycodapus fierasfer	1	1	1	1	1	1	1	1	1	1
Lycodes diapterus	1	1	1	1	1	1	1	1	1	1
Lycodes cortezianus	1	1	1	1	1	1	1	1	1	1
Lyconema barbatum	1	1	1	1	1	1	1	1	1	1
Melanostigma pamelas	1	1	1	1	1	1	1	1	1	1
Oncorhynchus gorbuscha	1	1	1	1	1	1	1	1	1	1
Paricelinus hopliticus	1	1	1	1	1	1	1	1	1	1
Pseudopentaceros wheeleri	1	1	1	1	1	1	1	1	1	1
Plectobranchus evides	1	1	1	1	1	1	1	1	1	1
Poroclinus rothrocki	1	1	1	1	1	1	1	1	1	1
Prionotus stephanophrys	1	1	1	1	1	1	1	1	1	1
Radulinus asprellus	1	1	1	1	1	1	1	1	1	1
Raja stellulata	1	1	1	1	1	1	1	1	1	1
Reinhardtius hippoglossoides	1	1	1	1	1	1	1	1	1	1
Remora australis	1	1	1	1	1	1	1	1	1	1
Sebastes aleutianus	1	1	1	1	1	1	1	1	1	1
Sebastes auriculatus	1	1	1	1	1	1	1	1	1	1
Sebastes entomelas	1	1	1	1	1	1	1	1	1	1
Sebastes chlorostictus	1	1	1	1	1	1	1	1	1	1
Sebastes rosaceus	1	1	1	1	1	1	1	1	1	1
Sebastes helvomaculatus	1	1	1	1	1	1	1	1	1	1
Sebastes jordani	1	1	1	1	1	1	1	1	1	1
Sebastes babcocki	1	1	1	1	1	1	1	1	1	1
Sebastes elongatus	1	1	1	1	1	1	1	1	1	1
Sebastes ruberrimus	1	1	1	1	1	1	1	1	1	1
Sebastes diploproa	1	1	1	1	1	1	1	1	1	1
Sebastes aurora	1	1	1	1	1	1	1	1	1	1
Sebastes melanostomus	1	1	1	1	1	1	1	1	1	1
Sebastes proriger	1	1	1	1	1	1	1	1	1	1
Sebastes alutus	1	1	1	1	1	1	1	1	1	1
Sebastes miniatus	1	1	1	1	1	1	1	1	1	1

Appendix 1-2. (continued)

	Latitude (°N)									
	41	40	39	38	37	36	35	34	33	32
Sebastes saxicola	1	1	1	1	1	1	1	1	1	1
Sebastes zacentrus	1	1	1	1	1	1	1	1	1	1
Sebastes carnatus	1	1	1	1	1	1	1	1	1	1
Sebastes rufus	1	1	1	1	1	1	1	1	1	1
Sebastes levis	1	1	1	1	1	1	1	1	1	1
Sebastes ovalis	1	1	1	1	1	1	1	1	1	1
Sebastolobus alascanus	1	1	1	1	1	1	1	1	1	1
Sebastolobus altivelis	1	1	1	1	1	1	1	1	1	1
Seriola lalandi	1	1	1	1	1	1	1	1	1	1
Tetragonurus cuvieri	1	1	1	1	1	1	1	1	1	1
Tetrapturus angustirostris	1	1	1	1	1	1	1	1	1	1
Thunnus alalunga	1	1	1	1	1	1	1	1	1	1
Thunnus obesus	1	1	1	1	1	1	1	1	1	1
Thunnus orientalis	1	1	1	1	1	1	1	1	1	1
Trachurus symmetricus	1	1	1	1	1	1	1	1	1	1
Xeneretmus triacanthus	1	1	1	1	1	1	1	1	1	1
Xeneretmus latifrons	1	1	1	1	1	1	1	1	1	1
Xiphias gladius	1	1	1	1	1	1	1	1	1	1
Zaniolepis frenata	1	1	1	1	1	1	1	1	1	1
Zaniolepis latipinnis	1	1	1	1	1	1	1	1	1	1
Zesticelus profundorum	1	1	1	1	1	1	1	1	1	1
Balistes polylepis	1	1	1	1	1	1	1	1	1	1
Nezumia stelgidolepis	1	1	1	1	1	1	1	1	1	1
Lepidopus fitchi		1	1	1	1	1	1	1	1	1
Physiculus rastrelliger		1	1	1	1	1	1	1	1	1
Sebastes constellatus		1	1	1	1	1	1	1	1	1
Kathetostoma averruncus			1	1	1	1	1	1	1	1
Lagocephalus lagocephalus			1	1	1	1	1	1	1	1
Oligocottus rubellio			1	1	1	1	1	1	1	
Icelinus quadriseriatus				1	1	1	1	1	1	1
Phanerodon atripes				1	1	1	1	1	1	1
Zalembius rosaceus				1	1	1	1	1	1	1
Cephaloscyllium ventriosum					1	1	1	1	1	1
Echinorhinus cookei					1	1	1	1	1	1
Etrumeus teres					1	1	1	1	1	1
Mycteroperca xenarcha					1	1	1	1	1	1
Orthonopias triacis					1	1	1	1	1	1
Parmaturus xaniurus					1	1	1	1	1	1
Remora remora					1	1	1	1	1	1
Remora albescens					1	1	1	1	1	1
Sebastes serriceps					1	1	1	1	1	1
Sebastes hopkinsi					1	1	1	1	1	1
Sebastes ensifer					1	1	1	1	1	1
Sebastes eos					1	1	1	1	1	1
Sebastes rosenblatti					1	1	1	1	1	1
Sebastes semicinctus					1	1	1	1	1	1
Semicossyphus pulcher					1	1	1	1	1	1
Sebastes phillipsi					1	1	1	1	1	
Zenopsis nebulosa					1	1	1	1		
Ruscarius creaseri						1	1	1	1	1
Caranx caballus						1	1	1	1	1
Citharichthys xanthostigma						1	1	1	1	1
Decapterus muroadsi						1	1	1	1	1
Desmodena lorum						1	1	1	1	1
Hippoglossina stomata						1	1	1	1	1
Icelinus cavifrons						1	1	1	1	1
Lethops connectens						1	1	1	1	1
Lythrypnus dallii						1	1	1	1	1
Lythrypnus zebra						1	1	1	1	1
Naucrates ductor						1	1	1	1	1
Neoclinus stephensae						1	1	1	1	1
Polydactylus approximans						1	1	1	1	1

Appendix 1-2. (continued)

	Latitude (°N)									
	41	40	39	38	37	36	35	34	33	32
Ruvettus pretiosus						1	1	1	1	1
Scomberomorus concolor						1	1	1	1	1
Sebastes umbrosus						1	1	1	1	1
Sebastes gilli						1	1	1	1	1
Sebastes macdonaldi						1	1	1	1	1
Sebastes simulator						1	1	1	1	1
Ulvicola sanctaerosae						1	1	1	1	1
Ernogrammus walkeri						1	1	1		
Icelinus fimbriatus						1	1	1	1	
Plagiogrammus hopkinsii						1	1	1	1	
Agonopsis sterletus							1	1	1	1
Euthynnus lineatus							1	1	1	1
Pteraclis aesticola							1	1	1	1
Ranzania laevis							1	1	1	1
Thunnus albacares							1	1	1	1
Typhlogobius californiensis							1	1	1	1
Alloclinus holderi								1	1	1
Cetengraulis mysticetus								1	1	1
Chaenopsia alepidota								1	1	1
Cryptotrema corallinum								1	1	1
Pteroplatytrygon violacea								1	1	1
Epinephelus analogus								1	1	1
Fodiator acutus								1	1	1
Gnathophis cinctus								1	1	1
Gymnothorax mordax								1	1	1
Leiocottus hirundo								1	1	1
Lophotus capellei								1	1	1
Mobula japanica								1	1	1
Lactoria diaphana								1	1	1
Pristigenys serrula								1	1	1
Rimicola dimorpha								1	1	1
Tetrapturus audax								1	1	1
Trachinotus rhodopus								1	1	1
Xanthichthys mento								1	1	1
Xeneretmus ritteri								1	1	1
Zalieutes elater								1	1	1
Rimicola cabrilloi								1	1	
Radulinus vinculus								1		
Oligoplites saurus									1	1
Allothunnus fallai									1	1
Antennarius avalonis									1	1
Apogon guadalupensis									1	1
Assurger anzac									1	1
Auxis thazard									1	1
Auxis rochei									1	1
Bagre panamensis									1	1
Bellator xenisma									1	1
Calamus brachysomus									1	1
Carcharhinus obscurus									1	1
Carcharhinus leucas									1	1
Carcharhinus remotus									1	1
Prognathodes falcifer									1	1
Chaetodon humeralis									1	1
Chilomycterus reticulatus									1	1
Chloroscrombrus orqueta									1	1
Cynoscion parvipinnis									1	1
Decodon melasma									1	1
Diplectrum maximum									1	1
Dormitator latifrons									1	1
Echeneis naucrates									1	1
Eucinostomus currani									1	1
Euleptorhamphus longirostris									1	1

Appendix 1-2. (continued)

	Latitude (°N)									
	41	40	39	38	37	36	35	34	33	32
Euthynnus affinis									1	1
Fistularia corneta									1	1
Galeocerdo cuvier									1	1
Gempylus serpens									1	1
Gobiesox papillifer									1	1
Gobiesox eugrammus									1	1
Hemiramphus saltator									1	1
Hippocampus ingens									1	1
Lobotes pacificus									1	1
Macroramphosus gracilis									1	1
Makaira indica									1	1
Makaira mazara									1	1
Manta birostris									1	1
Myrophis vafer									1	1
Myxine circifrons									1	1
Nematistius pectoralis									1	1
Nicholsina denticulata									1	1
Odontaspis ferox									1	1
Grammonus diagrammus									1	1
Phtheirichthys lineatus									1	1
Plagiotremus azaleus									1	1
Polydactylus opercularis									1	1
Pseudupeneus grandisquamis									1	1
Regalecus glesne									1	1
Rhizoprionodon longurio									1	1
Rhombochirus osteochir									1	1
Rimicola eigenmanni									1	1
Scomberomorus sierra									1	1
Scorpaenodes xyris									1	1
Sebastes lentiginosus									1	1
Selene peruviana									1	1
Seriola rivoliana									1	1
Sphoeroides lobatus									1	1
Sphyraena ensis									1	1
Sphyrna tiburo									1	1
Synchiropus atrilabiatus									1	1
Taractichthys steindachneri									1	1
Trachinotus paitensis									1	1
Trachipterus fukuzakii									1	1
Trichiurus nitens									1	1
Uraspis secunda									1	1
Zu cristatus									1	1
Apogon pacificus										1
Caranx caninus										1
Carcharhinus longimanus										1
Chaetodipterus zonatus										1
Cheilopogon heterurus										1
Diodon hystrix										1
Diodon holocanthus										1
Engyophrys sanctilaurentii										1
Epinephelus niphobles										1
Eucinostomus dowii										1
Ctenogobius sagittula										1
Harengula thrissina										1
Hyporhamphus naos										1
Istiophorus platypterus										1
Melichthys niger										1
Mycteroperca jordani										1
Remora brachyptera										1
Rhincodon typus										1
Sphoeroides annulatus										1