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CHAPTER 5

Bays and Estuaries

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Introduction to Estuarine Systems

Few habitats offer a more challenging environment to marine fishes than bays and estuaries. These interfaces between land and sea at river mouths present highly variable physical and chemical conditions for marine fishes most of which usually have narrow tolerances to these environmental gradations. Virtually all of the prominent physical and chemical characteristics of water, such as temperature, salinity, dissolved oxygen, and pH, change dramatically over space and time in these relatively shallow habitats. Tidal exchange, especially over the sometimes extensive mudflats and salt marshes, creates additional variability associated with strong currents, possible aerial exposure, and isolation in pools. Despite these dramatic environmental fluctuations, bays and estuaries throughout the world are recognized as important fish habitats, serving especially as spawning and nursery sites, migration routes, and areas naturally supporting large populations of certain coastal fish species (e.g., McHugh, 1967; Haedrich, 1983; Elliott, 2002).

The complex and dynamic qualities of estuaries have fostered continuing discussion in the literature as to their definition and classification and to their role as nursery grounds. Elliott and McLusky (2002) point out that the basic challenge of defining and classifying estuaries stems from their prominence as habitats that represent spatial and temporal continua, for example, in the environmental variable of salinity and the biological variable of community structure. These authors argue for an "expert judgment checklist" that involves assessment of physical, chemical, and biological characteristics to help define, delimit, and classify estuaries for both scientific and managerial needs while still recognizing the inherent variability of these systems. The nursery role of different habitats within and among estuaries has continued to be a topic of research, and Beck et al. (2001) have proposed a nursery-role hypothesis for marine and estuarine habitats that, if tested adequately, would result in a more rigorous assessment of the nursery value of nearshore areas.

Estuaries are among the most productive areas on earth, and fish biomass in these habitats ranks with that of the marine regions of upwelling, coral reefs, and kelp beds (table 5-1). Based on energy fixed by plants and algae, estuaries and associated salt marshes may offer the greatest availability of food of any habitat types in the world (see Whittaker and Likens, 1973). These unique environments are sinks for nutrients that flow from the land or are tidally transported from the sea. The concentrations of nutrient levels coupled with the shallow, well-mixed, and well-lit nature of these areas are primarily responsible for the high seasonal productivity that characterizes estuaries. The same turbid conditions and reduced water flows that result in deposition of nutrient-containing sediment in estuaries also trap contaminants, thus creating one of the chronic environmental problems of these habitats (see Marchand et al., 2002).

Various taxonomic groups of marine fishes, many of commercial importance, are represented in estuarine systems throughout the world. In the northeastern Atlantic and Mediterranean estuaries, the main species are anguillifoms (eels), mugiliforms (mullets), perciforms (especially temperate basses), and pleuronectiforms (flatfishes) (Costa et al., 2002). In South Africa, the prominent species are clupeiforms (anchovies and herrings), mugiliforms , atheriniforms (silversides), perciforms (especially sparids and gobies), and pleuronectiforms (Day et al., 1981). In New England, estuarine fish assemblages are dominated by salmoniforms (salmon and smelts), atheriniforms (silversides and killifishes), and gasterosteiformes (sticklebacks) (Haedrich and Hall, 1976). These groups include eurythermal and euryhaline species that are adapted for estuarine existence; however, major marine groups such as gadiforms (cods), clupeiforms (herrings), anguilliforms, and perciforms are represented by relatively few species that have adapted to thrive in estuarine systems of New England (Haedrich and Hall, 1976). Along the southern Atlantic and Gulf coasts of the United States, perciforms (especially croakers, porgies, and mojarras), clupeiforms (anchovies and menhaden), and mugiliforms become more important in estuaries (Peterson and Ross, 1991; Houde and Rutherford, 1993).

Although fishes can move from one area to another within an estuarine system, some degree of temperature tolerance (Hubbs, 1965) and osmoregulatory ability (Carpelan, 1961; Haedrich 1983) is required for success in these variable habitats. As implied above, predominantly estuarine species typically belong to groups that have evolved broad tolerance to changes

TABLE 5-1
Fish Biomass Density in Various Aquatic Ecosystems

Ecosystem	*Biomass Density g m^{-2}*
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

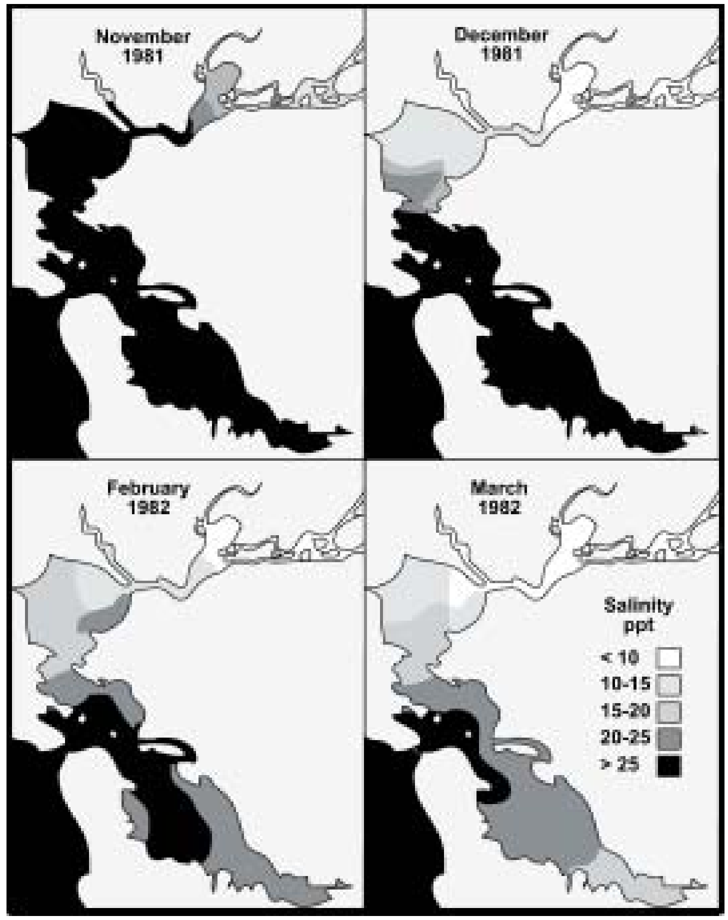


FIGURE 5-2 Large-scale variation in depth-averaged salinity (parts per thousand) in San Francisco Bay before and after the freshwater pulses of November to December 1981 and February to March 1982 (after Armor and Herrgesell, 1985).

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 (Bolinas 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, Carpenteria 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

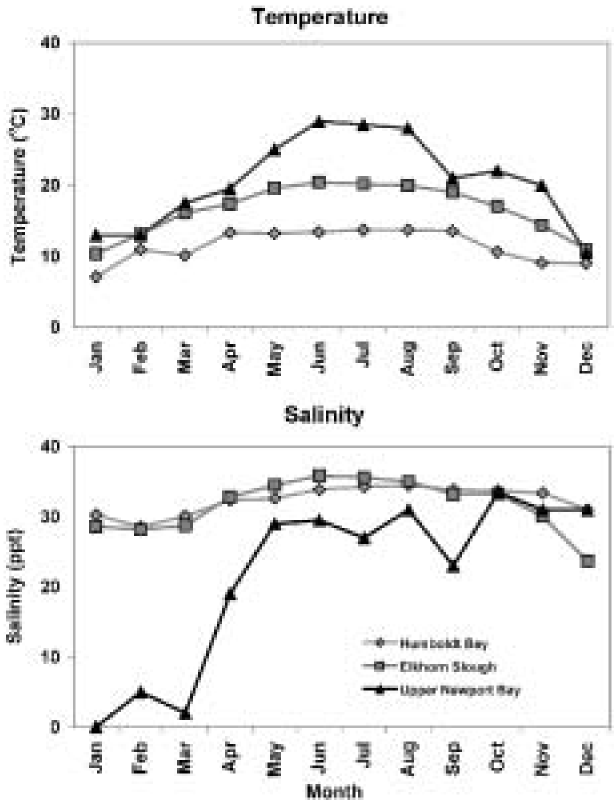


FIGURE 5-3 Monthly variation in temperature and salinity within three California bay/estuaries from northern to southern California: Humboldt Bay (1960), Elkhorn Slough (2000), and Upper Newport Bay (1978).

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

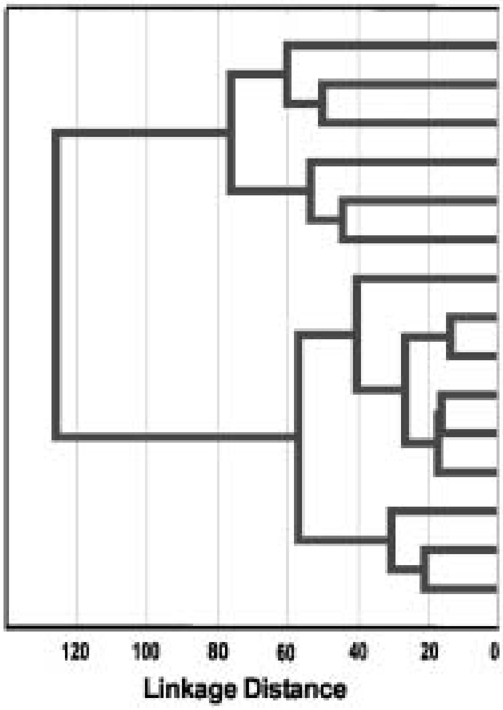
Bay-estuarine System	*References*
Humboldt Bay	Monroe, 1973; Barnhart et al., 1992
Tomales-Bodega Bay	Bane and Bane, 1971; Hardwick, 1973
Bolinas Lagoon	Giguere, 1970
San Francisco Bay	Ganssle, 1966; Aplin, 1967; Green, 1975; Armor and Herrgesell, 1985; Matern et al., 2002
Elkhorn Slough	Browning, 1972; 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).



	Widespread	Northern	Southern
Tomales-Bodega Bay	25	78	0
Humboldt Bay	22	66	0
San Francisco Bay	34	88	3
Bolinas Lagoon	20	22	0
Elkhorn Slough	33	55	9
Morro Bay	31	24	6
Mugu Lagoon	29	16	37
Alamitos Bay	19	0	23
Anaheim Bay	27	1	29
Newport Bay	33	3	45
Mission Bay	32	3	40
San Diego Bay	30	4	48
Capinteria Marsh	13	1	14
Los Penasquitos Lagoon	8	2	12
Tijuana Estuary	14	0	15

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 (anadromus 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

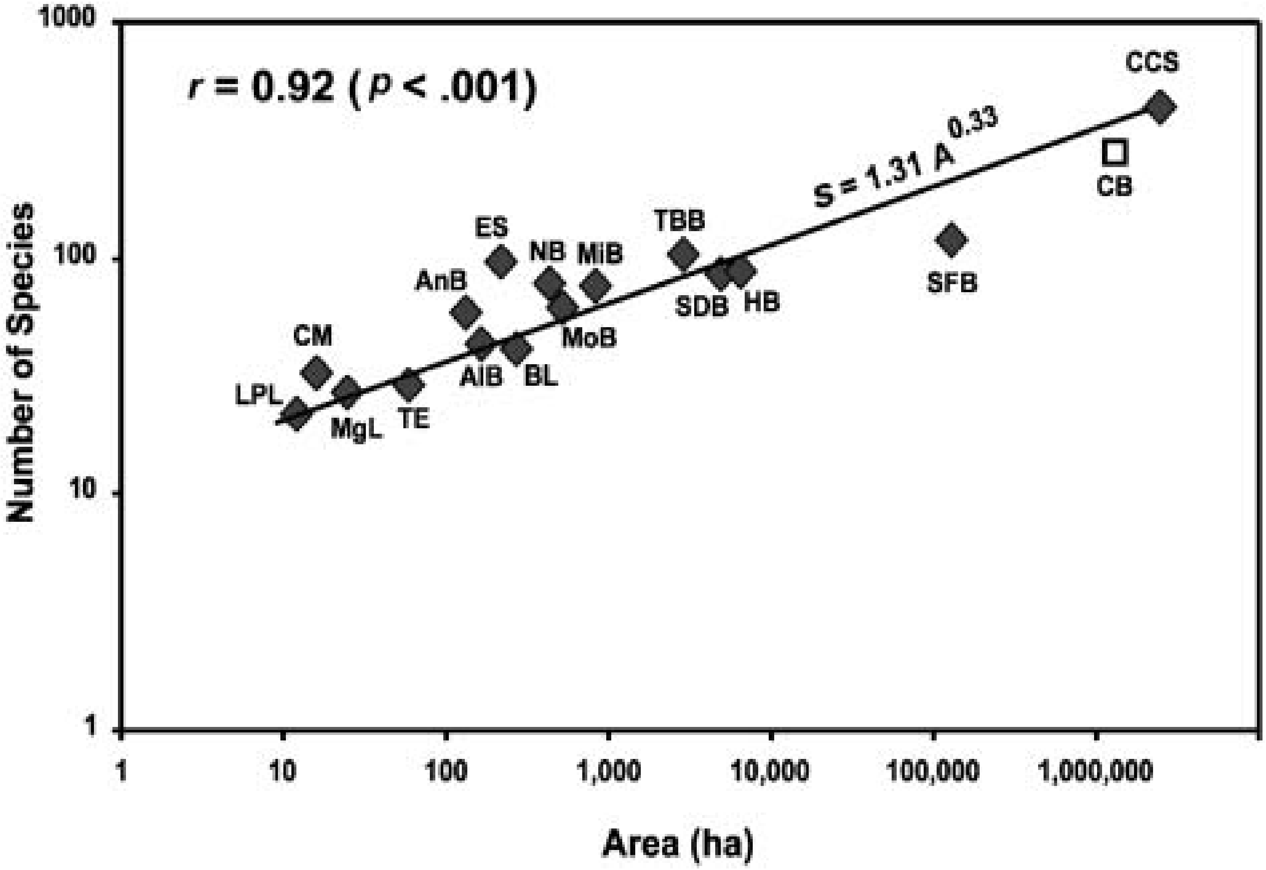


FIGURE 5-5 Relationship of number of species (S) and surface area (A) of 15 California bays and estuaries, plus the continental shelf (CCS) and Chesapeake Bay (CB) for comparison. The equation is based on California bays and estuaries and the continental shelf. AL = Alamitos Bay; AnB = Anaheim Bay; BL = 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

TABLE 5-3

Ecological Classification of Some Principal Fishes in 13 Bays and Estuaries in California and Baja California

Species Category	*Common Name*	*Scientific Name*	Klamath River	Humboldt Bay	Eel River	Tomales Bay	San Francisco Bay	Elkhorn Slough	Morro Bay	Alamitos Bay	Newport Bay	Mission Bay	San Diego Bay	Estero de Punta Banda	Bahia de San Quintin
FRESHWATER (BRACKISH)	Threespine stickleback	*Gasterosteus aculeatus*	X	X	X	X	X	X	X						
	Tidewater goby	*Eucyclogobius newberryi* #						X	X						
	Western mosquitofish	*Gambusia affinis* *						X							
	Prickly sculpin	*Cottus* asper		X	X		X	X							
DIADROMOUS ANADROMOUS	Coho salmon	*Oncorhynchus kisutsch* #	X	X	X	X									
	Chinook salmon	*Oncorhynchus tshawytscha* #	X	X	X		X								
	Steelhead	*Oncorhynchus mykiss* #	X	X	X	X	X								
	American shad	*Alosa sapidissima* *	X		X		X								
	White sturgeon	*Acipenser transmontanus*	X				X								
	Green sturgeon	*Acipenser medirostrus*	X	X	X		X								
	Striped bass	*Morone saxatilis* *				X	X								
CATADROMOUS	Striped mullet	*Mugil cephalus*								X	X	X	X	X	X
ESTUARINE RESIDENTS	Longfin smelt	*Spirinchus thaleichthys*	X	X	X		X								
	Delta smelt	*Hypomesus transpacificus* #					X								
	Bay goby	*Lepidogobius lepidus*		X		X	X	X	X						
	Pacific staghorn sculpin	*Leptocottus armatus*	X	X	X	X	X	X	X	X	X	X	X	X	X
	Bay pipefish	*Syngnathus leptorhynchus*		X	X	X	X	X	X	X	X	X	X	X	X
	Arrow goby	*Clevelandia ios*		X		X	X	X	X	X	X	X	X	X	X
	Longjaw mudsucker	*Gillichthys mirabilis*					X	X	X	X	X	X	X	X	X
	Cheekspot goby	*Ilypnus gilberti*					X			X	X	X	X	X	X
	Shadow goby	*Quietula ycauda*							X	X	X	X	X		
	Yellowfin goby	*Acanthogobius flavimanus* *					X				X		X		
	California killifish	*Fundulus parvipinnis*							X	X	X	X	X	X	X
	Slough anchovy	*Anchoa delicatissima*								X	X	X	X		X
	Deepbody anchovy	*Anchoa compressa*								X	X	X	X	X	X
	Spotted sand bass	*Paralabrax maculatofasciatus*								X	X	X	X	X	
	Barred pipefish	*Syngnathus auliscus*									X	X	X	X	
	Bay blenny	*Hypsoblennius gentilis*										X	X	X	X

MARINE MIGRANTS	Pacific herring	*Clupea pallasi*	X	X	X	X	X	X	X						
	Starry flounder	*Platichthys stellatus*	X	X	X	X	X	X	X						
	English sole	*Pleuronectes vetulus*	X	X	X	X	X	X	X						
	Leopard shark	*Triakis semifasciata*		X		X	X	X	X						
	Bat ray	*Myliobatis californicus*		X		X	X	X					X	X	X
	Jacksmelt	*Atherinopsis californiensis*	X			X	X	X			X	X	X	X	X
	Shiner perch	*Cymatogaster aggregata*	X	X	X	X	X	X	X	X	X	X	X	X	X
	Topsmelt	*Atherinops affinis*		X	X	X	X	X	X	X	X	X	X	X	X
	California halibut	*Paralichthys californicus*				X	X	X	X	X	X	X	X	X	X
	Diamond turbot	*Hypsopsetta guttulata*					X	X	X	X	X	X	X	X	X
	Black perch	*Embiotoca jacksoni*						X	X	X	X	X	X	X	X
	Spotted turbot	*Pleuronichthys ritteri*							X	X	X	X	X	X	X
	Yellowfin croaker	*Umbrina roncador*								X	X	X	X	X	X
	Surf smelt	*Hypomesus pretiosus*	X	X	X	X	X	X							
MARINE	Brown smoothhound	*Mustelus henlei*		X		X	X	X							
	Northern anchovy	*Engraulis mordax*	X	X	X	X	X	X	X	X	X	X	X	X	X
	Speckled sanddab	*Citharichthys stigmaeus*		X		X	X	X	X						
	White seaperch	*Phanerodon furcatus*					X	X	X		X				
	Gray smoothhound	*Mustelus californicus*						X	X	X	X	X	X	X	
	Round stingray	*Urolophus halleri*								X	X	X	X	X	X
	Barred sand bass	*Paralabrax nebulifer*								X	X	X	X	X	X

NOTE: Based on salt tolerance and life- history pattern. X = species present; # = species is endangered, threatened, or contains one or more populations with this status; * = alien species. Modified from Moyle and Cech, 2000.

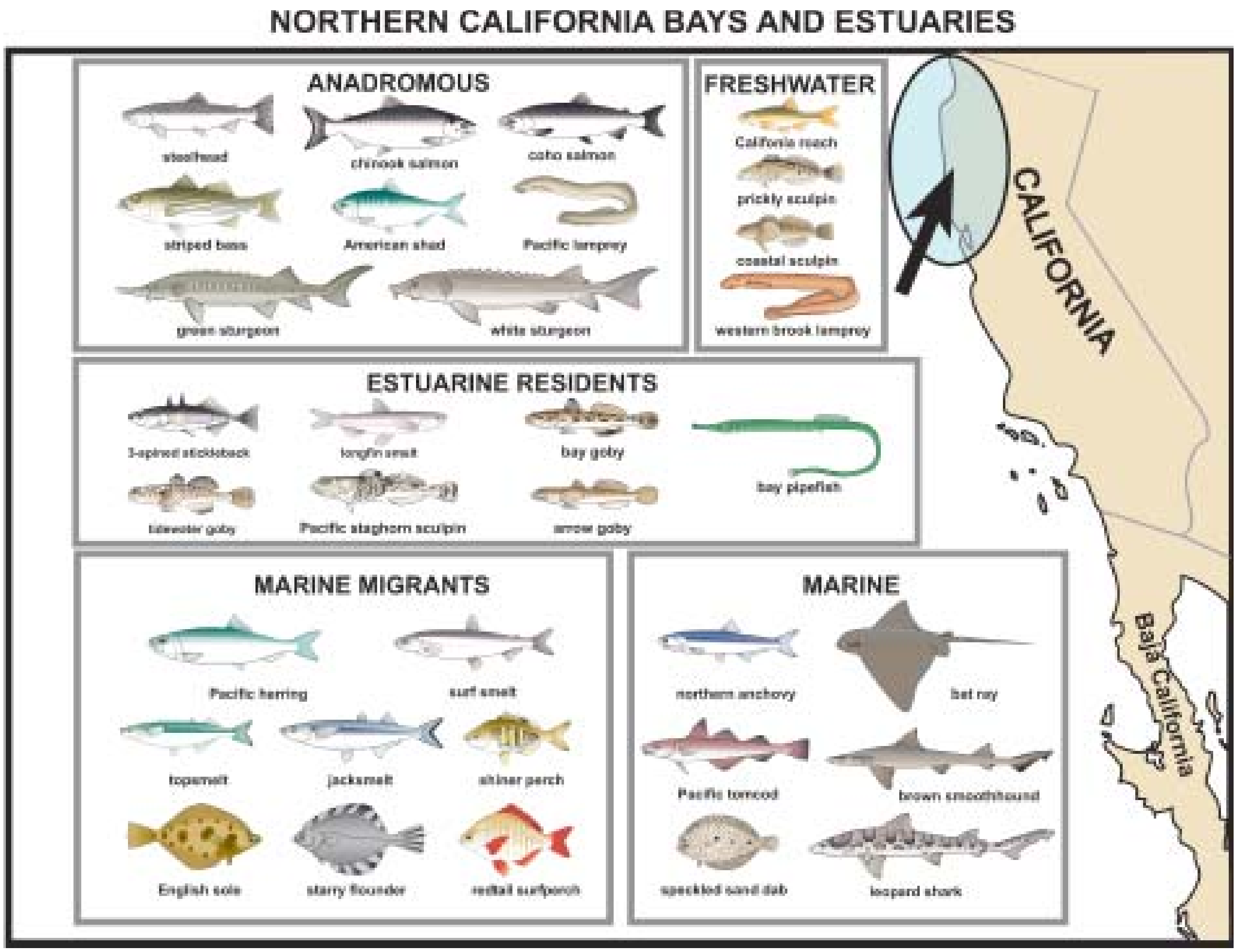


FIGURE 5-6 Profiles of fishes in northern California bays and estuaries representing five ecological categories based on salt tolerance and life-history pattern: freshwater taxa, anadromous taxa, estuarine residents, marine migrants, and marine species that seasonally or occasionally enter these habitats.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

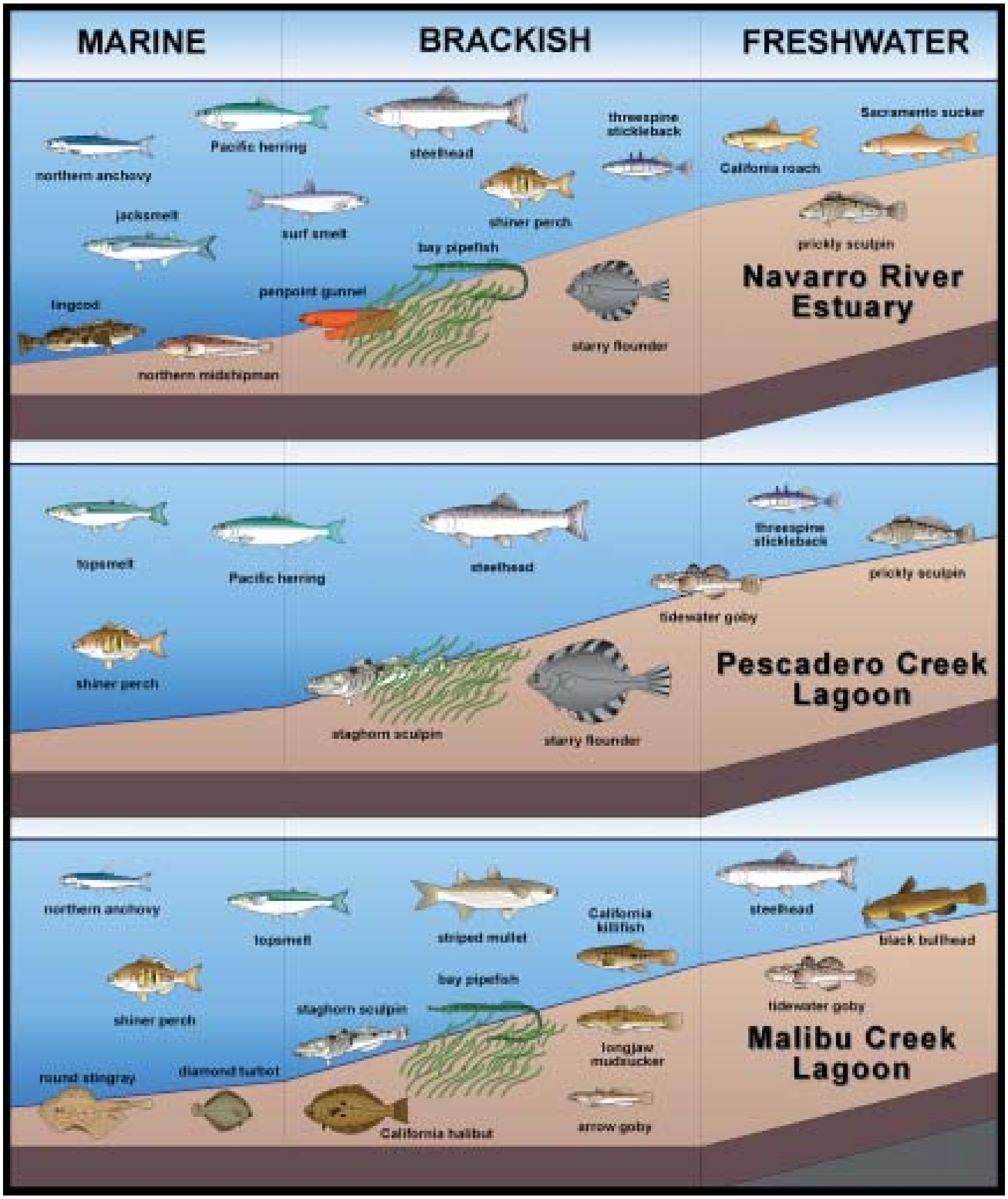


FIGURE 5-7 Profiles of principal fish species in three small canyon- or river-mouth estuaries. Navarro River estuary is located in Northern California south of Humboldt Bay, Pescadero Creek lagoon in Central California near Monterey Bay, and Malibu Creek lagoon in Southern California in the city of Malibu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

TABLE 5-4

Bay-Estuarine Fish Taxa in California That Are in Some State of Jeopardy

Common Name	*Scientific Name*	*Status in California*
Pacific lamprey	*Petromyzon tridentata*	Watch list
Green sturgeon	*Acipenser medirostris*	State special concern
Delta smelt	*Hypomesus transpacificus*	Federally threatened
Longfin smelt	*Spirinchus thaleichthys*	State special concern
Eulachon	*Thaleichthys pacificus*	State special concern
Coho salmon	*Oncorhynchus kisutch*	Northern ESU: federally threatened Central ESU: federally threatened and state endangered
Chinook salmon	*Oncorhynchus tshawytscha*	Seventeen runs: ranging from extirpated to stable or increasing
Pink salmon	*Oncorhynchus gorbuscha*	Extirpated
Chum salmon	*Oncorhynchus keta*	Near extirpation
Steelhead	*Oncorhynchus mykiss*	At least eight ESUs; ranging from watch list to candidate for federally threatened to federally threatened to federally endangered
Coastal cutthroat trout	*Oncorhynchus clarki clarki*	State special concern
Tidewater goby	*Eucyclogobius newberryi*	Federally endangered; state fully protected

NOTE: Based on information in Moyle, 2002. ESU = Evolutionary Significant Unit, a geographic group of populations that share common genetic, life-history, ecological, and other traits and that seem to be on a common evolutionary trajectory (Waples, 1991).

TABLE 5-5

Alien Fishes Established in Bay-Estuarine Habitats in California

Common Name	*Year of Introduction*	*Origin*	*Main Reason for Introduction*	*Current Distribution in California*
American shad	1871	Eastern USA	Food	Mainly north
Striped bass	1879	Eastern USA	Sport/food	Mainly San Francisco Bay
Rainwater killifish	1950s	Eastern USA	Hitchhiker	Mainly San Francisco Bay, also Newport Bay
Wakasagi	1959	Japan	Forage	Mainly San Francisco Bay
Yellowfin goby	Early 1960s	Eastern Asia	Ballast water	Tomales Bay, San Francisco Bay, and south
Chameleon goby	1962	Japan	Ballast water	Mainly San Francisco Bay
Shimofuri goby	~1980	Japan	Ballast water	Mainly San Francisco Bay and reservoirs
Shokihaze goby	~1995	Japan	Ballast water	Mainly San Francisco Bay

NOTE: Based on information in Dill and Cordone, 1997; and Moyle, 2002.

Another species in jeopardy is the tidewater goby, a species listed as federally endangered since 1994 and fully protected by the state since 1987 (Moyle, 2002). This small, annual fish originally occurred in coastal lagoons in northern California and also all along the coast from Del Norte County in the north to San Diego County in the south. The species has been extirpated from San Francisco Bay and numerous other localities, especially south of Point Conception. Tidewater gobies prefer shallow, well-oxygenated lagoons with salinities <10 ppt, but they can live over a much broader range. Populations rarely intermingle, and therefore sites of extirpation are unlikely to be recolonized. Causes of decline and extirpation of tidewater goby populations include farming, logging, and urbanization upstream, draining of wetlands, opening of coastal lagoons to tidal flushing, and encountering nonnative species that either prey upon or compete with them. This species, however, seems to be a sensitive indicator of environmental conditions and responds quickly to improved health of coastal lagoons and adjoining watersheds.

Alien Species

References were made to the impacts of alien species (also referred to as introduced or exotic species) in the above discussion of species in jeopardy. Other than in freshwater habitats, alien fish species in California are most common and diverse in bay-estuarine systems (see chapter 24). Several exotic species occur in both freshwater and bay-estuarine habitats, in part a reflection of their tolerance of a wide range of salinity conditions. Alien species in bays and estuaries in California are listed in table 5-5, and detailed accounts are provided in Dill and Cordone (1997) and Moyle (2002). Some of these nonnative species have been members of northern bay-estuarine ecosystems for such a long time that they are undoubtedly considered native species by some people. Prominent among these alien forms are two anadromous species, American shad and striped bass. Shad were introduced from Atlantic coastal waters to the Sacramento River in 1871, and since that time they have been a highly successful transplant, becoming first an important commercial species and then a popular sport fish. Although now distributed from Alaska to northern Baja California, American shad spawn mainly in larger rivers from the Sacramento drainage northward with lesser runs in smaller streams in northern California. No negative impacts of this planktivorous species on native fishes have been documented. Shad populations have declined in recent decades, probably as a result of water diversions from spawning tributaries and, in turn, reduced attraction of potential spawners to these diminished flows.

The striped bass, even though also in decline in California, presents a different picture of an alien species and its impacts (Moyle, 2002). Introduced first from a New Jersey river to San Francisco Bay in 1879, the population of this piscivorous fish increased dramatically in the early decades and may have been responsible for changes in the estuarine food web and in part for declines in some native species, including Central Valley chinook salmon populations. The striped bass is still one of the most abundant fish species in San Francisco Bay, which is home to the main breeding population even though this euryhaline species has been widely planted in reservoirs in California and other states. The decline in striped bass numbers may be the result mainly of water diversion, as is the case for numerous other species, but also of several other interacting factors including climatic fluctuations, pollution, reduced estuarine productivity, invasions of alien species, and harvesting, especially of large females. The impacts of new alien species on this established alien species are fascinating to contemplate. A recent invader in particular, the overbite clam, has reduced plankton populations in San Francisco Bay thus decreasing the food available to larval and juvenile striped bass. Juvenile bass, in turn, are the principal prey of adult striped bass. Importantly, management of the San Francisco Bay ecosystem has focused heavily on striped bass with the thought that the measures that benefit this species also help other species. As Moyle (2002) points out, however, striped bass is a unique species and, among other differences, mostly spawns later than native species, so that the management practices of timing increased outflows for this species will not necessarily enhance the reproduction of native fishes.

Some of the more recent fish introductions appear to have the potential for serious detrimental effects on native fishes. We refer here to small Asian species, in particular a smelt and several species of goby that have become established in California estuarine waters in the last 50 years, also as reviewed by Moyle (2002). Wakasagi is a planktivorous smelt intentionally introduced from Japan into California reservoirs in 1959 to provide forage for rainbow trout and other salmonids. By the 1990s, it had spread through water diversions into the San Francisco Bay estuary where it has already hybridized with delta smelt and shows the potential to compete with this endangered species for food and spawning sites. Interestingly, however, even though wakasagi has broader salinity and temperature tolerances than delta smelt, it had not become abundant in San Francisco Bay as of 2001, perhaps because of its vulnerability as a schooling species to predation by striped bass.

In contrast to wakasagi, the exotic estuarine gobies in California were not the result of deliberate introductions but accidental transplants presumably arriving in ballast water of ships from Japan or other parts of Asia (Moyle, 2002). The earliest of these arrivals was yellowfin goby, a relatively large species, which appeared in San Francisco Bay in the early 1960s and subsequently colonized other bay-estuarine habitats, especially Elkhorn Slough in central California and Newport Bay and San Diego Bay in southern California. This species is broadly tolerant of fluctuating temperatures, salinities, and oxygen levels. It can survive in freshwater but requires some salt content for breeding and can complete its life cycle entirely in the ocean. Although the yellowfin goby has become one of the most abundant species in San Francisco Bay and Newport Bay and is still increasing its range, its effect on native species remains unknown. Other alien gobies established in California include shimofuri goby, chameleon goby, and shokihaze goby, all of which belong to the genus *Tridentiger*. Shimofuri goby has expanded rapidly, and, as is characteristic of many successful introduced species, exhibits high dispersal ability, broad tolerance to changing environmental conditions, high reproductive output, aggressive behavior, and a flexible diet that includes exotic invertebrates. Although its impact on native species in San Francisco Bay is largely unknown, its expected invasion of smaller lagoons in southern California may spell trouble for the tidewater goby because, as Matern (1999) has shown in laboratory experiments, shimofuri gobies win out in interactions with this endangered species. Moyle (2002) has cautioned that tidewater goby habitats should be protected from invasion by this alien species wherever possible.

Rainwater killifish is another small alien species that has become established in San Francisco Bay and a few freshwater habitats, and apparently in Newport Bay in southern California (table 5-5). This species is native to coastal waters of the Atlantic and Gulf coasts as well as some rivers in Texas and New Mexico and may have been introduced from the Atlantic coast into San Francisco Bay and Yaquina Bay in Oregon as embryos attached to live oysters (Moyle, 2002). The rainwater killifish obviously tolerates a range of salinities and feeds opportunistically on a variety of invertebrates. Like the western mosquitofish, which it resembles superficially, the fish is known to consume mosquito larvae, and its spread may be aided by attempts to use it for mosquito control (Moyle, 2002).

CENTRAL CALIFORNIA

Elkhorn Slough and Morro Bay (fig. 5-1) are the largest bay-estuarine systems on the central California coast. Smaller wetlands also form seasonally at the mouths of the numerous creeks along the central coast (Ferren et al., 1996a,b,c). The fish assemblages of Elkhorn Slough have been well studied, those of Morro Bay less so, and those occurring in the smaller systems have been surveyed in only a few cases.

Each of the two large systems supports a fish assemblage with varying numbers of year-round estuarine residents, freshwater occupants, and marine species from nearshore waters that enter the estuary to feed, mate, and spawn (table 5-3; fig. 5-8). In contrast to northern California bays and estuaries, both Elkhorn Slough and Morro Bay are characterized by fewer diadromous species, given that sturgeon, shad, salmon, and striped bass are absent or rare in these systems. Elkhorn Slough, a part of the National Estuarine Research Reserve System, is a shallow, tidal embayment and seasonal estuary at the head of the Monterey submarine canyon in Monterey Bay. The slough system comprises several distinct fish habitats, including the Moss Landing harbor, adjacent Bennett Slough, the main channel extending inland about 10 kilometers and fringed by extensive mudflats, a network of tidal creeks that meander through pickleweed marshes, and salt-evaporation ponds. All of these habitats are connected by the exchange of

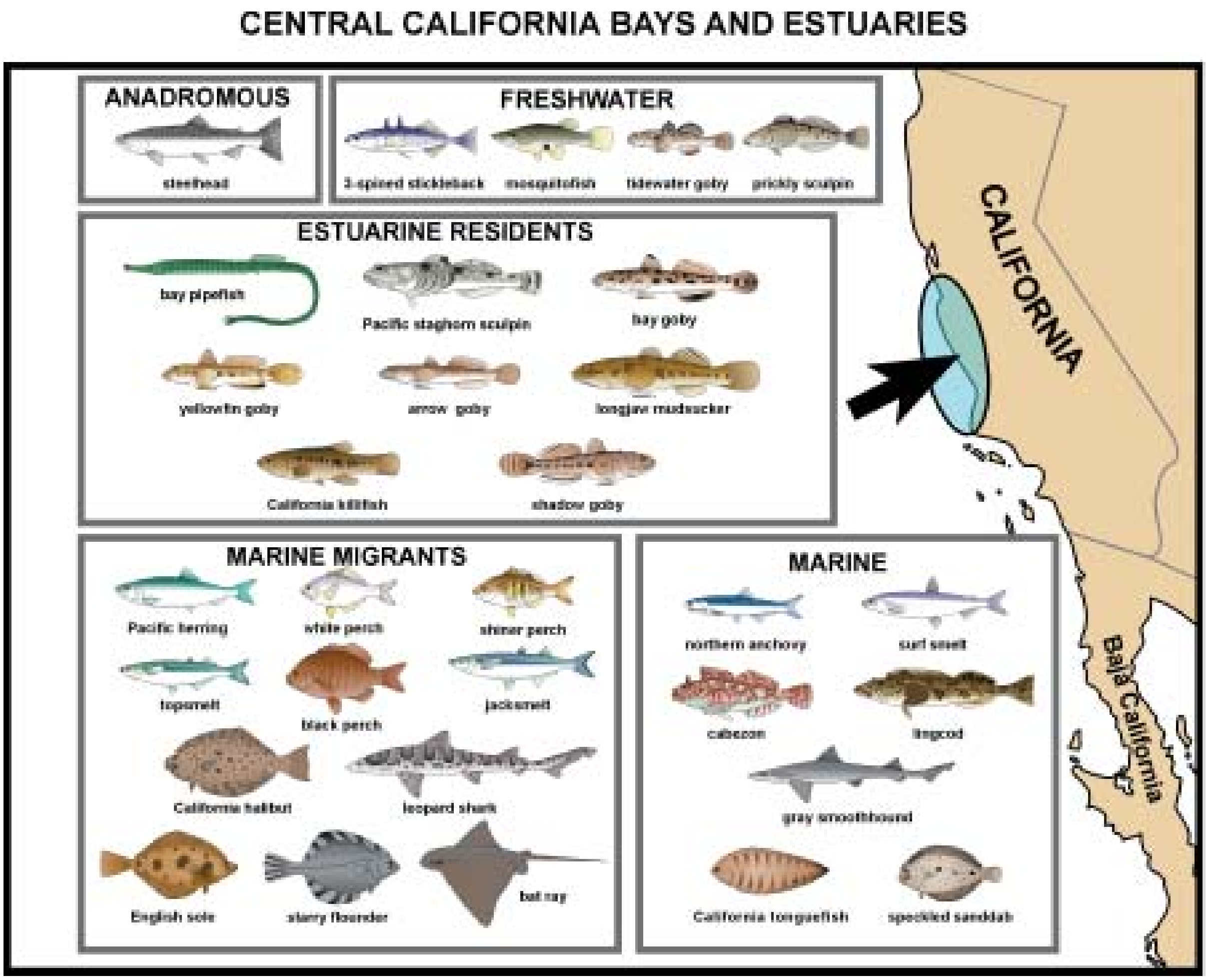


FIGURE 5-8 Profiles of fishes in central California bays and estuaries representing five ecological categories based on salt tolerance and life-history pattern: freshwater taxa, anadromous taxa, estuarine residents, marine migrants, and marine species that seasonally or occasionally enter these habitats. (See Table 5-3.)

tidal water, but differ in water depth, tidal influence (primarily salinity and current flow), and biological components such as plants that provide spawning sites and refuge for their particular assemblages of invertebrates and juvenile fishes. As in most bays and estuaries, fish distribution patterns vary with distance from the mouth of Elkhorn Slough. For example, marine species typically reside in the lower slough and harbor, where waters are strongly influenced by ocean and bay hydrographic properties such as higher salinity, lower water temperature, and variable turbulence compared with upper reaches of the slough. Resident fishes are distributed widely but most are abundant in the upper slough. Freshwater species occupy middle and upper slough habitats, including tidal creeks, ponds, and salt marshes. Dominant species of the upper slough and tidal creeks are best characterized as euryhaline with affinities toward higher temperature.

At least 102 fish species from 43 families have been identified in Elkhorn Slough, and most (82 species) of them are marine fishes from Monterey Bay (Yoklavich et al., 1991). The most prevalent freshwater species are threespine stickleback, western mosquitofish, and prickly sculpin. Numerically dominant estuarine residents are bay pipefish, Pacific staghorn sculpin, and several species of goby. Principal species of marine migrants are topsmelt, jacksmelt, shiner perch and white seaperch, leopard shark, and bat ray. Some of the most abundant marine migrant species that visit the slough seasonally (e.g., Pacific herring, topsmelt, and shiner perch) are important forage species for coastal birds, fishes, and mammals. Other marine migrants, including economically valuable species such as English sole and California halibut, use Elkhorn Slough as a nursery ground and inhabit the relatively warm, calm slough waters as juveniles before moving offshore to continue development as adults. Gray smoothhound, northern anchovy, and speckled sanddab are marine species that also commonly occur in the Slough. Notably, only four alien species, American shad, western mosquitofish, striped bass, and yellowfin goby, occur in the Elkhorn Slough system. Compared to San Francisco Bay, Elkhorn Slough seems to have offered little opportunity for the introduction of exotic fish species. The Slough's narrow opening may isolate it from tanker traffic and mariculture operations, two activities usually implicated in the introduction of non-native fishes (Yoklavich et al., 1991). Various aspects of the fish assemblages in Elkhorn Slough have been studied in recent decades, including temporal and spatial patterns in abundance and diversity of juvenile and adult fishes (Talent, 1985; Yoklavich et al., 1991; Yoklavich et al., 2002), species composition and seasonality of larval fishes (Yoklavich et al., 1992), feeding ecology and energetics (Talent 1976, 1982; Yoklavich 1982a,b; Barry et al., 1996), and growth and reproduction of elasmobranchs (Martin and Cailliet, 1988a,b; Yudin and Cailliet, 1990; Kusher et al., 1992).

The fish assemblages of Morro Bay, a designated National Marine Estuary, have been investigated in only two surveys. Fierstine et al. (1973) used small otter trawls to characterize the fish species in five zones during a 1-year period, and Horn (1980) sampled fishes with a beach seine at one location for 24-hour periods each quarter for a year. These two studies are complementary in that they used different sampling gear and, in part because of this difference, overlapped only slightly in habitats sampled. Whereas Fierstine et al. (1973) sampled the main channels and collected 66 species, Horn (1980) collected over the large mudflats of the Baywood Park area, along with some of the main channel west of these shallow areas, and captured 21 species, most of which had been taken in the earlier study. The combined list of species from the two studies is dominated by topsmelt, shiner perch, Pacific staghorn sculpin, and northern anchovy. Depending upon habitat and time of year sampled, the next species of numerical importance were California killifish, bay pipefish, shadow goby, bay goby, and tidewater goby, in addition to several species of surfperch and shark.

The importance of habitat heterogeneity and environmental gradients in supporting fish species diversity is clearly demonstrated in Morro Bay, as it is in Elkhorn Slough, despite the limited number of studies of Morro Bay fishes. These relationships hold whether the focus is on the distinctiveness of fish assemblages in different habitats or on the classification of species based on salinity tolerance and life-history pattern. Fierstine et al. (1973) showed that zonation patterns occur in Morro Bay similar to those reported by Yoklavich et al. (1991) for Elkhorn Slough. For example, the sandy habitat near the entrance of Morro Bay was dominated by walleye surfperch, diamond turbot, sand sole, and speckled sanddab. In contrast, the area just inside the bay near the power plant was populated mainly by pelagic species, including northern anchovy, jack mackerel, and Pacific pompano, and by more inshore species such as topsmelt. Based on Fierstine's (1973) trawl samples, silty areas containing eelgrass in the channels and mudflats of the southern part of Morro Bay were dominated by surfperches, including shiner perch and black perch plus walleye surfperch and white seaperch, flatfishes such as English sole, starry flounder, and diamond turbot, and two silversides, topsmelt and jacksmelt. Pacific staghorn sculpin was also relatively abundant as were juveniles of lingcod and several species of rockfishes. Six species of elasmobranchs—bat ray, round stingray, horn shark, shovelnose guitarfish, gray smoothhound, leopard shark, and thornback—were collected in the spring and summer months. Horn's (1980) beach seine hauls in shallower areas of the southern part of the bay were more heavily dominated by topsmelt, contained more gobies, and, uniquely, captured bay pipefish and California killifish.

Unfortunately, fishes occupying tidal creeks or habitats other than mudflats and channels in Morro Bay have not been sampled. Both Yoklavich et al. (1991) and Barry et al. (1996) noted that tidal creeks are most likely to be the main nursery habitats in Elkhorn Slough and that this function could be diminished by human-induced physical processes such as erosion. Similar studies and predictions need to be conducted in Morro Bay so that human influences on the habitats and their fish assemblages can be understood and minimized.

In terms of salt tolerance and life-history pattern, Morro Bay fish assemblages are similar to those of Elkhorn Slough with a few differences based largely on latitudinal distinctions (table 5-3; fig. 5-8). The principal freshwater species in Morro Bay is threespine stickleback. As mentioned above, diadromous fishes are uncommon in both Morro Bay and Elkhorn Slough. Dominant estuarine residents are similar to those in Elkhorn Slough, except that two species of southern affinity, California killifish and shadow goby, reach the northern extent of their ranges in Morro Bay. Marine migrants that commonly enter Morro Bay include forage species such as Pacific herring, topsmelt, and shiner perch and commercially important species such as English sole and California halibut. Another marine migrant, spotted turbot, extends northward only to Morro Bay and thus further distinguishes the fish assemblages of this system from those in Elkhorn Slough. Principal marine species that enter Morro Bay at least occasionally include gray smoothhound, northern anchovy, and speckled sanddab, as in Elkhorn Slough, but two other marine species, brown smoothhound and surf smelt, occur more commonly in the latter system. No alien species appears to have established itself in Morro Bay. The reasons proposed for the limited number of exotic species in Elkhorn Slough, isolation from tanker traffic and mariculture operations, also may be largely responsible for the absence of such species in Morro Bay.

SOUTHERN CALIFORNIA

Bays and estuaries in southern California are nestled within an arid region of Mediterranean climate and are fed by small, seasonal rivers and streams. As a result, these systems are mostly small and mainly marine in character, with fish assemblages that are largely devoid of freshwater and anadromous species and are dominated by estuarine residents and marine migrants (table 5-3 and fig. 5-9). Nevertheless, bays and estuaries in the region vary greatly in size from numerous small, canyon-mouth estuaries such as Malibu Lagoon to a few large systems, especially Anaheim Bay, Newport Bay, and San Diego Bay. The larger bays and estuaries display considerable habitat diversity and develop environmental gradients, especially during the winter months when the most rainfall occurs. These seasonal variations in habitat conditions combined with the warm-temperate geographic setting result in dynamic and distinctive fish assemblages occupying southern California bays and estuaries.

These bay-estuarine assemblages (table 5-3, fig. 5-9) are distinguished, as mentioned, by lack of a freshwater component, except during occasional wintertime floods (see Horn and Allen, 1985), and also by lack of anadromous species, other than small runs of Pacific lamprey and mostly historic runs of the now endangered southern steelhead population (see table 5-4). Further distinction is achieved by the presence of striped mullet, the only catadromous species in the state. Principal estuarine residents in the larger bays and estuaries in southern California include Pacific staghorn sculpin, bay pipefish, and arrow goby, all virtually ubiquitous in these habitats in the state. Other common estuarine species are California killifish, slough anchovy, deepbody anchovy, spotted sand bass, and several other species of goby. Marine migrants are dominated by topsmelt, shiner perch, black perch, diamond turbot, juvenile California halibut, spotted turbot, and yellowfin croaker. Marine species that move into bays and estuaries in spring and summer include northern anchovy, gray smoothhound, round stingray, and barred sand bass. The most abundant alien

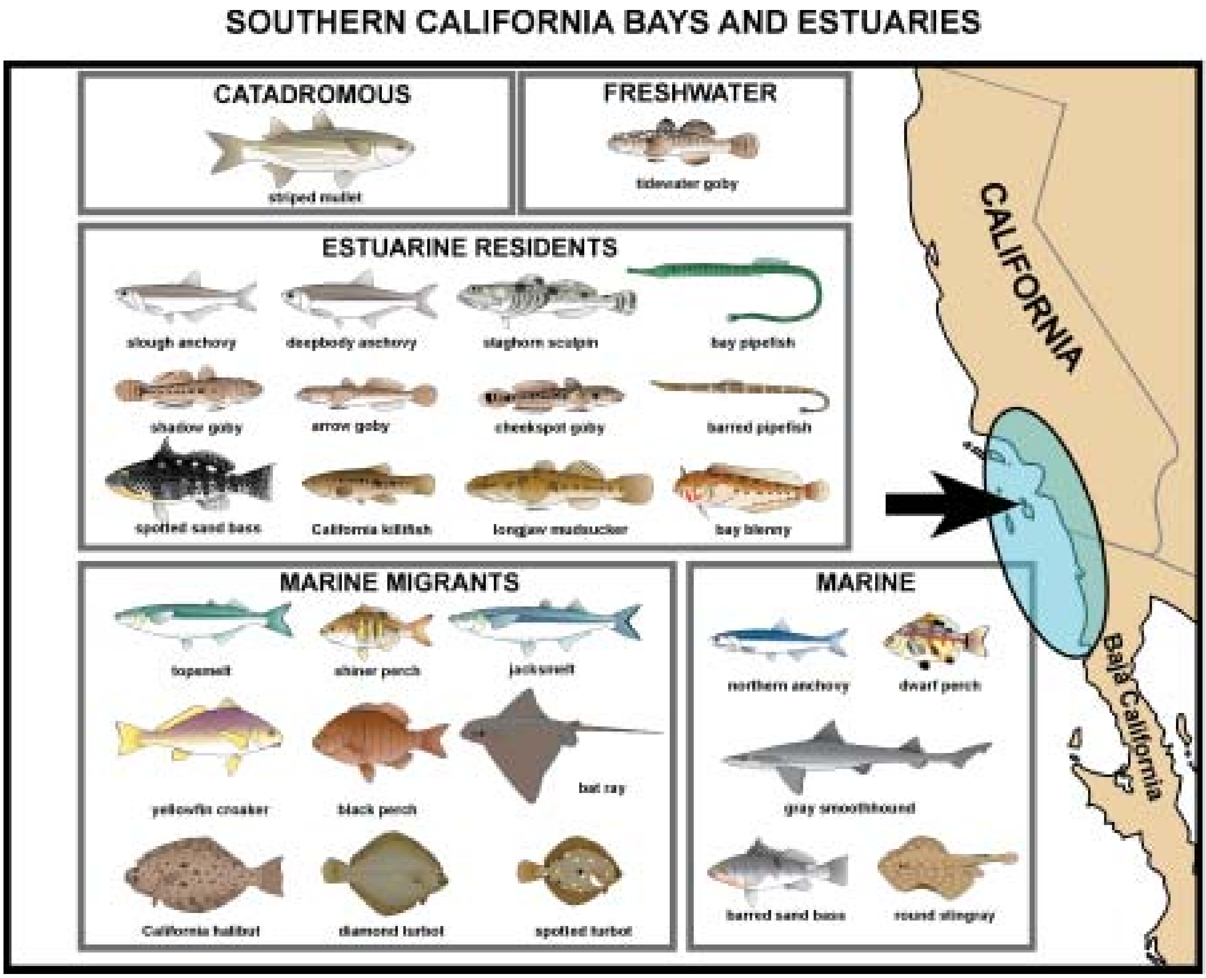


FIGURE 5-9 Profiles of fishes in Southern California and Northern Baja California bays and estuaries representing four ecological categories based on salt tolerance and life-history pattern: catadromous taxa, estuarine residents, marine migrants, and marine species that seasonally or occasionally enter these habitats. (See Table 5-3.)

species in southern California bay-estuarine systems is probably yellowfin goby. A few other alien species, such as rainwater killifish, which has been collected in upper Newport Bay, chameleon goby, now known from Los Angeles Harbor, and shimofuri goby have the potential to expand broadly into southern California bays and estuaries (Moyle, 2002). Attempts by the California Department of Fish and Game to introduce striped bass into Newport Bay in the 1970s eventually failed even though, for several years, the species was a reasonably abundant member of the top carnivore guild in that system (Horn and Allen, 1985). Reproductive failure occurred apparently because of insufficient amounts of low-salinity water required by the species for spawning (Horn et al., 1984).

Differential habitat use characterizes the bay-estuarine fish assemblages in southern California just as in the other parts of the state (see Horn and Allen, 1985; Valle et al., 1999; Allen et al., 2002). The tidal channels of salt marshes are occupied primarily by California killifish and longjaw mudsucker. Shallow benthic areas of mudflats are inhabited most abundantly by four other species of goby, whereas the adjacent water column of both the shoreline and main channels are occupied by several common species, especially topsmelt, striped mullet, deepbody anchovy, and slough anchovy. Deeper areas of bay-estuarine habitats are populated mainly by marine migrants, including black perch, spotted sand bass, diamond turbot, and juvenile California halibut, and by marine species such as round stingray and barred sand bass. Eelgrass beds provide important habitat for several bay-estuarine fish species, including bay pipefish, barred pipefish, shiner perch, and giant kelpfish (Allen et al., 2002). Recent eelgrass transplants on mitigation sites in San Diego Bay indicate that successful restoration of eelgrass habitat can be achieved with fish densities quickly reaching those of a natural, reference eelgrass bed in the bay (Pondella et al., 2003).

The fish assemblages of several small to large bay-estuarine systems in southern California have been studied intensively in recent decades. The major findings of studies in Malibu Lagoon, Anaheim Bay, Newport Bay, San Diego Bay, Sweetwater Marsh, and Tijuana Estuary are highlighted here. Malibu Lagoon is one of the small, canyon-mouth estuaries that occur throughout coastal southern California and contain relatively diminished fish assemblages, including endangered steelhead and tidewater goby (Lafferty et al., 1999; Dawson et al., 2001) and small populations of common estuarine residents. This small lagoon has a continuous freshwater inflow, but this flow varies seasonally in magnitude (Swift et al., 1989,

TABLE 5-6
Tropical/Subtropical Fishes Captured During a 1994 to 1999 Study of Fish Assemblages in San Diego Bay

Common Name	*Scientific Name*	*Total Number Collected*
California halfbeak	*Hyporhamphus rosae*	410
Bonefish	*Albula vulpes*	175
California needlefish	*Strongylura exilis*	42
Shortfin corvina	*Cynoscion parvipinnis*	30
Pacific seahorse	*Hippocampus ingens*	13
California butterfly ray	*Gymnura marmorata*	4
Banded guitarfish	*Zapteryx exasperata*	2
Red goatfish	*Pseudoupeneus grandisquamosus*	1
	Total	677
	Percent of grand total of fishes collected	0.14%

NOTE: After Allen et al., 2002.

1993). A study by Ambrose and Meffert (1999) showed that this system contains typical salt marshes species, such as topsmelt, California killifish, arrow goby, and longjaw mudsucker, near its mouth plus steelhead, tidewater goby, and various freshwater species in the upstream areas (fig. 5-7).

Anaheim Bay (fig. 5-1), a part of the National Wildlife Refuge system since 1972, consists mainly of a relatively undisturbed salt marsh within the United States Naval Weapons Station near Seal Beach, California. Dredging of the mouth and adjacent harbor has allowed uninterrupted tidal flow into the marsh over the years. The main habitats within this bay-estuarine system include salt marsh, tidal mud flats, and subtidal channels. About the time that Anaheim Bay became a refuge, its fish assemblage and other marine resources were examined in a multifaceted study that was published as an edited volume by Lane and Hill (1975). This work included an annotated checklist of 45 fish species in Anaheim Bay and 42 in the outer harbor and detailed life-history accounts of six of the most common species: California killifish, shiner perch, arrow goby, Pacific staghorn sculpin, California halibut, and diamond turbot. Overall, these studies indicated that the Anaheim Bay salt marsh is highly productive and supports rapid growth rates of the resident fish populations.

Upper Newport Bay (fig. 5-1) was purchased by the state of California in 1975 and since then has been managed as an ecological reserve by the California Department of Fish and Game. The upper portion represents one of the largest, least altered salt marsh systems in the state south of Morro Bay. Shortly after Upper Newport Bay was established as a reserve, comprehensive 1-year (1978–1979) studies of the fish assemblages were conducted (Allen, 1982; Horn and Allen, 1985) and were followed by a 2-year monitoring survey in 1986–1987 to assess the effects of additional estuarine habitat on fishery-related species (Allen, 1988). In these investigations, topsmelt made up the majority of individuals in seine hauls, and this species along with striped mullet accounted for most of the fish biomass in the samples. Typically, topsmelt was followed in numerical abundance in these studies by California killifish, arrow goby, western mosquitofish, deepbody anchovy, and slough anchovy. Heavy rainfall in the first few months of the 1978–1979 study was responsible for the relatively high abundance of western mosquitofish during that period in this normally marine-dominated estuary.

San Diego Bay (fig. 5-1), the third largest California bay-estuarine system in California after San Francisco Bay and Humboldt Bay, provides expansive and diverse habitats for fishes, including deep channels, marinas, and extensive shallows largely covered with eelgrass. The southern half of the bay is relatively unaltered and represents more natural condition of the system. In a 5-year (1994–1999) study of the bay's fish assemblages by Allen et al. (2002) using a variety of sampling gear, just three of the 78 species collected, northern anchovy, topsmelt, and slough anchovy, accounted for most of the total numbers, whereas five species, round stingray, spotted sand bass, northern anchovy, bat ray, and topsmelt, made up two-thirds of the total biomass. In terms of an Index of Community Importance incorporating numbers, biomass, and frequency of occurrence, topsmelt, round stingray, and northern anchovy were the top-ranked species.

One of the striking outcomes of the 5-year study by Allen and co-workers (2002) was the variety of tropical/subtropical species that were captured in San Diego Bay (table 5-6). Six of these species ranked in the top 50 in the Index of Community Importance: California halfbeak, shortfin corbina, California needlefish, California butterfly ray, bonefish, and Pacific seahorse (in descending index value). All warm-water species listed in Table 5-6 occur mainly farther south in the Mexican and Panamic biogeographic provinces (see Hastings, 2000), and each reaches the northern limit of its range in Southern California (Allen and Robertson, 1994). The shallow portions of San Diego Bay, as well as other bays and estuaries in the southern part of southern California, seem to act as refuges for these species. The frequent occurrence of El Niño events starting in 1982–1983 and culminating in the 1997–1998 event, along with the sustained warming trend in the region during the same time period (Smith, 1995), appears to have promoted the establishment of these otherwise tropical and subtropical fishes in Southern California.

Studies of the fish assemblages in Sweetwater Marsh and Tijuana Estuary by Joy Zedler and associates are important contributions to bay-estuarine fish ecology in the region. Sweetwater Marsh, the largest remaining wetland on San Diego Bay and a part of the National Wildlife Refuge system, is continuously open to tidal action and comprises a mosaic of salt marsh vegetation and channels along with dredged channels and elevated roadways (Zedler, 2001). Tijuana Estuary (fig. 5-1), one of the most nearly intact salt marshes in southern California and a National Estuarine Research Reserve since 1981, also has retained its connection to the ocean almost continuously and persisted as an important bay-estuarine habitat

TABLE 5-7
20 Most Abundant Species Captured in Beam Trawl Sampling

Estero de Punta Banda				Bahia de San Quintin			
Common Name	Scientific Name	Number	% of Total	Common Name	Scientific Name	Number	% of Total
Kelp bass	*Paralabrax clathratus*	353	38.1	Bay pipefish	*Syngnathus leptorhynchus*	790	41.0
Bay blenny	*Hypsoblennius gentilis*	119	12.9	Shiner perch	*Cymatogaster aggregata*	205	10.6
Bay pipefish	*Syngnathus leptorhynchus*	107	11.6	Cheekspot goby	*Ilypnus gilberti*	183	9.5
California halibut	*Paralichthys californicus*	105	11.3	California tonguefish	*Symphurus atricauda*	162	8.4
Barred sand bass	*Paralabrax nebulifer*	58	6.3	California halibut	*Paralichthys californicus*	137	7.1
Spotted turbot	*Pleuronichthys ritteri*	56	6.0	Black perch	*Embiotoca jacksoni*	127	6.6
Spotted sand bass	*Paralabrax maculatofasciatus*	32	3.5	Bay blenny	*Hypsoblennius gentilis*	87	4.5
Diamond turbot	*Hypsopsetta guttulata*	23	2.5	Diamond turbot	*Hypsopsetta guttulata*	55	2.9
Shiner perch	*Cymatogaster aggregata*	22	2.4	Mussel blenny	*Hypsoblennius jenkinsi*	40	2.1
Salema	*Xenistius californiensis*	13	1.4	Specklefin midshipman	*Porichthys myriaster*	33	1.7
Giant kelpfish	*Heterostichus rostratus*	11	1.2	Giant kelpfish	*Heterostichus rostratus*	28	1.5
Sargo	*Anisotremus davidsoni*	6	0.6	Reef finspot	*Paraclinus integripinnis*	19	1.0
California tonguefish	*Symphurus atricauda*	4	0.4	Arrow goby	*Clevelandia ios*	15	0.8
Senorita	*Oxyjulis californica*	4	0.4	Round stingray	*Urolophus halleri*	8	0.4
Queenfish	*Seriphus politus*	2	0.2	Spotted turbot	*Pleuronichthys ritteri*	7	0.4
Deepbody anchovy	*Anchoa compressa*	2	0.2	Spiny dogfish	*Squalus acanthias*	5	0.3
Mussel blenny	*Hypsoblennius jenkinsi*	1	0.1	Longjaw mudsucker	*Gillichthys mirabilis*	5	0.3
Opaleye	*Girella nigricans*	1	0.1	Spotted scorpionfish	*Scorpaena guttata*	4	0.2
California halfbeak	*Hyporhamphus rosae*	1	0.1	Plainfin midshipman	*Porichthys notatus*	3	0.2
California corbina	*Menticirrhus undulatus*	1	0.1	Kelp bass	*Paralabrax clathratus*	3	0.2
	Totals	926			Totals	1929	

NOTE: Sampling occurred at 5 m depth in two northern Baja California bays and estuaries, Estero de Punta Banda and Bahia de San Quintin. After Rosales-Casian 1997.

despite problems of water quality and sedimentation (Zedler, 2001). The experimental and modeling approaches taken by Zedler and co-workers have demonstrated the importance of salt marsh vegetation and tidal creeks for fish inhabitants. Dominant species at both the Sweetwater and Tijuana sites are the longjaw mudsucker, California killifish, and arrow goby (Desmond et al., 2000). California killifish with access to the rich foraging areas of marsh surfaces consume much more food than killifish confined to creek habitats (West and Zedler, 2000). Applying a bioenergetics model to California killifish growth, Madon et al. (2001) showed that members of this species grow faster if they can feed on the marsh surface than if they are restricted to subtidal channels. These and other findings by the Zedler team make a strong case for including salt marshes and interconnecting tidal creeks in mitigation and restoration projects involving bay-estuarine fish habitats in southern California.

NORTHERN BAJA CALIFORNIA

The bays and estuaries of northern Baja California (fig. 5-1) support fish assemblages generally similar to those of southern California (table 5-3; fig. 5-9). Comparisons are limited, however, because the two Baja California systems, Estero Punta Banda and Bahia de San Quintin, have been sampled using mainly benthic trawls with lesser use of beach seines and gill nets (Hammann and Rosales-Casian, 1990; Rosales-Casian, 1996, 1997) rather than with several types of sampling gear used in the more comprehensive studies in southern California. In particular, the differences in the types of gear employed precludes comparison of schooling and midwater fishes from the southern California and northern Baja California systems.

Beam trawl samples taken in the two Northern Baja California systems were dominated by species commonly collected in trawls in bays and estuaries in southern California (table 5-7). The most abundant species sampled in Estero Punta Banda in 1992–1993 were kelp bass (juveniles), bay blenny, bay pipefish, California halibut, barred sand bass, and spotted turbot. Together, these six species accounted for 86% of the total catch. In Bahia de San Quintin in 1994, the most common species in the trawls were bay pipefish, shiner perch, cheekspot goby, California tonguefish, California halibut, and black perch, which, together, made up 83% of the total numbers of fish collected.

Both Estero Punta Banda and Bahia de San Quintin have been characterized as highly productive bay-estuarine systems that are nursery areas for a number of marine fish species (Rosales-Casian, 1997). Three of these species, California halibut, kelp bass, and barred sand bass, are of major economic importance in both Mexico and the United States (see chapter 22). Baja de San Quintin, which is similar in size to San Diego Bay, may be the more important of the two systems because it is one of the largest, most nearly pristine such habitats on the Pacific coast of Baja California (Zedler, 2001); it also contains extensive eelgrass beds and features an almost permanent upwelling zone near its mouth (Rosales-Casian, 1997). This complex and heterogeneous embayment serves as a reference ecosystem for coastal wetland restoration efforts in southern California, but its pristine status is threatened by several potential development projects (Zedler, 2001).

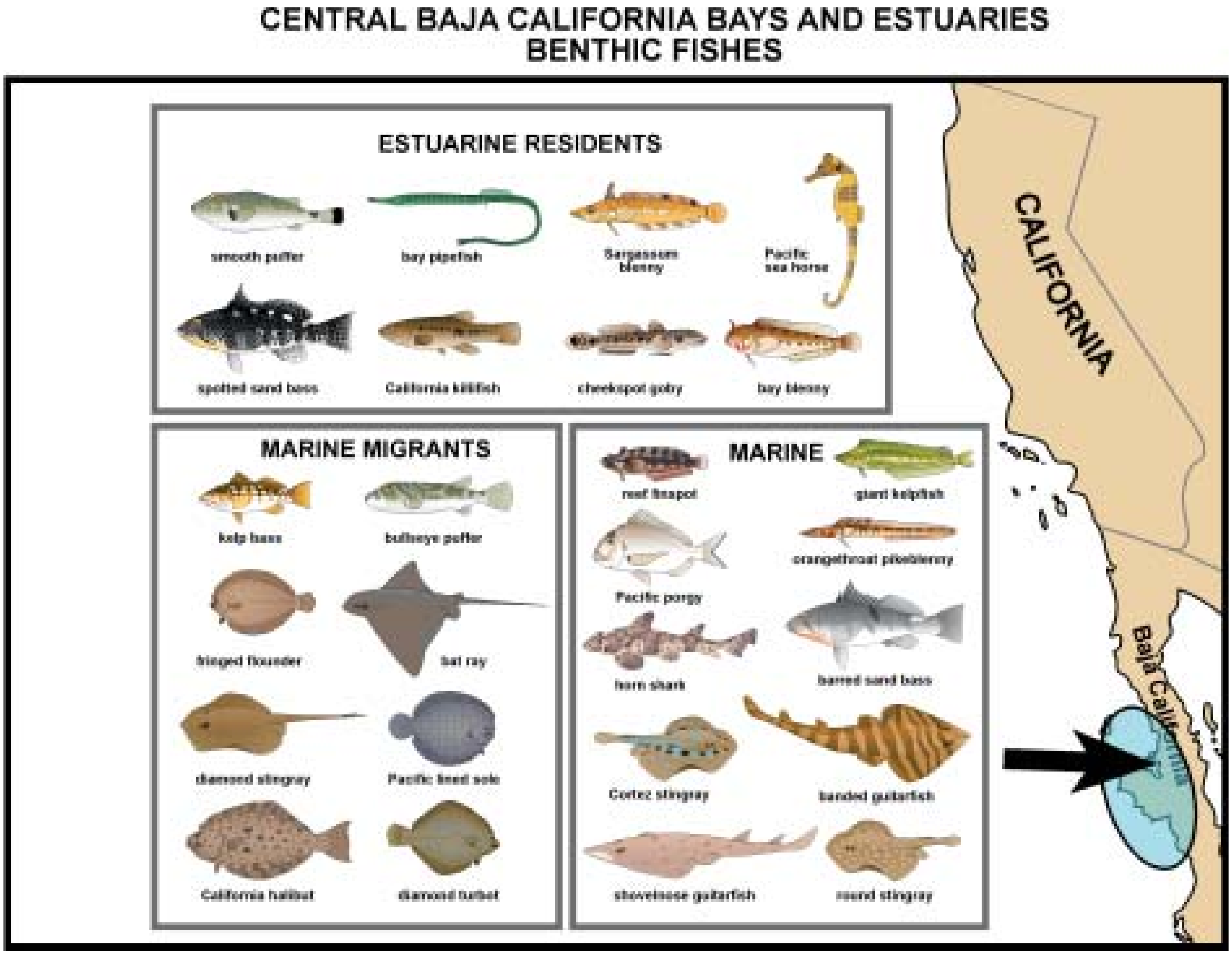


FIGURE 5-10 Profiles of fishes in Central Baja California bays and estuaries representing three ecological categories based on salt tolerance and life-history pattern: estuarine residents, marine migrants, and marine species that seasonally or occasionally enter these habitats. (See Table 5-3.)

CENTRAL BAJA CALIFORNIA

Based on benthic trawl samples, Laguna de Ojo Liebre (fig. 5-1), also known as Scammon's Lagoon, supports a fish assemblage with distinct southern affinities and therefore is substantially different from those in the bays and estuaries of northern Baja California and southern California (fig. 5-10). These trawl samples, containing a mixture of estuarine residents, marine migrants, and marine species, were dominated numerically by spotted sand bass, smooth puffer (*Sphoeroides lispus*), stingrays (*Urolophus halleri* and *U. maculates*), sargassum blenny (*Exerpes asper*), bay pipefish, and diamond turbot (Galván et al., 2000). Only three of these eight species are represented in the bays and estuaries of southern California. Overall, the Ojo Liebre fish assemblage shows a greater affinity with the assemblage in Bahia de Magdalena on the coast of southern Baja California.

Major Ecological Features of Bay-Estuarine Fish Assemblages in California

The fish assemblages inhabiting bays and estuaries in California share several major ecological characteristics, at least some of which are common to bay-estuarine assemblages in other parts of the world. Most of these features have been mentioned in the foregoing sections but are summarized explicitly in this section.

LOW SPECIES DIVERSITY

Bay-estuarine fish assemblages in California and elsewhere in the temperate zone tend to be dominated in abundance by a few (usually ≤5) species (table 5-8) and therefore have relatively low diversity even though many other, but much less common, species are typically encountered (Allen and Horn, 1975; Horn, 1980; Haedrich, 1983; Able and Fahay, 1998). This observation is supported by recent studies in New Zealand (Morrison et al., 2002), Germany (Thiel and Potter, 2001), the northeastern United States (Able and Fahay, 1998; Hughes et al., 2002; Hagan and Able, 2003; Lazzari et al., 2003) and California (Allen et al., 2002; Desmond et al., 2002; Matern et al., 2002). The five or fewer most abundant species in these systems are low in the trophic structure as would be expected from general patterns of relative abundance at different trophic levels. Thus, Allen and Horn (1975) observed that these species are usually planktivores (e.g., anchovies and herrings), omnivores (e.g., silversides, mullets, killifishes), or low-level

TABLE 5-8

Relative Proportions of the Five Most Abundant Fishes Sampled in Eight California Bays and Estuaries

Species	*San Pablo Bay (Ganssle, 1966)*	*Elkhorn Slough (Yoklavich et al., 1991)*	*Morro Bay (Horn, 1980)*	*Carpinteria Marsh (Brooks, 2001)*	*Mugu Lagoon (Onuf and Quammen, 1983)*	*Upper Newport Bay (Allen, 1982, 1988)*	*South San Diego Bay (Allen et al., 2002)*	*Tijuana Estuary, (Williams et al., 2001)*
Topsmelt	—	22.3	31.1	30.6	10.7	66.3	18.3	36.0
Arrow goby	—	15.5	—	50.3	—	13.9	3.2	46.2
Shiner perch	—	10.8	26.6	—	54.7	—	5.5	—
Northern anchovy	57.7	—	11.2	—	—	—	4.2	—
Slough anchovy	—	—	—	—	—	1.2	60.5	—
Pacific staghorn sculpin	—	15.6	23.9	3.2	11.4	—	—	2.8
California killifish	—	—	2.2	9.8	5.4	6.1	—	12.6
Pacific herring	29.3	—	—	—	—	—	—	—
Starry flounder	—	8.5	—	—	—	—	—	—
California halibut	—	—	—	—	4.8	—	—	—
Longfin smelt	4.7	—	—		—	—	—	—
Longjaw mudsucker	—	—	—	2.5	—	—	—	1.1
Striped bass	3.1	—	—	—	—	—	—	—
Deepbody anchovy	—	—	—	—	—	2.6	—	—
Jacksmelt	1.9	—	—	—	—	—	—	—
	—	—	—	—	—	—	—	—
Totals for top 5 species	96.6	72.6	95.1	96.4	87.0	90.1	96.1	98.7

NOTE: Percentage of total. Sites arranged left to right to portray their north to south latitudinal positions.

carnivores (e.g., gobies and flatfishes). In a 5-year study of San Diego Bay fishes by Allen et al. (2002) in which 78 species were collected, northern anchovy, topsmelt, and slough anchovy were the most abundant species, together accounting for 86% of the total catch. Similarly, in an 11-year survey of the fish assemblages in three Southern California estuaries by Desmond et al. (2002) in which 37 species were collected, arrow goby, topsmelt, and California killifish made up 70–95% of the cumulative abundance over all sites and years. In those studies that have determined biomass as well as numerical abundance, the results also show that only a few species, most of which are omnivores or planktivores, dominate the system. For example, in Upper Newport Bay, two species (striped mullet and topsmelt) accounted for almost 60% of the biomass, and three other species (yellowfin croaker, deepbody anchovy, and shiner perch) represented 14% of the total (Horn and Allen, 1985). In San Diego Bay, five species (round stingray, spotted sand bass, northern anchovy, bat ray, and topsmelt) accounted for 66% of the biomass (Allen et al., 2002). The preponderance of lower trophic-level species affects the overall trophic structure of bay-estuarine fish assemblages resulting in a shorter, "telescoped" (Odum, 1970) food chain.

HIGH PRODUCTIVITY AND BIOMASS

Bays, estuaries, and salt marshes are among the most productive habitats in the world. They rank with tropical rain forests and coral reefs in net annual primary productivity (Whittaker and Likens, 1973). Swamps and marshes, including salt marshes that form at the edges of estuaries, emerge at the highest level in such a ranking. Given their extraordinarily high primary productivity and disproportionate abundance of low trophic-level fishes, bay-estuarine systems should be expected to support high secondary productivity. Though still sparse, the data that have been obtained so far bear out this prediction.

The scarcity of studies on fish production in bays and estuaries is understandable because of the difficulties in obtaining meaningful information (Costa et al., 2002). Attempts to obtain productivity estimates based on biomass increase of a cohort of fish through the year must contend with an environment that is constantly changing because of tidal and stream inflow and with species that grow rapidly, migrate according to age and hydrologic condition, and recruit in several temporal pulses or perhaps in continuous immigration. Such a project requires that the collecting gear be chosen to sample all juvenile stages effectively; otherwise, the results may represent an artifact of sampling. In addition, other factors that must be considered include variability in local climate, food availability, and cohort mortality resulting from disease, predation, and fishing.

These challenges help to explain why, to our knowledge, only one estimate of fish production exists for a bay-estuarine assemblage in California, and only a few have been completed for assemblages or individual species occurring in Atlantic coast systems of the United States and Europe. The single production estimate for a California assemblage of 9.4 g dry weight m^{-2} yr^{-1} was obtained in 1978 by Allen (1982) for the littoral portion of the fish assemblage in Upper Newport Bay (table 5-9). Young-of-the-year topsmelt accounted for ~85% of the total production followed by deepbody anchovy (~5%), and California killifish (~4%). Productivity was highly seasonal, the main peak occurred in August and a much smaller peak in October. The annual value obtained must be considered an underestimate because adult striped mullet, even though the major contributor to fish biomass in a concurrent study (Horn and Allen, 1985), were inadequately sampled and therefore excluded from the calculations. Despite this underestimate, the annual productivity for the Upper Newport Bay littoral fish assemblage may be the highest yet recorded for any aquatic system using comparable methods of determination

TABLE 5-9

Annual Fish Production Estimates for Marine and Bay-Estuarine Systems with Comparable Production Determinations

System	*Annual Production gDW m^{-2} yr^{-1}*	*Source*
Estuary, Upper Newport Bay, California	9.4	Allen (1982)
Coastal lagoon, Mexico	8.6	Warburton (1979)
Restored salt marsh, New Jersey	8.4	Teo and Able (2003)
Salt marsh creek, Delaware	8.1*	Meredith and Lotrich (1979)
Freshwater lagoons, Cuba	6.2	Holcik (1970)
Eelgrass beds, North Carolina	4.6	Adams (1976)
Coral reef, Bermuda	4.3	Bardach (1959)
Coastal lagoon, Laguna Madre, Texas	3.8	Hellier (1962)
Kiel Bay, Sweden	1.9	Pihl and Rosenberg (1982)
Salt marsh, Massachusetts	1.6*	Valiela et al. (1977)
Forth estuary, Scotland	1.1	Elliott and Taylor (1989)
English Channel	1.0	Harvey (1950)
Georges Bank (commercial fishes)	0.4	Clarke (1946)

*Recalculated value by Teo and Able (2003) from the original published value.
NOTE: Wet weights converted to dry weights using a conversion factor of 0.25.

(table 5-9). The estimate of 10.2 g dry weight m^{-2} yr^{-1} reported for mummichog (*Fundulus heteroclitus*) inhabiting a tidal creek in Delaware (Meredith and Lotrich, 1979) was considered earlier (Allen, 1982) the highest fish productivity determination available. This value, however, has been recalculated down to 8.14 g dry weight m^{-2} yr^{-1} by Teo and Able (2003), who themselves obtained a productivity estimate of 8.37 g dry weight m^{-2} yr^{-1} for mummichog in a restored salt marsh in New Jersey (table 5-9). Other fish productivity estimates for European estuaries and a variety of marine systems are considerably lower than the above values (table 5-9).

Although no estimates of annual productivity have been reported for other bay-estuarine fish assemblages in California, standing stock estimates (biomass densities, g m^{-2}) are available for a few systems in the state and in Northern Baja California. Generally, similar values have been obtained for Morro Bay (3.1 g m^{-2}) by Horn (1980), Upper Newport Bay (4.1 g m^{-2}) by Allen (1982), and San Diego Bay (7.1 g m^{-2}) by Allen et al. (2002), all using a beach seine in shallow-water areas of these three bay-estuarine systems. The similarity of the Morro Bay and San Diego Bay densities to the Upper Newport Bay estimate, which was associated with high productivity estimates for that system, suggests that these two bays also contain highly productive fish assemblages. In contrast, biomass densities estimated for the fish assemblages in Estero de Punta Banda and Bahia de San Quintin in northern Baja California by Rosales-Casian (1997) from beam trawl catches were about 100 times lower (0.05–0.07 g m^{-2}) than those for the three California systems. This discrepancy may have resulted from the absence of midwater, schooling fishes in the Baja California samples and also from the use of a beam trawl, which is less effective than a beach seine in capturing certain bottom species.

MARKED SEASONALITY

California spans latitudes characterized by temperate conditions, cooler in the north and warmer in the south. Thus all shallow-water habitats in California experience some degree of seasonal temperature change. Moreover, precipitation varies dramatically during the year at most latitudes of the state because a large portion of the coast is under the influence of a Mediterranean-type climate with warm, dry summers and cool, wet winters. In an earlier section, the higher rainfall of the northern part of California was contrasted with the lower rainfall conditions of the central and especially the southern parts of the state. Therefore, both a seasonal and a latitudinal component contribute to variations in temperature and rainfall (and freshwater inflow) experienced by the bay-estuarine systems of the state.

Not surprisingly, the fish assemblages in the bays and estuaries of California undergo marked seasonal fluctuations in abundance, diversity, and composition that are correlated with variations in temperature and salinity during the year. Virtually all studies of these fish assemblages carried out for at least 1 year show a seasonal pattern of change, whether in the northern, central, or southern part of the state, in northern Baja California, or in expansive embayments such as San Diego Bay or small canyon-mouth estuaries such as Mugu Lagoon.

The basic seasonal pattern in California bay-estuarine systems involves a few common species (e.g., gobies, Pacific staghorn sculpin) that reside year-round in the system and are joined in the spring and summer months by several abundant species entering as juveniles (e.g., northern anchovy, California halibut) or reproductively active adults (e.g., topsmelt, shiner perch). Studies in Elkhorn Slough (Yoklavich et al., 1991), Morro Bay (Horn, 1980), Colorado Lagoon in Alamitos Bay (Allen and Horn, 1975), Upper Newport Bay (Horn and Allen, 1985), and San Diego Bay (Allen et al., 2002), among others, provide evidence to support this general pattern of abundance and diversity on monthly (fig. 8-11), seasonal (fig. 8-12), and interannual scales (fig. 8-13). Salinity and especially temperature are identified most commonly as the environmental factors associated with these patterns in fish assemblages.

The relationship between the biotic and abiotic variables, however, is often more complicated than may be appreciated at first, and we highlight several examples here. For instance, Desmond et al. (2002) concluded that variation in the fish assemblages of three southern California estuaries resulted from seasonal differences driven by changes in temperature but in the same study found that the invertebrate assemblages showed little seasonal variation. The variations that were

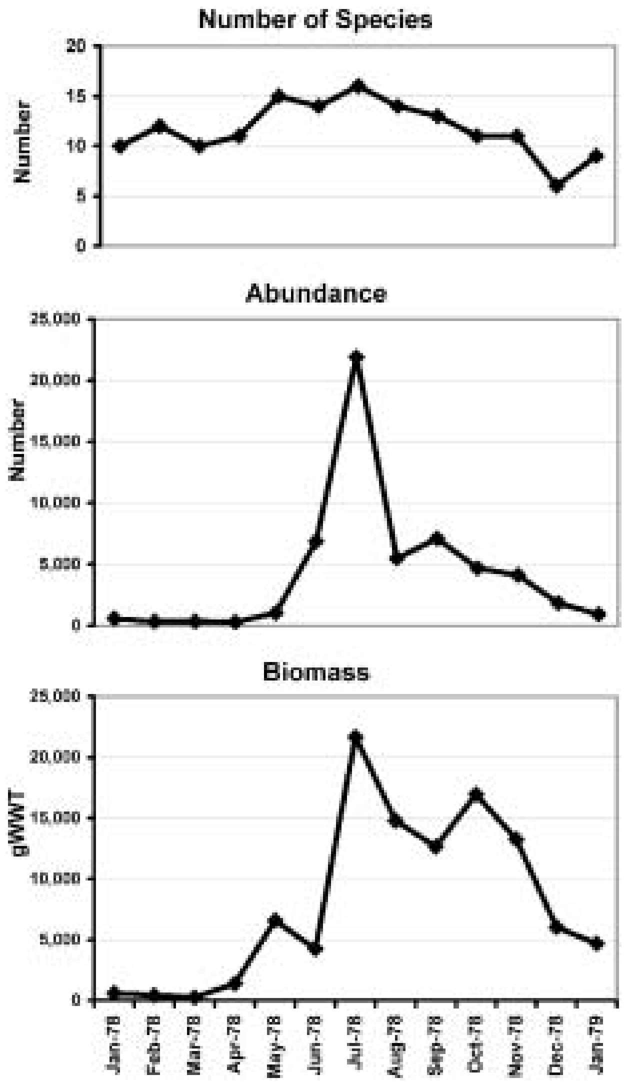


FIGURE 5-11 Monthly variation in number of species, abundance, and biomass of the littoral fishes from Upper Newport Bay, California in 1978 (after Allen 1982).

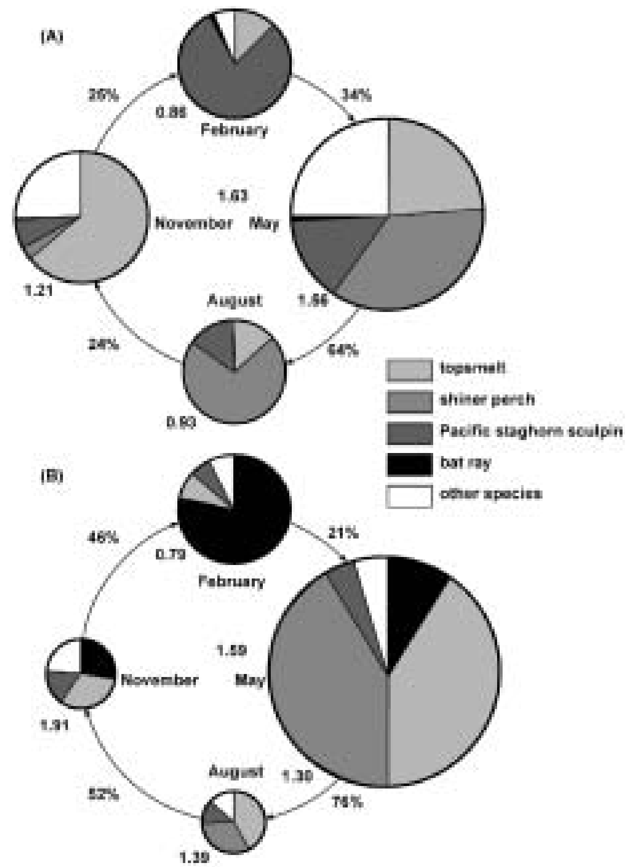


FIGURE 5-12 Seasonal pie diagrams depicting the annual cycle of (A) numbers and (B) biomass of four of the most common fish species and the remaining species collected by beach seine in the Baywood Park section of Morro Bay. Total diversity (H′) is given in the center of each cycle; the area of each circle is proportional to sample size, the number to the lower left of each circle is quarterly diversity H′, and the number on the connecting arrow is percentage similarity between months (after Horn, 1980).

shown by the invertebrates were more related to stream flow and dissolved oxygen levels than to temperature. For the Upper Newport Bay fish assemblage, Horn and Allen (1985) emphasized that temperature was the main factor influencing the annual cycle of abundance and diversity but recognized the importance of salinity especially because their study was conducted during a year (1978) marked by heavy rainfall during the first few months. Increased sedimentation accompanying the elevated freshwater inflow was a complicating factor in attempts to account for the seasonal pattern of upper bay fishes. Major storms and associated flooding impacted the fish populations in Mugu Lagoon, as documented during a 5-year study conducted in the late 1970s by Onuf and Quammen (1983). Water-column fishes, especially topsmelt and shiner perch, were more severely affected than bottom-dwelling species because the additional sediment inflow reduced the low tide volume of the lagoon and destroyed the eelgrass beds. El Niño events, which raise water temperatures and affect other habitat conditions as well, also create a set of complicating factors that can influence fish assemblages within an annual cycle. Allen et al. (2002) provided evidence that the 1997–1998 El Niño measurably reduced fish abundance in San Diego Bay in 1997, especially of schooling, planktivorous species. One of these species, northern anchovy, the most abundant fish overall in the 5-year study, was virtually absent during 1997, apparently in response to the increased temperatures associated with the El Niño. A final example of the influence of complicating factors is provided by Matern et al. (2002) in their long-term (21-year) study of fishes in Suisun Marsh, a part of the San Francisco Bay estuary. Although these investigators acknowledged that temperature and salinity were factors correlated with variations in abundance in some fish species, they concluded that the lack of predictable assemblage structure in the system was also significantly affected by human-caused disturbances (e.g., changes in freshwater input) and frequent invasions by alien species.

STRONG INTERANNUAL VARIABILITY

Only a small number of long-term investigations, of 5 years or longer, have been conducted on bay-estuarine fish assemblages in California or, for that matter, in other temperate regions of the world. Yet, bays and estuaries are widely recognized as highly variable systems inhabited by fluctuating populations of fishes

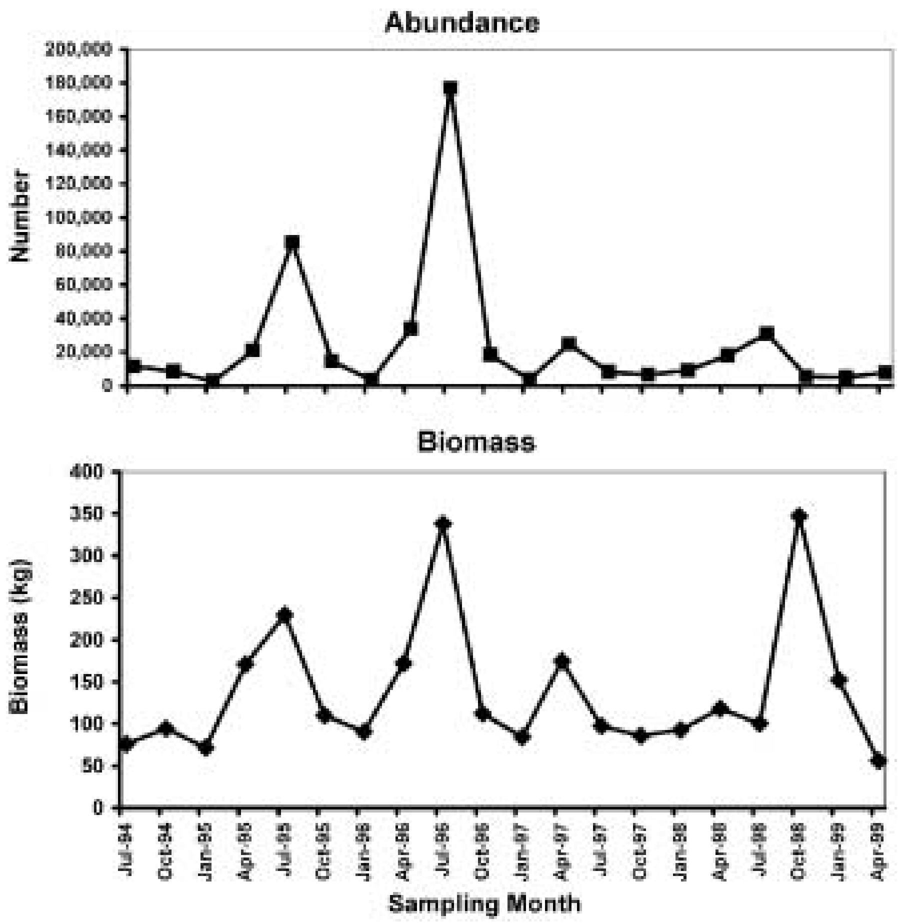


FIGURE 5-13 Seasonal variation in fish abundance (number) and biomass (kg) during a 5-year period in San Diego Bay (1994–1999) (after Allen et al., 2002).

and other organisms that are not likely to remain the same year after year because of natural changes in the environment. Bay-estuarine systems, however, have been subjected to more than natural forces, i.e., to degradation by human activities and invasion by alien species. Their recognized importance as fish habitats and growing efforts to restore them create the need for long-term surveys of their fish and invertebrate assemblages to assess the variability of these assemblages over space and time and to attempt to understand the causes of the variations.

Here we review some of the long-term studies of bay-estuarine fish assemblages in California in part to justify our use of the word "strong" in the subheading for this section of the chapter, remembering that the overall purpose of the section is to summarize five general ecological features of bay-estuarine fish assemblages and their habitats. We have used a minimum of 5 years to define a long-term survey in part because the recruitment dynamics of short-lived species such as silversides, killifish, and gobies ought to be observable in this length of time. Another reason stems from the value derived from two 5-year studies that were mentioned in the previous subsection. In the first of these investigations, Onuf and Quammen (1983) evaluated the impact of major storms and flooding on the fish assemblage in Mugu Lagoon, a small, canyon-mouth estuary in southern California. Occurring at the start of the second and fourth years of the 5-year study, these disturbances were substantial enough to account for most of the annual changes seen in the fish populations inhabiting the lagoon. Accumulation of sediment resulting from the storms reduced the available habitat for water-column fishes such as topsmelt and shiner perch and destroyed the eelgrass beds, which were used for feeding and refuge sites by several fish species. Onuf and Quammen (1983) reasoned that major disturbances that sharply and somewhat irreversibly reduce fish abundance are to be expected in small embayments along steep coastlines in regions of Mediterranean-type climate in southern California where winter storms are common and occasionally severe in magnitude. In the second 5-year study, which spanned 1994–1999, Allen et al. (2002) detected the apparent impacts of the 1997–1998 El Niño on the fish assemblage in San Diego Bay. Schooling, planktivorous fishes were most heavily affected. Among these species, northern anchovy, which ranked first in overall abundance in the study, almost disappeared in 1997. None was recorded in the samples taken in July 1997 in contrast to nearly 150,000 captured in July of the previous year. Simply stated, these two studies were long enough to have included infrequent but powerful environmental events and to have allowed evaluation of their impacts on fish assemblages.

A few longer term surveys of bay-estuarine fish assemblages in California have been conducted, and three recently completed such works are summarized here with an emphasis on the value of an extended investigation in highly variable systems. Matern et al. (2002) documented the changing and unpredictable composition of the fish assemblages of Suisun Marsh in the San Francisco Bay estuary in a 21-year otter trawl and beach seine survey. The fauna of 53 total species comprised a mixture of native and alien species and a combination of freshwater, estuarine, and marine representatives in this brackish tidal marsh. Not only was the assemblage structure unpredictable over time, but overall abundance declined, particularly among native

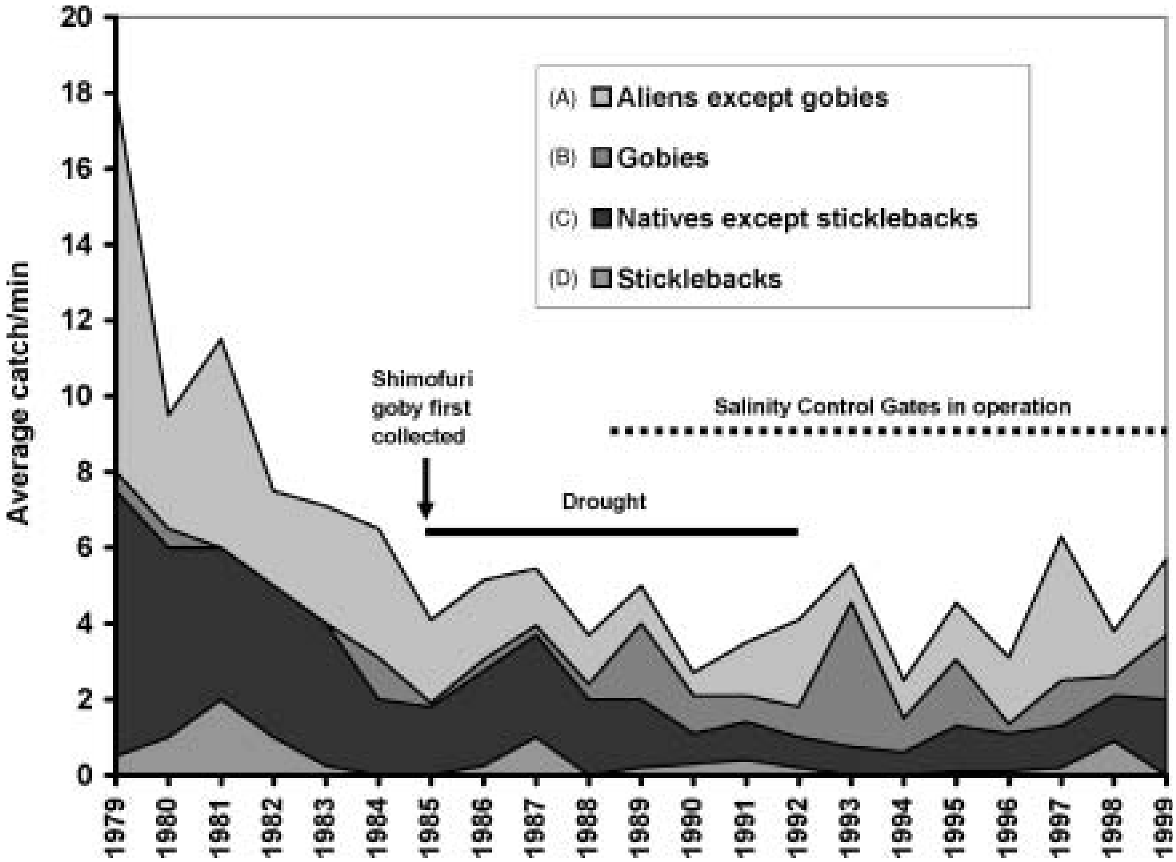


FIGURE 5-14 Average yearly catch per minute of (A) alien fishes excluding yellowfin goby and shimofuri goby, (B) yellowfin goby plus shimofuri goby, (C) native fish species excluding threespine stickleback, and (D) threespine stickleback in Suisun Marsh, San Francisco Bay estuary, 1979–1999. The timing of some major events is indicated (after Matern et al., 2002).

resident and seasonal species but not among alien species (fig. 5-14). The investigators attributed the lack of assemblage structure to naturally fluctuating conditions of the estuary, to species declines probably related to anthropogenic disturbances, and to the frequent invasions of alien species of both fishes and invertebrates. According to Matern and co-workers, some degree of predictable assemblage structure and stabilized abundances of native species will not be achieved until human disturbances and alien invasions are reduced.

High year-to-year variability in abundance of resident species was also supported by long-term data from Tijuana Estuary, a relatively small embayment in southern California adjacent to the U.S.-Mexican border (Williams et al., 2001) (fig. 5-15). The annual abundance of the top five species (arrow goby, topsmelt, California killifish, staghorn sculpin, and longjaw mudsucker) recorded from Tijuana Estuary varied dramatically from 1986 to 1999 with coefficients of variation ranging from 350% to 195% of the mean for each species.

In a third, related survey, Desmond et al. (2002) sampled both fish and invertebrate assemblages in three southern California estuaries (Los Penasaquitos Lagoon, Sweetwater Marsh, and Tijuana Estuary) during an 11-year period. For fishes, which were sampled using a bag seine and blocking nets, the study focused on resident rather than transient species because sampling was conducted only at low tide. Perhaps as expected given the fluctuating character of estuaries, the investigators found high variation in fish (fig. 5-16) and invertebrate species, within and among the three estuaries. Less expected, however, were results showing that the fish assemblage varied seasonally in abundance and species richness, whereas the invertebrate assemblage varied little over the seasons but exhibited a much higher degree of interannual variation than the fishes. Variation in the fish assemblage was driven primarily by seasonal changes in temperature, as has been shown for other bay-estuarine fish assemblages in southern California (e.g., Allen and Horn, 1975; Horn and Allen, 1985; Allen et al., 2002). In contrast, the invertebrate assemblage responded more predictably to interannual changes in stream flow and dissolved oxygen levels, indicating that irregular disturbances such as flooding have a more profound effect on these inhabitants than predictable, seasonal changes in temperature. Clearly, a value of this long-term study was the discovery that the fish and invertebrate assemblages vary differently in space and time. These results can be applied to the design of monitoring programs for wetland restoration or mitigation.

PROMINENT NURSERY FUNCTION

The role as nursery area for juveniles of coastal fish species is probably the most widely recognized and accepted func-

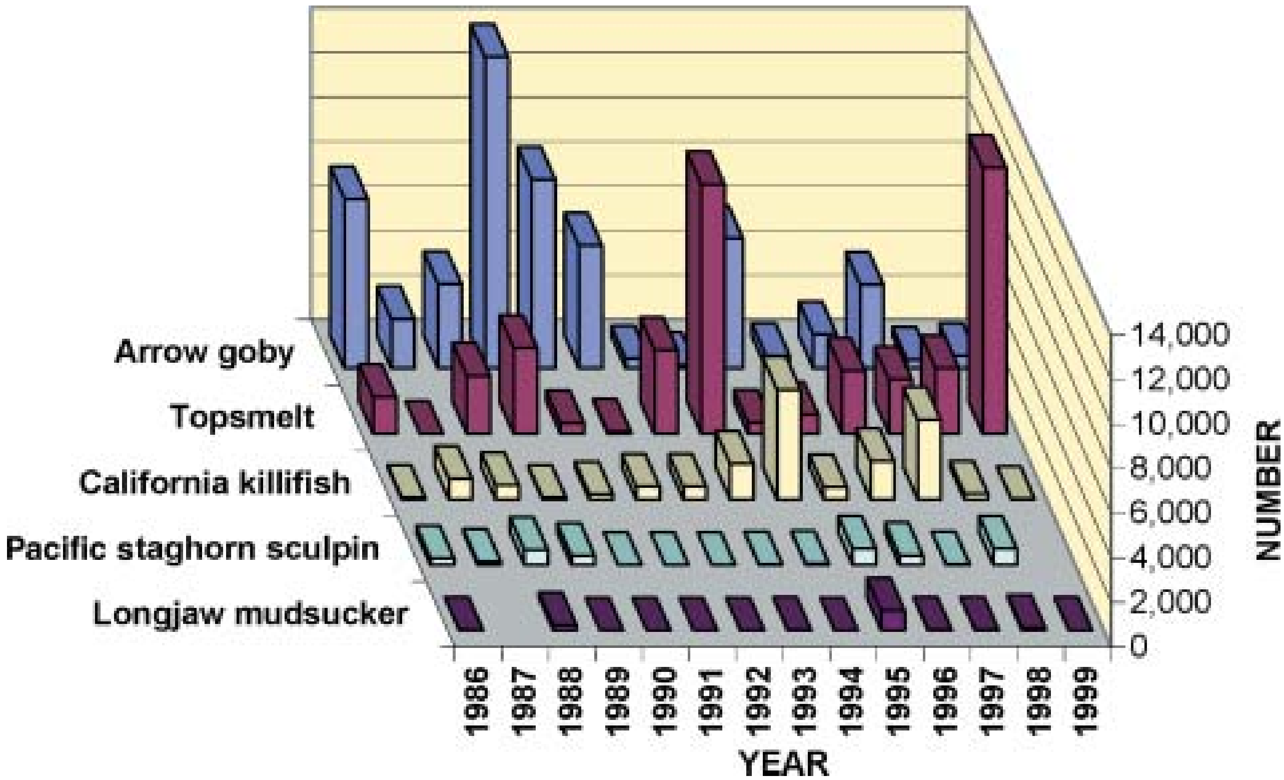


FIGURE 5-15 Annual variation in abundance of the most common bay and estuarine species captured in Tijuana Estuary from 1986 through 1999 (after Williams et al., 2001).

tion of bays and estuaries in their overall status as important fish habitats. Pihl et al. (2002) defined a nursery as a concentration of juvenile stages that are feeding and growing and listed nursery area as one of the four main habitat functions of estuaries along with spawning ground, feeding ground, and pathway for spawning migrations of diadromous species. In their survey of 26 European estuaries, Pihl and co-workers found that more than 60% of the fish species recorded in these habitats were using them as nurseries. Numerous recent publications on bay-estuarine, salt marsh, and other near shore coastal fishes contain “nursery” in the title, an indication of the continued importance of evaluating this function in shallow-water habitats (e.g., Forrester and Swearer, 2002; Gillanders et al., 2003; Lazzari et al., 2003; Minello et al., 2003). In California, most of the sampling studies of bay-estuarine fish assemblages mention the importance of the nursery function and often that a large proportion of the catch were juveniles (e.g., Yoklavich et al., 1991; Matern et al., 2002). Length-frequency analyses further show the predominance of juveniles among the most abundant species (Horn, 1980; Horn and Allen, 1985; Valle et al., 1999), as well as differential habitat use in tidal creek habitats by juveniles and adults (Desmond et al., 2000). The only bay-estuarine study to date in California to report the actual percentages of juveniles for a large portion of the total number of species captured is that by Allen et al. (2002) in their 5-year survey of fish assemblages in San Diego Bay. Nearly 70% of all fishes captured were juveniles, and for 27 of the 34 most abundant fish species, more than half of the individuals sampled were juveniles (table 5-10). Collections of four species, northern anchovy, spotted kelpfish, giant kelpfish, and kelp bass, consisted entirely of juveniles, and more than 90% of the individuals of six other species were juveniles.

Despite the wide acceptance of a nursery function for bays and estuaries and associated salt marshes, concern has been raised about the rigor that been applied in ascribing a nursery function to bays and estuaries and other coastal habitats. In a seminal paper authored by 13 estuarine fish ecologists, Beck et al. (2001) criticize the ambiguity that they claim surrounds the nursery-role concept and interferes with its use as a tool in conservation and management. To strengthen the concept, they propose a hypothesis built on the prevailing notion that some inshore juvenile habitats contribute disproportionately to the production of juveniles that recruit to adult populations. Their hypothesis states that “a habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur.” A nursery habitat in the terms of Beck et al. (2001) supports a greater than average combination of higher density, growth, and survival of juveniles and movement to adult habitats. This demanding but testable hypothesis holds promise for increasing the rigor of research in estuarine fish ecology. Papers already are being published that address components of the nursery-role hypothesis (e.g., Gillanders et al., 2003; Heck et al., 2003; Minello et al., 2003), and it is important to test the hypothesis in California bay-estuarine systems.

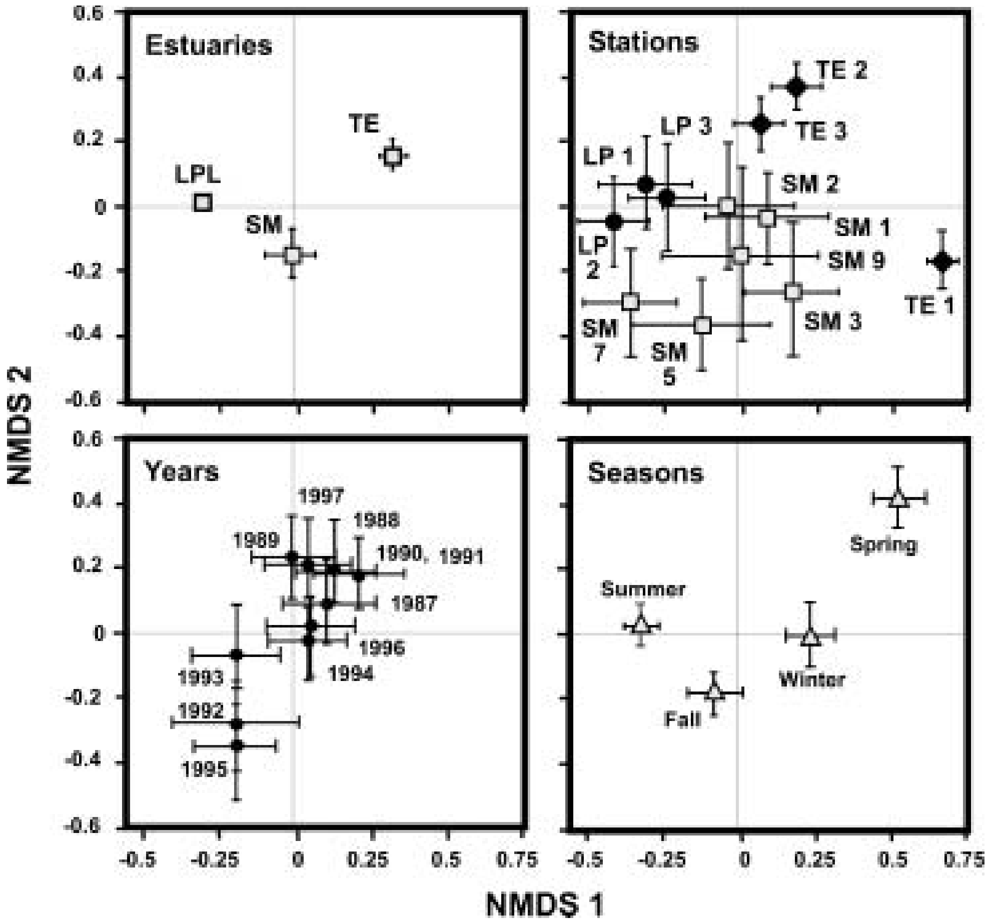


FIGURE 5-16 Biplots of non-metric multidimensional scaling (NMDS) analysis of fish assemblage data collected in three southern California bays and estuaries from 1987 to 1998. LPL = Los Penasquitos Lagoon, SM = Sweetwater Marsh, and TE = Tijuana Estuary. NMDS axis 1 was significantly affected by estuary, station, and season but not year; NMDS axis 2 was significantly affected by station, year, and season but not estuary. Values are means ± standard errors for all samples (after Desmond et al., 2002).

Recommendations for Future Studies

Several types of studies are needed if we are to deepen our understanding of the structure and function of bay-estuarine fish assemblages in California and Baja California and to enhance our abilities to conserve and manage these impacted species and their diminished habitats more effectively. Here are some of the types of projects and problems that are worthy of attention in future research.

1. Conduct comprehensive surveys in understudied bays and estuaries to establish baseline information on their fish assemblages and undertake new surveys of systems studied decades ago to detect any changes, both using an array of the most effective types of sampling gear.
2. Revive ichthyoplankton surveys after a few decades of reduced activity for the same purposes as stated in 1 above. Excellent baseline studies exist from previous works, and an outstanding atlas of egg and larval types for California marine fishes (Moser, 1996) is available to facilitate the renewed efforts. Relevant here is the impression gained by Matern et al. (2002) that environmental variables act mainly on very young life stages rather than on the larger juveniles and adults usually captured in trawls and seines.
3. Initiate or continue long-term surveys (of 5 or more years) for both juvenile-adult and ichthyoplankton assemblages. Such studies yield expected and unexpected results of value especially with regard to understanding interannual variability and the effects of pulsed disturbances such as flooding or ENSO events on these assemblages. The several studies summarized in this chapter produced both types of results.
4. Determine food origins and trophic positions using stable isotopes and lipid biomarkers. A variety of carbon and energy sources are potentially available in bay-estuarine habitats, especially for abundant species such as topsmelt ands striped mullet that feed on a wide range of food sources including detritus, which may have multiple origins. The comprehensive food web analysis of two bay-estuarine systems in southern California by Kwak and Zedler (1997) using multiple stable isotopes provides a solid basis for further research.
5. Estimate production for fish populations in a variety of bay-estuarine systems. To our knowledge, only one such estimate of fish production exists for a California system, and that study yielded what may be the highest value yet determined for an aquatic habitat. For European estuaries, Costa et al. (2002) emphasized the need to assess fish production in areas with contrasting features, to quantify the loss of production in degraded habitats, to determine what production is exported to marine areas, and to estimate the relative proportions of production of migrating marine species that have some production in both estuarine and marine habitats. These needs seem even greater

TABLE 5-10
Estimated Percent of Juveniles Among the 34 Most Abundant Fishes in a 1994–1999 Study in San Diego Bay

Common Name	*Scientific Name*	*% Juveniles*
Northern anchovy	*Engraulis mordax*	100
Spotted kelpfish	*Gibbonsia elegans*	100
Giant kelpfish	*Heterostichus rostratus*	100
Kelp bass	*Paralabrax clathratus*	100
California halibut	*Paralichthys californicus*	99
Bonefish	*Albula vulpes*	99
Barred sand bass	*Paralabrax nebulifer*	97
Pacific sardine	*Sardinops sagax*	96
Striped mullet	*Mugil cephalus*	95
Salema	*Xenistius californiensis*	94
Arrow goby	*Clevelandia ios*	79
Barred pipefish	*Syngnathus auliscus*	78
Bay pipefish	*Syngnathus leptorhynchus*	76
Topsmelt	*Atherinops affinis*	73
Queenfish	*Seriphus politus*	73
California killifish	*Fundulus parvipinnis*	72
Shadow goby	*Quietula y-cauda*	71
Jacksmelt	*Atherinopsis californiensis*	69
Specklefin midshipman	*Porichthys myriaster*	67
Cheekspot goby	*Ilypnus gilberti*	67
Black perch	*Embiotoca jacksoni*	66
California grunion	*Leuresthes tenuis*	66
Yellowfin croaker	*Umbrina roncador*	66
Dwarf perch	*Micrometrus minimus*	63
Fantail sole	*Xystreurys liolepis*	61
Round stingray	*Urolophus halleri*	53
Shiner perch	*Cymatogaster aggregata*	51
Slough anchovy	*Anchoa delicatissima*	43
Bay blenny	*Hypsoblennius gentilis*	37
Black croaker	*Cheilotrema saturnum*	36
Spotted turbot	*Pleuronichthys ritteri*	35
Deepbody anchovy	*Anchoa compressa*	23
Spotted sand bass	*Paralabrax maculatofasciatus*	22
Diamond turbot	*Hypsopsetta guttulata*	18
	Average % juveniles/species	69

NOTE: After Allen et al., 2002.

in California given the near absence of fish production studies in the state's bays and estuaries.

6. Investigate estuarine–coastal coupling using up-to-date tagging procedures, molecular genetic techniques, and stable isotope and lipid biomarkers as in 5 above. Research is still needed to determine whether certain especially abundant species move from estuaries into coastal waters and transport outward the high secondary production characteristic of bay-estuarine systems.
7. Test the nursery-role hypothesis of Beck et al. (2001) for different habitats within and among bay-estuarine systems in California. If tested as proposed, this challenging hypothesis ought to increase the effectiveness of conserving and managing bay-estuarine habitats and their fish assemblages.
8. Design and implement studies to test the impacts of alien fish and invertebrate species on native fish populations. Continued monitoring is required to detect the occurrence and spread of alien species, and manipulative field and laboratory experiments similar to those conducted by Matern (1999) on shimofuri goby are needed to assess the impact and predict the spread of such invaders. Alien species, especially gobies, continue to appear and establish breeding populations and to spread from their site of introduction.
9. Determine the impacts of nutrient pollution (eutrophication) on bay-estuarine fish assemblages in California. A recent study on an Atlantic coast bay-estuarine system shows that, as the nitrogen load increases, macroalgal biomass increases, eelgrass density and biomass diminish, and fish abundance, diversity, and growth decline (Deegan et al., 2002). Such studies are rare in California systems (see Minello et al., 2003), but nutrient loading is a widespread phenomenon in temperate bays and estuaries, including many in California such as Upper Newport Bay (Kamer et al., 2001).
10. Assess and predict the impacts of climate change from long-term monitoring of fish assemblages in California's bays and estuaries. Climate change is likely to exacerbate the effects of eutrophication and other stresses through higher water temperatures and alterations in sea level, freshwater input, and ocean exchange (Scavia et al., 2002). Restoration projects and water management plans involving bays and estuaries should take into account longer term changes anticipated as a result of climate change.

Acknowledgments

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