

TABLE 5-1
Fish Biomass Density in Various Aquatic Ecosystems

<i>Ecosystem</i>	<i>Biomass Density g m⁻²</i>
Unpolluted rivers	1-5
Georges Bank	1.6-7.4
Matamek River, Quebec	2.1-17.8
Narragansett Bay	3.2
Gulf of Mexico	5.6-31.6
Flax Pond (Long Island) Estuary	24.0
California kelp bed	33.2-37.6
Bermuda coral reef in summer	59.3
Narragansett Bay salt marsh embayment	69.2
Peruvian upwelling in autumn	216.7

NOTE: After Haedrich and Hall 1976.

in temperature and salinity. Salmon, true smelts (osmerids), killifishes, and sticklebacks can adjust rapidly to abrupt changes in salinity by having (1) low permeability of body surfaces, (2) marked activity of the kidneys, and (3) highly functional salt glands in their gills (Haedrich and Hall, 1976).

Quantitative sampling of estuarine fish populations presents several difficulties and has been the topic of much discussion (e.g., Haedrich and Hall, 1976; Kjelson and Colby, 1976, Smith et al., 1984; Horn and Allen, 1985; Moyle et al., 1986; Rozas and Minello, 1997; Hemingway and Elliott, 2002). The fish assemblages of estuaries and other nearshore habitats, unlike the benthos or plankton, comprise many different groups representing different niches and thus requiring diverse but complementary collecting methods (Hemingway and Elliott, 2002). Each of the several subhabitats of estuaries, e.g., tidal channels, mudflats, eelgrass beds, and marsh pools, support their own suite of associated fish species in various life stages (Allen, 1982; Yoklavich et al, 1991; Valle et al., 1999; Allen et al., 2002). Some types of gear are much more effective at sampling these various subhabitats and particular life stages than others (Allen et al., 2002; see review by Hemingway and Elliott, 2002). For instance, purse seines are superior for sampling and estimating densities of midwater, schooling species and large, mobile taxa. Square enclosures, seines, and channel nets are most useful for estimating intertidal densities of cryptic, demersal, and schooling juvenile fishes. Beam trawls and drop nets more effectively assess the abundance of eelgrass-associated species and some larger demersal species. Otter trawls are needed to collect large, demersal fishes in the deeper channels. Therefore, programs using several types of gear are required to sample all species and subhabitats effectively. Unfortunately, many studies of estuarine fish assemblages completed to date have not employed multiple gear strategies, thus limiting our ability to compare species assemblages that are represented in different systems.

California Bays and Estuaries and Their Fish Assemblages

Background and Organization of the Chapter

Embayments come in many forms along the nearly 2600 km expanse of the California and Baja California coastline. Depending on size, general characteristics, and local custom, they are variously referred to as bay (bahia), estuary (estero),

slough, lagoon (laguna), and marsh (fig. 5-1). Most qualify as estuaries in the broadest sense because they are diluted with freshwater during a portion of the year, but, because of the limited freshwater input into some of the systems, we use the collective name of "bays and estuaries" in this chapter. The arid climate of much of the California coast, especially from the central region southward into Baja California, can give the impression that such estuarine habitats are few in number and small along this coastline. These habitat types are scarcer and smaller than those on the Atlantic and Gulf coasts of the United States. Nevertheless, bays and estuaries as broadly defined above are diverse in size and type in California and Baja California and present an array of different environmental conditions for coastal fishes. Large embayments, such as San Francisco Bay and San Diego Bay, generally represent the broadest range of habitats including deep to shallow channels, mudflats, eelgrass beds, and salt marshes. The deep portions of these large systems are peninsular extensions of the shallow continental shelf and therefore offer habitat to many species of nearshore fishes. The smallest bays and estuaries predictably contain some reduced combination of shallow channels, mudflats, eelgrass beds, and salt marshes and are inhabited by a smaller number of typical bay-estuarine fish species.

The wide variety of bay and estuaries in California is largely a result of the diverse geology, climate, and topography of the state, and these systems have been described and classified by Ferren (1996a,b,c). In northern California, the relatively high annual rainfall results primarily in river-dominated estuaries. These systems usually receive frequent freshwater influx and develop classic estuarine salt-wedge characteristics, sharp gradients of salinity with depth that move upstream or downstream depending on variations in the input of fresh water over the annual hydrologic cycle (fig. 5-2). Southward along the California coast, these relatively large bays and estuaries give way to smaller embayments where freshwater input is largely restricted to the winter months when rainfall is most prevalent (fig. 5-3). These types of embayments have sometimes been referred to as "intermittent estuaries," and those of central and southern California generally fall into this category. Ferren et al. (1996a,b,c) classified the wetlands of central and southern California into five types, including estuarine systems, and, in turn, recognized seven kinds of estuaries for these two sections of the state's coastline, a reflection of the remarkable geomorphological and climatic diversity of California. The very small bay-estuarine systems at the creek mouths of canyons and structural basins in the classification of Ferren and co-workers have rather distinctive fish assemblages because of the relatively consistent freshwater inflow into a limited space. In the bays and estuaries on the Pacific coast of Baja California, where annual rainfall is especially low, evaporation may exceed precipitation, resulting in hypersaline conditions during much of the year; these systems are sometimes referred to as "negative estuaries." The upper portions of most of the bay-estuarine systems in California and northern Baja California are fringed by salt marshes, which are characterized by shallow channels, mudflats, and islands that support salt-tolerant plants.

California bays and estuaries have received a great deal of study during the last 40 years (table 5-2). This heightened attention has been prompted mainly by the alarming and ever-increasing rate of human modification and destruction of these unique habitats and the continuing accumulation

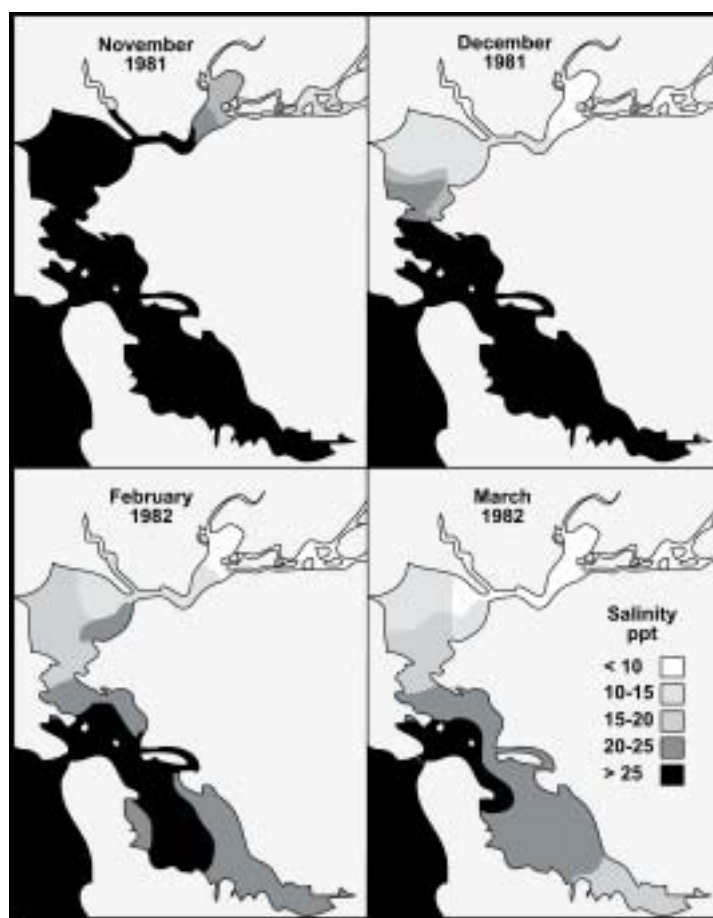


FIGURE 5-1 Map of the coastline of California and Baja California with locations of 19 bay-estuarine systems.

of pollutants in them. Estimates of the degree of loss of coastal wetlands, including bays, estuaries, and salt marshes range as high as 90% in southern California (Zedler et al., 2001). Types of pollution in California bay-estuarine systems range from nutrient loading (e.g., Kamer et al., 2001) to organochlorine and heavy metal contamination (e.g., Davis et al., 2002). Habitat loss and environmental pollution are discussed in a broader context of California marine fish habitats in Chapter 23. Recognition of the biological importance and the diminished number and quality of these habitats in California has resulted in a growing number of restoration projects in estuaries and salt marshes in recent years (Zedler, 2001).

We characterize California bay-estuarine fish assemblages below from two broad perspectives, each with links to other chapters in this book: (1) latitudinal distribution patterns, and (2) major ecological features. The coastline from Humboldt Bay in northern California to Laguna de Ojo Liebre in central Baja California spans about 11° of latitude (fig. 5-1) and crosses biogeographic boundaries and environmental gradients, especially of temperature and rainfall. As such, the latitudinal perspective treated here is related to the larger scale distributional analyses in chapters 1 and 2. This perspective can be divided into two components: (a) species-area relationships, and (b) classification based on salt tolerance and life-history pattern, which relate generally to the

FIGURE 5-2 Large-scale variation in depth-averaged salinity (parts per thousand) in San Francisco Bay before and after the freshwater pulses of November to December 1981 and February to March 1982 (after Armor and Herrgesell, 1985).



ecological classification of the entire California marine fish fauna (chapter 4). The overarching ecological features of diversity, productivity, seasonality, interannual variability, and nursery function are important in portraying and understanding bay-estuarine fish ecology, and they link to varying degrees to the conceptual topics discussed in Unit III on Population and Community Ecology, especially feeding and trophic interactions (chapter 14) and recruitment (chapter 15).

Latitudinal Distribution Patterns

SPECIES-AREA RELATIONSHIPS

In an earlier analysis of the relationships among California bays and estuaries based on presence/absence of fish species, the seven sites studied in southern California formed a distinctive unit (Horn and Allen, 1976). The six bays and estuaries studied in central and northern California (i.e., north of Point Conception) also grouped together in the analysis; however, the group of large bays and estuaries in the north (Humboldt Bay, Tomales-Bodega Bay, and San Francisco Bay) and the smaller, intermittent estuaries of Northern and central California (Bolinus Bay, Elkhorn Slough, and Morro Bay) clustered as separate subunits. We have updated the Horn and Allen (1976) analysis here by (1) adding two sites, Carpinteria Estuary (Brooks, 2001) and Mugu Lagoon (Onuf and Quammen, 1983), and (2) using the species lists from Elkhorn Slough (Yoklavich et al., 1991) and San Diego Bay (Allen et al., 2002). From this revised analysis, a group of 38

species was identified that occur widely in California bays and estuaries, a group of 60 species that inhabits bays and estuaries primarily in southern California, and a group of 133 species that occurs mainly in bay-estuarine habitats north of Point Conception. These three geographic categories are listed adjacent to an updated dendrogram (fig. 5-4) and permit recognition of the faunal composition of each bay and estuary in the cluster according to these categories.

As was found for the 13 bays and estuaries in the original Horn-Allen analysis, variation in the number of species among the 15 sites in the new analysis was driven largely by the size (surface area) of the habitat. Multiple regression analysis was used to determine the relative contributions of six independent environmental variables (surface area, latitude, mean annual sea surface temperature, diurnal tidal range, distance to nearest neighboring site, and mean annual rainfall) to explain the variation in the number of species recorded from each bay-estuarine site. Surface area was the only significant independent variable and accounted for 81% ($R^2 = 0.81$) of the variation in species richness.

As in the previous paper, our new analysis yielded a statistically significant relationship between the number of species and the area of the bay-estuarine habitat. This species-area relationship (fig. 5-5) is best described by the power function $S = 1.31 A^{0.33}$ (where S = the number of species and A = the surface area of the bay-estuarine system) for log-transformed data ($r = 0.92$; $p < 0.001$) and $S = 12.44 A^{0.24}$ for nontransformed data ($r = 0.96$; $p < 0.001$). The latter equation is a more easily accessible model to predict the species richness of any bay-estuarine system in California. The width of the mouth of

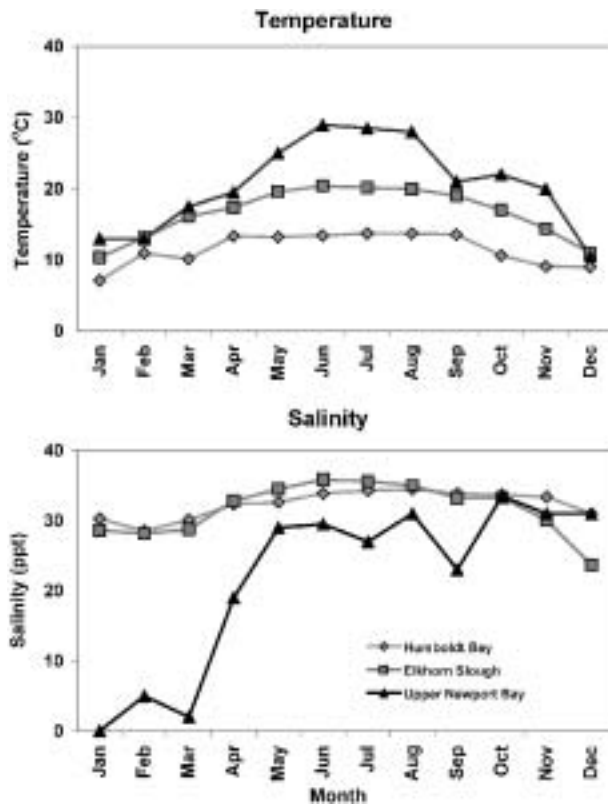


FIGURE 5-3 Monthly variation in temperature and salinity within three California bay/estuaries from northern to southern California: Humboldt Bay (1960), Elkhorn Slough (2000), and Upper Newport Bay (1978).

each habitat also was significant when included in the species-area analysis. Mouth width and surface area, however, were highly intercorrelated variables thus adding undesirable redundancy to the analysis.

Recognition of three broad distributional categories (widespread, southern, and northern) of bay-estuarine fish assemblages illustrates the complex and dynamic character of the California coastal fauna that Hubbs (1974) emphasized. Many species cross faunal boundaries, some as a result of local or seasonal fluctuations in environmental variables, especially temperature. Hubbs (1948, 1960) noted the general tendency for primarily southern species to occur in bays and estuaries in central and northern parts of California and for primarily northern species to occur in deeper (hence, cooler) waters in southern California and in cool, upwelling areas off northern Baja California. As a result, Horn and Allen (1976) hypothesized that of the 224 species in California's bays and estuaries, southern ones would be more likely in systems north of Point Conception than would northern species in this type of habitat south of Point Conception. The results of their study supported this view because of 55 primarily southern species, 25% occurred in one to three northern bays and estuaries, whereas of 128 northern species, only 9% variously occurred in no more than one of the southern systems. A comparison of the remaining, generally deeper dwelling, coastal fishes (Horn and Allen 1978) showed the opposite trend, i.e., Point Conception is less of a boundary to northern species than to southern ones. Our update of the Horn and Allen (1976) database and the new analysis did not change these general conclusions.

TABLE 5-2

References to Works on Fish Assemblages in 18 Bays and Estuaries in California and Baja California

Bay-estuarine System	References
Humboldt Bay	Monroe, 1973; Barnhart et al., 1992
Tomales-Bodega Bay	Bane and Bane, 1971; Hardwick, 1973
Bolinas Lagoon	Giguere, 1970
San Francisco Bay	Ganssle, 1966; Aplin, 1967; Green, 1975; Armor and Herrgesell, 1985; Matern et al., 2002
Elkhorn Slough	Browning, 1972; Cailliet et al., 1977; Yoklavich et al., 1991; Yoklavich et al., 1992; Barry et al. 1996
Morro Bay	Fierstine et al., 1973; Gerdes et al., 1974; Horn, 1980
Carpinteria Lagoon	Brooks, 2001
Mugu Lagoon	Onuf and Quammen, 1983
Alamitos Bay	Allen and Horn, 1975; Valle et al., 1999
Anaheim Bay	Lane and Hill, 1975
Newport Bay	Allen, 1982, 1988; Horn and Allen, 1985
Los Penasquitos Lagoon	Mudie et al., 1974; Williams et al., 2001; Desmond et al., 2002
Mission Bay	Chapman, 1963
San Diego Bay	Peeling, 1974; Allen et al., 2002
Tijuana Estuary	White and Wunderlich, 1976; Williams et al., 2001; Desmond et al., 2002
Estero de Punta Banda	Beltran-Felix et al., 1986; Rosales-Casian, 1997
Bahia de San Quintin	Rosales-Casian, 1996, 1997
Laguna de Ojo Liebre	Galvan et al., 2000

NOTE: Arranged in order from north to south; see Fig. 1 for locations.

Ecological Classification Based on Salt Tolerance and Life History Pattern

DESCRIPTION OF THE MODEL ADOPTED

Several attempts have been made to classify the bay-estuarine fishes of California based on their life histories as well as on temporal and spatial distributions. These efforts have resulted in a number of different ecological classifications specific to particular habitats. The fish species of Newport Bay and San Diego Bay in southern California have been grouped into residents, spring-summer seasonals (periodics), and visitors (Allen, 1982; Allen et al., 2002). Similarly, Yoklavich et al. (1991) categorized the fishes in Elkhorn Slough in central California as either marine species, marine immigrants, slough residents, partial residents, or freshwater species. Using salinity tolerance more explicitly, Armor and Herrgesell (1985) classified fish species in San Francisco Bay as freshwater (occurrence at salinities <1 ppt), anadromous, estuarine (occurrence at 1-20 ppt), marine estuarine (9-30 ppt), or marine (only >20 ppt). These several, overlapping classification strategies emphasize the need for a composite model applicable to California bay-estuarine systems in general. Therefore, we have adopted here a scheme based on the general classification proposed by Moyle and Cech (2000), with modifications derived from Armor and Herrgesell (1985) and Yoklavich et al. (1991).

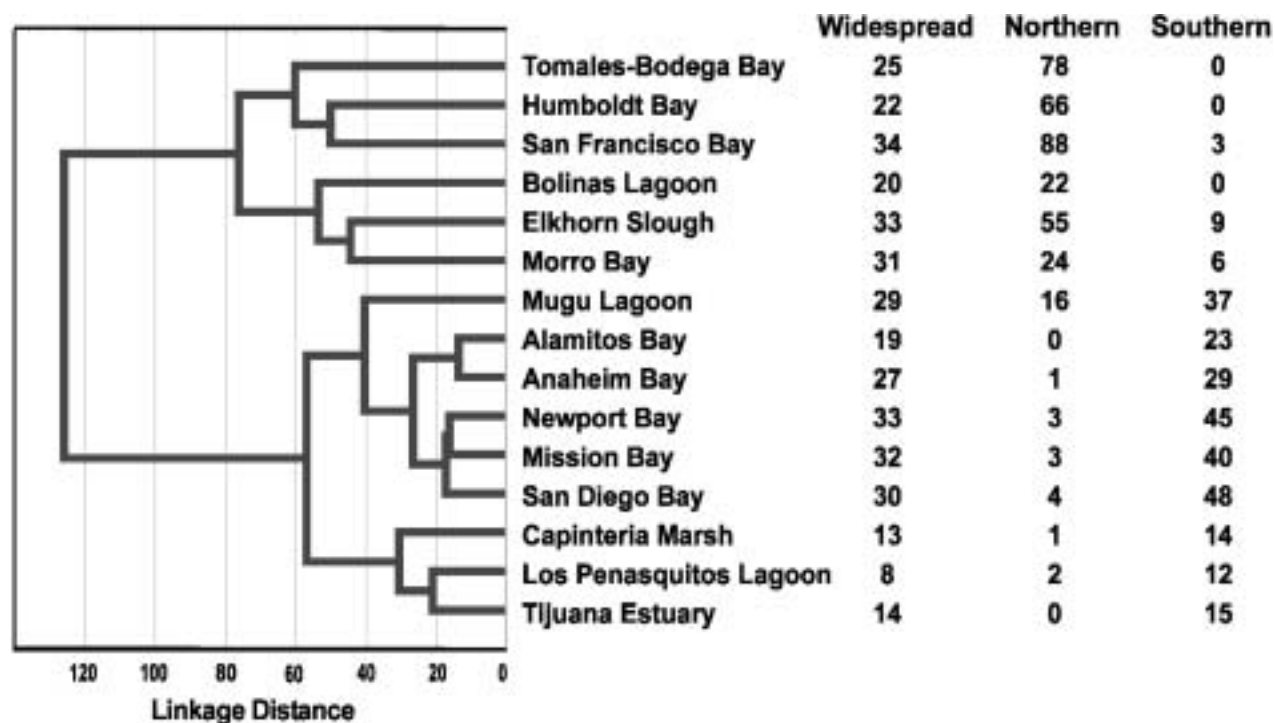


FIGURE 5-4 Dendrogram of the clustering of 15 California bays and estuaries based on the presence/absence of fish species using correlation coefficients (r) and complete linkage. The species of each bay-estuarine system are grouped into three broad distributional categories (widespread, northern, and southern) based on a two-way table (bay vs. species) generated in the cluster analysis (after Horn and Allen, 1976).

Our classification, shown in table 5.3, recognizes the fish species of California bay-estuarine systems as either freshwater taxa, diadromous (anadromous or catadromous) taxa, estuarine residents, marine migrants, or marine species that seasonally or occasionally enter the system. These five categories are defined as follows: (1) Freshwater taxa are those forms that occur only in upstream (sometimes brackish) areas where salinities are generally less than 1 ppt. (2) Diadromous taxa are those that migrate between marine and freshwater (or brackish) environments for spawning purposes. Most common among these species are anadromous fishes, which mature in the ocean and enter freshwater to spawn. Catadromous fishes are much rarer in California, but one species, striped mullet, may qualify in southern California bays and estuaries because small juveniles recruit to brackish and freshwaters from the open sea during the winter months (Horn and Allen, 1985). (3) Estuarine residents are those euryhaline and eurythermal species that complete their entire life cycle in bays and estuaries. This category contains species that are widespread in the state and also those that mainly inhabit the salt marsh areas of southern California bays and estuaries. (4) Marine migrants include both species that migrate into bays and estuaries to spawn or give birth (sharks, rays, herrings, and surfperches) and species that are spawned offshore, recruit into bays and estuaries, and then use these habitats as nurseries during their juvenile stage (e.g., some flatfishes). (5) Marine species are those that occur broadly in all life-history stages in the nearshore environment and enter bays and estuaries at certain times of the year or at varying intervals. This scheme has the advantage of combining salt tolerance, life-history pattern, and latitudinal occurrence for each fish species. Latitudinal change in species composition occurs in part because thermal and biogeographic boundaries are crossed, as discussed in the

previous section, and in part because freshwater input decreases from north to south in California and into Baja California. Given these considerations, the bay-estuarine habitats and their associated fish assemblages in this coastal expanse are portrayed in four segments and discussed in turn below.

NORTHERN CALIFORNIA

This part of the coast contains the two largest bay-estuarine environments in California: San Francisco Bay and Humboldt Bay. More than 100 species of fishes have been reported from each of these systems (Armor and Herrgesell, 1985; Barnhart et al., 1992). Even though the fishes in the two systems represent the entire spectrum of salinity tolerance, the consistent inflow of freshwater greatly influences the composition of both fish assemblages. As a result, they are dominated seasonally by a relatively small number of anadromous and otherwise euryhaline species of mainly northern affinities, including salmon and trout, true smelts, cods, and herrings (table 5-3; fig. 5-6). Among the most prevalent freshwater brackish species in northern bays and estuaries are threespine stickleback and prickly sculpin. Diadromous (anadromous) species in California are largely confined to northern bays and estuaries and include white sturgeon, American shad, chinook salmon, and striped bass. A relatively small number of species of estuarine residents occur in these systems and are represented mainly by longfin smelt, bay pipefish, Pacific staghorn sculpin, and several species of goby. Dominant marine migrants include pelagic species, especially Pacific herring, silversides (jacksmelt and topsmelt), and shiner perch, as well as benthic (demersal) forms such as starry flounder and English sole. The most

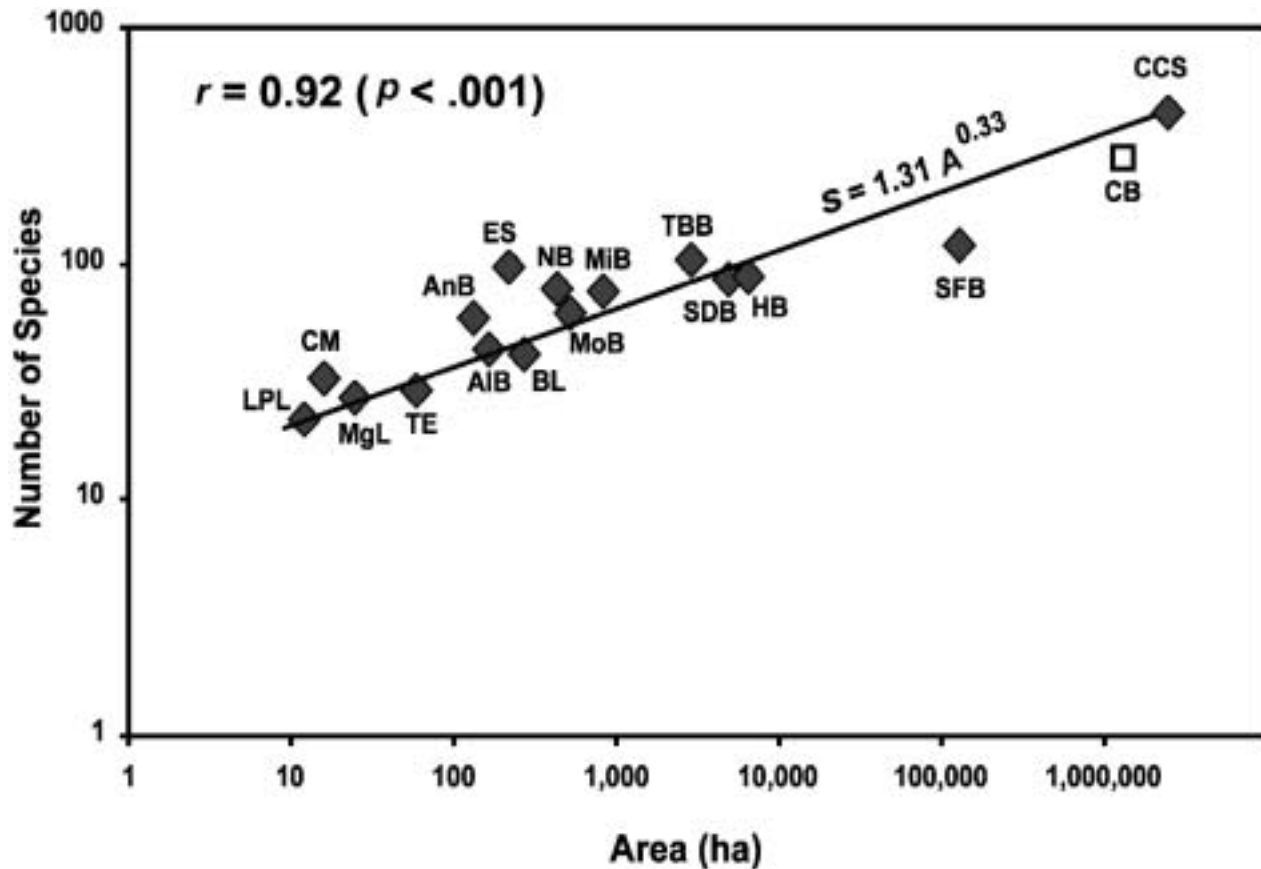


FIGURE 5-5 Relationship of number of species (S) and surface area (A) of 15 California bays and estuaries, plus the continental shelf (CCS) and Chesapeake Bay (CB) for comparison. The equation is based on California bays and estuaries and the continental shelf. AL = Alamitos Bay; AnB = Anaheim Bay; BL = Bolinas Lagoon; CM = Carpenteria Marsh; ES = Elkhorn Slough; HB = Humboldt Bay; LPL = Los Penasquitos Lagoon; MB = Morro Bay; MgL = Mugu Lagoon; MiB = Mission Bay; NB = Newport Bay; SDB = San Diego Bay; SFB = San Francisco Bay; TBB = Tomales-Bodega Bay; TE = Tijuana Estuary (after Horn and Allen, 1976).

abundant marine species in these northern systems appears to be northern anchovy. Finally, freshwater brackish and diadromous species such as three-spine stickleback, starry flounder, tidewater goby, steelhead, and juvenile salmon are well represented in the low-salinity regions of these larger bays and estuaries, and have been the prevalent species in smaller, river-mouth systems throughout the region (fig. 5-7). Many of the species in northern bays and estuaries, including starry flounder (Orcutt, 1950), striped bass (Raney, 1952), threespine stickleback (Snyder, 1991), and jacksmelt (Clark, 1929), have been the subject of life-history investigations. The life histories of Chinook salmon, coho salmon, steelhead, English sole, and other species are well summarized in Emmett et al. (1991), Leet et al. (2001), and Moyle (2002).

Species in Jeopardy

Those bay-estuarine species in decline and threatened with extinction in California are discussed in this northern section because of the relatively high diversity of such fish taxa in this region. The bay-estuarine fish assemblages of northern California are a remarkable mixture of species in terms of origins, life history, and status and include icons of rarity, decline, and success. Anadromous fishes, in particular sturgeon and salmon, are more diverse and abundant in

northern compared to central and southern parts of the state. Habitat loss and alteration involving dams, water diversions, and pollution have played major roles in reducing fish populations, especially of anadromous species. These and other impacts on California's native bay-estuarine fish faunas are described in Leet et al. (2001) and by Moyle (2002). Such perturbations have resulted in several species and populations being recognized as endangered, threatened, or in some lesser state of jeopardy by the federal or state government (table 5-4).

Although most species of sturgeon worldwide are listed as in trouble, one of the two species in California, at least, appears to be faring better in recent years than in earlier decades as a result of improved fisheries management. White sturgeon, the largest fish species that enters fresh waters in North America (apparently reaching 6 m and 630 kg), spends most of its life in estuaries of large rivers. Recognition that this species requires at least 10 years to mature at a size of about 1 m or more led to closure of the commercial fishery in 1917. Effective management of the sport fishery in the state has resulted in white sturgeon being one of the few species in San Francisco Bay to sustain its population. In contrast, green sturgeon is a rarer species that spends most of its life in the ocean, spawns at an even older age (15–20 years), and is less well studied. Thus, it has not fared as well as white sturgeon and is currently listed as a species of special concern in California. Green sturgeon

NORTHERN CALIFORNIA BAYS AND ESTUARIES

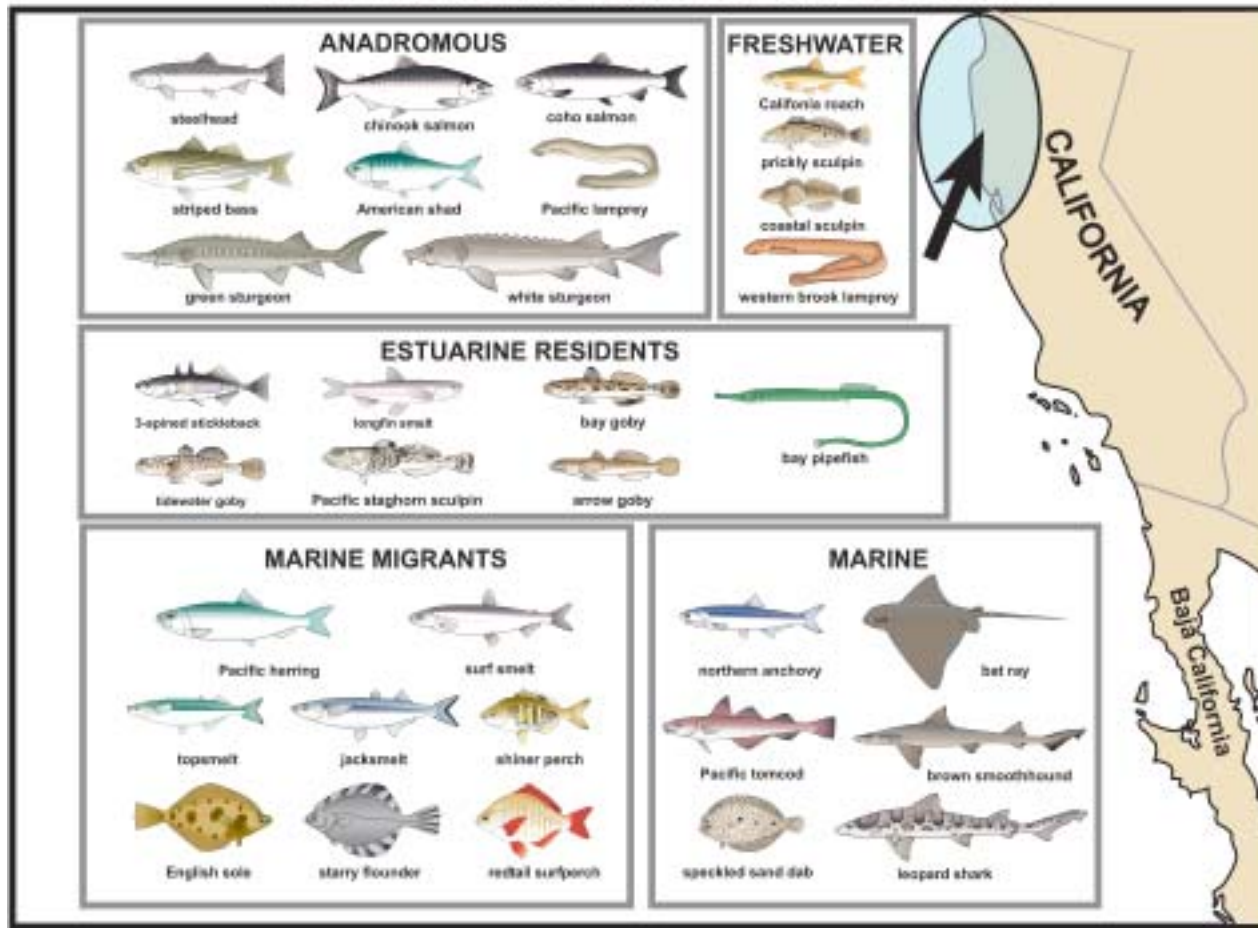


FIGURE 5-6 Profiles of fishes in northern California bays and estuaries representing five ecological categories based on salt tolerance and life-history pattern: freshwater taxa, anadromous taxa, estuarine residents, marine migrants, and marine species that seasonally or occasionally enter these habitats. (See Table 5-3.)

apparently spawn only in the Sacramento, Klamath, and Trinity rivers in California although there are recent signs of stable populations and increased spawning activity (Kohlhorst, 2001). In 2005, the federal government proposed to list the distinct population segment of green sturgeon in the Sacramento River as a threatened species under the Endangered Species Act.

Salmon are much better publicized as anadromous species in jeopardy, and there is much to justify this notoriety (see Moyle, 2002). Of the six species that historically occurred in and transcended estuaries in California, pink salmon have been extirpated from the state and certain populations of other species are extinct as well. The remaining five, coho, chinook, chum, steelhead, and cutthroat, have at least some populations threatened with extinction (table 5-4). As with sturgeon, the losses and declines can be linked mainly to large dams and water diversions that deny access of adult fish to spawning streams and disrupt the life cycle of these anadromous species. Other causes of decline include overfishing and additional sources of environmental damage such as loss of riparian habitat, siltation, pollution, effects of alien species, and competition from hatchery-reared juveniles for food and adults for spawning areas. The enormous reduction in salmon numbers and the concomitant loss of energy and nutrients that these fishes transport from the ocean to estuaries and inland streams undoubtedly have had

profound effects on these aquatic ecosystems (Gende et al., 2002). Recovery of salmon populations in California presents a tremendous challenge requiring major long-term investments in habitat restoration and improved management of hatcheries, fisheries, and spawning streams.

True smelts (Osmeridae) are part of the mix of native fishes in northern bays and estuaries, and they, too, have suffered large population declines (Moyle, 2002). Marked reduction in these small planktivorous fishes capable of occurring in great numbers seems unlikely and perhaps is even more alarming than that of the much larger and late-reproducing salmon and sturgeon. The status of three species, delta smelt, longfin smelt, and eulachon, is important to mention in this context. Delta smelt is a euryhaline species endemic to the upper San Francisco Bay estuary, mainly in Suisun Bay and the Delta. Although its population size has fluctuated greatly in the past, delta smelt was historically one of the most abundant species in the upper estuary. Beginning in the early 1980s, numbers declined precipitously, and the species was listed as threatened by both federal and state governments in 1993 with critical habitat (Suisun Bay and Suisun Marsh) defined in 1996. The causes of decline in delta smelt appear to be varied and include water diversion, fluctuating water flows, and invasive species that represent alternative, less preferred prey organisms or that

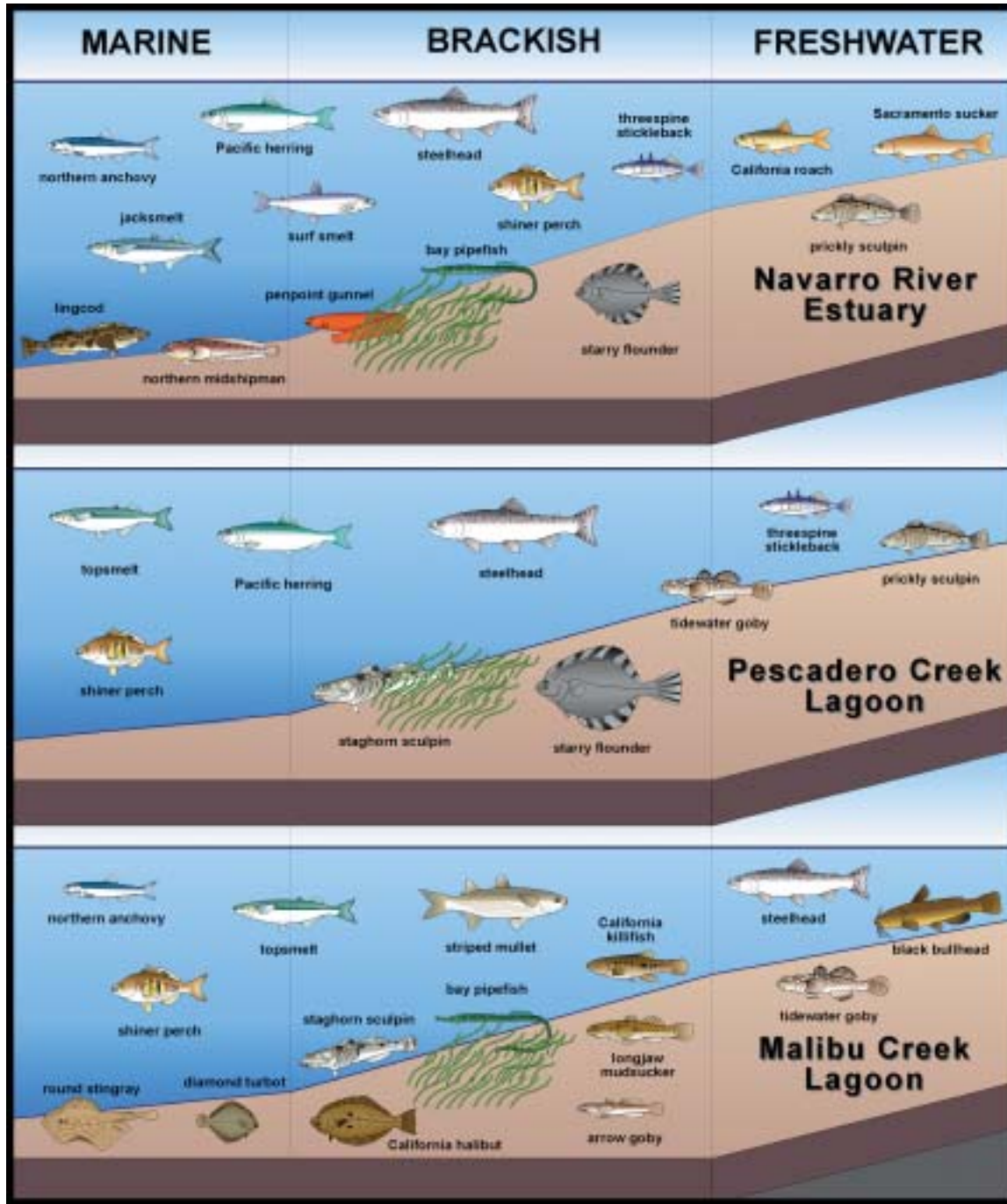


FIGURE 5-7 Profiles of principal fish species in three small canyon- or river-mouth estuaries. Navarro River estuary is located in Northern California south of Humboldt Bay, Pescadero Creek lagoon in Central California near Monterey Bay, and Malibu Creek lagoon in Southern California in the city of Malibu just northwest of Los Angeles.

hybridize with the species (see below). Longfin smelt is more widely distributed in northern bays and estuaries and once was one of the most abundant species in San Francisco Bay and Humboldt Bay and an important element of the food webs. Populations have declined in most locations, and the species is now listed by the state as a species of special concern. Like those of delta smelt, longfin smelt numbers declined abruptly in the early 1980s in San Francisco Bay and have remained low. Causes of the long-term decline there appear to be similar to those for delta smelt, and recovery probably depends on restoration of more natural cycles of water flow in estuaries. A

third smelt species in decline in California and also a state species of special concern is the eulachon, a fish famous for its high oil content and use by native people of the Pacific Northwest for food and candles. It spends most of its life in the ocean, returning to spawn in the lower reaches of coastal streams usually no farther south than the Klamath River and tributaries of Humboldt Bay. Numbers have been low for most of the last 30 years in the Klamath River, and, although the causes of the decline are unknown, ocean conditions, including El Niño–Southern Oscillation (ENSO) events as well as the quality of spawning habitat, may be important factors.

