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CHAPTER 7

# Continental Shelf and Upper Slope

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## Introduction

Historically, the continental shelf (conventionally defined from shore to 200 m) and the upper slope (depths of 200–500 m) have been the focus of much of the world's marine fishing. The predominant habitat of the shelf and upper slope consists of sandy and muddy sediments. Many species of fish characteristically occur in this habitat, and some of these show unique adaptations to life on a relatively flat and featureless benthic habitat. This soft-bottom habitat is easily fished using bottom trawls, and hence the soft-bottom fish fauna is often the source of important fisheries in much of the world. More recently, because of the ease of sampling and the discharge of wastewater onto this habitat, this fauna has become the focus of environmental assessments of human activities on the shelf. Because of the importance of the soft-bottom fish fauna to fisheries and to environmental assessments, the biology and ecology of the fauna have been relatively well studied. However, although the fauna has been relatively well studied off California and Pacific Baja California, there is no overall summary of the soft-bottom fish fauna and its ecology for the entire region.

This chapter provides a first recent attempt to summarize what is known about the ecology of the soft-bottom fish fauna of the continental shelf and upper slope of the California and the Pacific coast of the Baja California Peninsula (the deeper slope is discussed in Neighbors and Wilson in chapter 12 of this book). The chapter begins with an overview of the physical conditions of the habitat, followed by overviews of scientific study, sampling methods, the soft-bottom fish fauna of the Californias (e.g., taxonomic composition, biogeography, morphology, life-history traits, assemblages, and community organization), a brief comparison of this fauna to similar faunas elsewhere in the world, and ends with a prospectus for future research.

## Physical and Biological Conditions on the Shelf and Upper Slope

### Topography

The continental shelf is the gently sloping submerged continental margin that extends seaward to the steeply sloping continental slope. Conventionally, the continental shelf is considered to extend seaward to the 200 m isobath (Emery, 1969), although the geological shelf is somewhat shallower (Curray, 1966). The geological shelf extends seaward to the shelf break (a sharp change of slope), occurring at a depth of 130 m, in most places, worldwide (Curray, 1966). Although the shelf break is also at this depth off northern and central California (Jane A. Reid, United States Geological Survey Pacific Science Center [USGS, PSC], University of California, Santa Cruz, CA; pers. comm.), it ranges from 80 to 145 m in southern California (Emery, 1960).

Along California and the Pacific Coast of Baja California, the continental shelf occurs continuously along the mainland, with shelf areas also at coastal islands and some banks (Fig. 7-1). The shelf (shore to 200 m) is moderately wide off northern and central California (<1–50 km), very narrow along mainland southern California (0.06–13 km), moderate to narrow along northern Baja California (3–22 km), and very broad in Bahia Sebastian Vizcaino and along the west coast of Baja California Sur (85–135 km). The area of the California shelf is estimated at about 28,000 km$^2$ (25,000–30,000 km$^2$) (Jane A. Reid, USGS, PSC, pers. comm.). Although there are no similar estimates for the shelf off the Pacific coast of the Baja California Peninsula, most of the shelf area clearly lies off Baja California Sur.

The upper slope (between the 200 and 500 m isobaths) is generally much narrower than the shelf because of its steeper slope. It typically ranges from about 1 to 10 km wide but is relatively wide (75 km) west of southernmost Baja California Sur. A branch of the upper slope extends as a large submarine peninsula off southern California, extending 160 km south from Point Conception as the Santa Rosa–Cortez Ridge to San Nicolas Island. From Santa Rosa to San Nicolas Island, the upper slope extends 45 km in continuous length with additional large upper slope bank areas south to Cortez Bank.

### Soft-Bottom Habitat

The soft-bottom habitat is the dominant habitat of the shelf and upper slope. This habitat comprises more than 50% (and

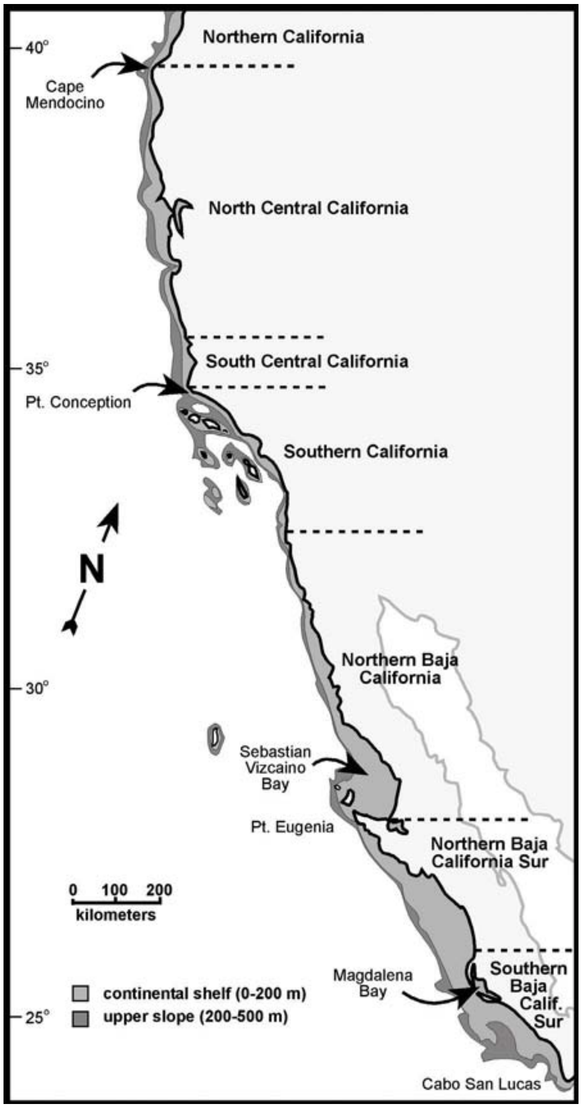



FIGURE 7-1 Shelf (shore to 200 m isobath) and upper slope (200–500 m) of California and Pacific Coast of Baja California, with analytical regions discussed in text.

probably from 70 to >90%) of the California shelf area (J. A. Reid, USGS, PSC, pers. comm.) and is probably the dominant habitat off the Pacific Coast of Baja California, particularly on broad shelf areas off Baja California Sur. Hard bottoms are most common inshore near rocky headlands, along steep narrow shelf areas (e.g., islands, central California), and the shelf break or submarine canyons. Some low-relief, hard-bottom areas are transitional between hard- and soft-bottom areas. Sandy sediments are more common in nearshore areas, along the shelf break, and on the island and bank shelf; silt, clay, and mud sediments are common between the shelf break and inshore sand zone and below the shelf break (Emery, 1960; Curray, 1966). Although the soft-bottom habitat is relatively flat, there is some microrelief resulting from water movement (waves, currents) or biological activity (e.g., excavations, burrows, protruding tubes).

### Changes in Physical Conditions with Depth

Temperatures off southern California decrease from 14.5 to 19.5°C at the surface to 8 to 9°C at 200 m, and to 6°C at 500 m (Emery, 1960). Oxygen decreases from 6 mL/L at the surface to 1.5 to 2 mL/L at 200 m and to about 0.6 mL/L at 500 m. Pressure changes from 2.1 kg/cm$^2$ (2 atmospheres) at 10 m to 21.7 kg/cm$^2$ (21 atm) at 200 m and 52.7 kg/cm$^2$ (51 atm) at 500 m. Light penetration decreases with depth more rapidly in coastal waters than in the clear open ocean; sufficient ambient light exists for vertebrate sight during the day to a depth of about 200 m (coastal turbidity further decreases light penetration) (Clarke and Denton, 1962). In contrast, similar light levels occur in clear open ocean water at depths of 1000 m in daylight and 600 m in moonlight. Bioluminescence becomes more important than ambient light at night or in deep water (Clarke and Denton, 1962).

## Overview of Scientific Studies of Soft-Bottom Fishes of the Californias

### Types of Studies by Focus

Information on soft-bottom fishes off the Californias has been gathered for more than 150 years. Most of this information is from three types of studies, each with a different focus: (1) taxonomic, (2) fisheries, and (3) pollution assessment (table 7-1). Taxonomic studies (conducted by museums) focused on species descriptions and have been conducted from the early 1850s to the present along the entire coast of the Californias. Fisheries studies that have been conducted since the early 1900s consist primarily of stock assessments and gathering of fisheries-relevant life-history information. These studies were done by the California Department of Fish and Game (CDFG) in state waters (less than 4.8 km from shore) and by the National Marine Fisheries Service (NMFS) in federal waters (more than 4.8 km from shore). Environmental studies in California since the late 1950s generally focus on assessment of pollution effects. These are usually monitoring studies that are required by the State Water Resources Control Board (SWRCB) or United States Environmental Protection Agency (USEPA), although research oriented studies are also conducted, particularly by the Southern California Coastal Water Research Project (SCCWRP).

### Early Studies (1850–1950)

The earliest scientific studies of the soft-bottom fish fauna of the Californias focused on species descriptions because almost the entire fauna was unknown to science. The first scientific collections of soft-bottom species began in the 1850s with the U.S. Pacific Railway surveys (table 7-1). Many fish species were collected from fish markets at this time and sent to the Smithsonian Institution for description by ichthyologists (e.g., C.F. Girard, W.O. Ayres, W.N. Lockington) (Hubbs 1964). The first scientific ocean surveys of this fauna were U.S. Fisheries Commission Steamer *Albatross* surveys, which were conducted from northern California to southern Baja California, and particularly off southern California during 1889–1916 (Hedgpeth, 1945; Moring, 1999). These surveys sampled stations at depths from 15 to 4100 m using beam trawls (USBF, 1906), and fishes were distributed to museum ichthyologists (e.g., Charles Henry Gilbert) for description. The next major scientific survey was the Allan Hancock Foundation *Anton Dohrn* survey conducted on the shelf in

TABLE 7-1

Historical Summary of Soft-Bottom Fish Studies on the Continental Shelf and Upper Slope off California and Baja California

- I. Types of studies by focus
  - A. Taxonomic studies (museum surveys), 1850s to present, used beam trawls early, otter trawls later
  - B. Fisheries studies (stock assessments, fisheries-relevant life-history studies), early 1900s to present
    1. CDFG—State waters (<4.8 km from shore)—12.2-m wide otter trawls, 20–30 min tows
    2. NMFS—Federal waters (>4.8 km from shore)—22–32 m wide otter trawls, 20–30 min tows
  - C. Environmental studies—late 1950s to present, water quality agencies, 7.6-m wide otter trawls, 10-min tows
    1. SWRCB—regulatory, by CDFG, POTWs, and consulting firms—5.3–12.2 m wide otter trawls, 5–20 min tows
    2. SCCWRP—research and assessment surveys—7.6-m wide otter trawls, 10-min tows
- II. Early studies (1850–1950)—unknown fauna, focus on species descriptions
  - A. U. S. Pacific Railway surveys of California, sampled fish markets (Hubbs, 1964)
  - B. U. S. Fisheries Commission Steamer *Albatross* surveys (California and Baja California), sampled depths of 15–4100 m with 2.2–4.9 m wide beam trawls towed for 20–25 min; species described by C. H. Gilbert (USBF, 1906)
  - C. USC, AHF Southern California surveys, 10–200 m, 1.5-m wide beam trawl, 20-min tow (Ulrey and Greeley, 1928)
- III. Studies since 1950 by region
  - A. Northern and Central California
    1. Environmental assessments of inner shelf (<30 m)
       - a. 1960s—Morro Bay (Heimann and Miller, 1960); Monterey Bay (Heimann, 1963); San Francisco Bay (Alpin, 1967)
       - b. 1970s—SWRCB predischarge surveys (Humboldt Bay, San Francisco Bay, Watsonville, central Monterey Bay, San Luis Obispo, Morro Bay)
       - c. 1980s to present—San Francisco Bay (CDFG; Baxter et al., 1999), San Francisco Coast (City of San Francisco)
    2. NMFS groundfish stock assessment surveys of shelf and slope (50–1280 m), 32 m wide nets, 30-min tows
       - a. Shelf and upper slope (50–366 m) (Gunderson and Sample, 1980; Weinberg et al., 1984; 1994; Coleman, 1986, 1988; Dark and Wilkins, 1994; Jay, 1996; Zimmerman et al., 1994; Wilkins et al., 1998; Shaw et al., 2000)
       - b. Slope (183–1280 m) Lauth (1997, 1999, 2000, 2001), Lauth et al. 1997)
  - B. Southern California
    1. Fishery surveys—CDFG (Jow, 1969); NMFS in 1977 (Gunderson and Sample, 1980) and 2002–2003
    2. Environmental surveys (SWRCB, USEPA, and SCCWRP)—7.6 m wide trawls, 10-min tows
       - a. CDFG—Santa Monica Bay, 1957–1963, 10–200 m (Carlisle 1969)
       - b. POTW Monitoring Surveys (USEPA-SWRCB NPDES and 301h Waiver)—POTW quarterly reports
         1. County Sanitation Districts of Los Angeles, Orange County Sanitation Districts (1970s to present)
         2. City of Los Angeles, City of San Diego (1980s to present)
       - c. SCCWRP research and assessement surveys (1970s to present)—SCCWRP (1973) and Annual Reports; M. J. Allen (1982a); Thompson et al. (1987, 1993); M. J. Allen et al. (1998, 2002)
    3. Educational surveys (1970s to present)
       - a. Occidental College (Stephens et al., 1973, 1974; Love et al., 1986); UCLA (Mearns and M. J. Allen, 1973);
       - b. Ocean Institute ( = Orange County Department of Education; Orange County Marine Institute)
  - C. Baja California—Hubbs (1960) provides some information on soft-bottom fishes of Pacific Coast
    1. Scripps Instititution of Oceanography (SIO) surveys, 1950–1984, >200 sites, 2–622 m (SIO Fish Collection)
    2. CalCOFI surveys—1970–1971, 27–95 m, incidental to plankton surveys, (R. N. Lea, CDFG, pers. comm.)
    3. Baja California University surveys
       - a. CICESE—Baja California, < 30 m depth (Hamman and Rosales Casian, 1990)
       - b. CICIMAR—Baja California Sur, 1990, 38–218 m, 21 m wide otter trawl (Murillo et al., 1998)

NOTE: CalCOFI = California Cooperative Oceanic Fisheries Investigations; CDFG = California Department of Fish and Game; CICESE = Centro de Investigación Científica y de Educación Superior de Ensenada; CICIMAR = Centro Interdisciplinario de Ciencias Marinas; NMFS = National Marine Fisheries Service; POTW = publicly owned treatment works; SCCWRP = Southern California Coastal Water Research Project; SWRCB = State Water Resources Control Board; UCLA = University of California, Los Angeles; USEPA = United States Environmental Protection Agency; USC, AHF = University of Southern California, Allan Hancock Foundation.

southern California at depths of 10–200 m from 1912 to 1922 using beam trawls (Ulrey and Greeley, 1928). This was the first survey where all species collected at a site were reported. Other scientific studies of these fishes made after 1922 were conducted by CDFG and a focused on life-history information on important fisheries species.

### Studies Since 1950 by Region

Since 1950, information on the soft-bottom fish fauna of the Californias has increased dramatically with routine fisheries and environmental monitoring surveys. The types and intensity of the surveys, as well as the sampling methods vary in each of three regions: (1) northern and central California, (2) southern California, and (3) Baja California (table 7-1).

Northern and central California surveys consist primarily of environmental assessments using small otter trawls on the inner shelf at depths less than 30 m and NMFS groundfish stock assessment surveys using large otter trawls on the deeper shelf and slope (50–1280 m) (table 7-1). The former have been conducted irregularly from the early 1960s to the present from Humboldt Bay to Morro Bay, usually in response to SWRCB regulatory requirements. The latter in some form have been conducted regularly since 1977. Data from the former studies are found in reports submitted to the SWRCB and in CDFG reports. Good and extensive data summaries from the NMFS studies are found in numerous technical reports (e.g., Coleman, 1986; Zimmerman et al., 1994; Lauth et al., 1997; Wilkins et al., 1998; Shaw et al., 2000), journals (e.g., Heimann and Miller, 1960; Heimann, 1963; Gabriel and Tyler, 1980; Gunderson and Sample, 1980; M.J. Allen and Smith, 1988; Wakefield and Smith, 1990; Dark and Wilkins, 1994; Weinberg, 1994; Jay, 1996; Williams and Ralston, 2002), and dissertations (Gabriel, 1980; Wakefield, 1990).

Southern California surveys consist primarily of environmental assessments using small otter trawls at depths mostly less than 200 m, but some to 1000 m (table 7-1). These have been conducted since the late 1950s by CDFG and publicly owned treatment works (POTWs) in response to USEPA or SWRCB requirements but also by SCCWRP. Educational surveys have been regularly conducted since the early 1970s. Most fisheries surveys have focused on single species collections, but recent NMFS surveys (2002–2003) are providing stock assessment information on more species. Although studied extensively, most information from this region is found in monitoring reports submitted by large POTWs to State Regional Water Quality Control Boards or USEPA, technical and annual reports produced by SCCWRP, CDFG internal reports, and reports submitted to California Sea Grant. Some studies in this region have been published in journals or books (e.g., Carlisle, 1969; Mearns, 1974; M.J. Allen, 1977; Mearns, 1979; Gunderson and Sample, 1980; M.J. Allen, 1982b; Love et al., 1986; Cross, 1987; Stull, 1995; Stull and Tang 1996) and dissertations (e.g., M.J. Allen, 1982a). The most extensive regionwide studies of this fauna in the Southern California Bight are M.J. Allen (1982a) and M.J. Allen et al. (1998, 2002).

Baja California surveys have been largely exploratory. Museum collections by Scripps Institution of Oceanography are the most extensive (more than 200 sites at depths of 2–622 m from 1950 to 1984) (table 7-1). Trawl samples were also conducted incidentally in 1970–1971 California Cooperative Oceanic Fisheries Investigation surveys. Baja California universities (Centro de Investigación Científica y de Educación Superior de Ensenada [CICESE] and Centro Interdisciplinario de Ciencias Marinas [CICIMAR]) have conducted more recent surveys along this coast (e.g., Hammann and Rosales Casián, 1990; Murillo et al., 1998). Hubbs (1960) described in general the fish fauna on the Pacific Coast of Baja California but provided little information on the soft-bottom fauna of the shelf and slope.

## Sampling Methods

Soft-bottom fishes live on a relatively flat, featureless bottom of sediment and hence can be effectively caught by dragging a net along the bottom. Beam trawl samples were used in the earliest scientific studies of this fauna (USBF, 1906; Ulrey and Greely, 1928); otter trawls were more commonly used after 1950. Beam trawls have metal rectangular mouth frames and hence a mouth opening with fixed dimensions. Otter trawls use otter boards attached to the wings of the net. As the net is towed, water force on the boards causes the net to spread open. In contrast to the fixed-opening beam trawls, otter trawls have mouths with more variably sized openings. However, the size and weight of the frame makes large beam trawls impractical, limiting beam trawls to small mouth openings (e.g., 1.0–1.6 m). Small beam trawls capture smaller and less mobile fishes than are caught by small otter trawls and are less useful for assessing soft-bottom assemblages. Nevertheless, they are valuable tools (with very fine net mesh) for capturing very small juveniles (L. G. Allen et al., 1990; M.J. Allen and Herbinson, 1990; Kramer and SWFSC, 1990; M.J. Allen and Herbinson, 1991; L. G. Allen and Franklin, 1992).

Otter trawl nets used in surveys range in width from 4.9–32.0 m (headrope). Small nets (4.9–12.2 m wide) are used on the inner shelf of central and northern California and across the southern California shelf and upper slope. Large nets (22–32 m) are used by CDFG and NMFS assessment surveys of the deeper shelf and upper slope (predominantly off central and northern California). However, the width of the net opening during a tow (board or net spread) is less than the actual headrope length; the actual board spread of small nets is 3.4 m for 4.9-m nets, 4.9 m for 7.6-m nets, and 7.9 m for 12.2-m nets (Mearns and Stubbs, 1974). This is likely to vary, depending on vessel speed, bottom type, and weight of catch in the bag. The actual horizontal sweep (net spread) of a 27-m headrope Nor'Eastern trawl is 13.4 m with a headrope height of 8.8 m (Gunderson and Sample, 1980). In 1972, sampling gear and protocol for environmental trawl surveys in southern California were standardized to 7.6-m wide (headrope) semi-balloon otter trawls with 1.3-cm cod-end mesh towed along isobaths for 10 minutes (Mearns and M. J. Allen, 1978). NMFS trawl surveys of the shelf and slope off California have used commercial nets (22–32 m headropes with roller gear) towed for 30 minutes to provide catches similar to those obtained by commercial fishermen (Gunderson and Sample, 1980; Dark and Wilkins, 1994).

Compared to other sampling methods, otter trawls provide the most information for assemblage studies and for assessment of population status and fish health (M. J. Allen, 1975, 1976). Relative to hook-and-line and observational techniques, otter trawls yield the most species and allow accurate identification of species; counts of individuals; measurement of biomass and lengths; examination of diseases; and collection of specimens for stomach analysis, age and growth studies, and tissue chemistry analysis. However, they provide little information on the behavior of the fishes in their natural environment. Depending on the net size, they underestimate the abundance of large individuals and fast swimming species (for small trawls) or small individuals and species (for large trawls). Jow (1969), using 22 and 32-m wide (headrope) otter trawls, caught larger individuals and missed many small species that are typically taken in smaller (7.6-m wide headrope) otter trawls (e.g., M. J. Allen et al., 1998). Large species are caught more efficiently with larger otter trawls or hook-and-line techniques.

Soft-bottom trawl (7.6-m headrope) stations have been sampled with hook-and-line methods on the shelf (M. J. Allen et al., 1975) and upper slope (Cross, 1987) to compare methods. Benthic set lines effectively sampled wide-ranging, benthic foraging species that may escape the net, whereas fishing by rod-and-reel in sonar-located schools near the bottom was a more effective way to catch highly clumped fishes likely missed by chance in a trawl (M.J. Allen et al., 1975; M.J. Allen 1976). Although most individuals caught were equivalent to large-sized trawl-caught individuals, fewer small individuals were taken by hook-and-line. Cross (1987) caught more species by longline than trawl on the upper slope but attributed this to more fishing on banks, with more vertical relief, than strictly on a softbottom.

Observational sampling (diver observation—M. J. Allen et al., 1976; remote photographs or videos—SCCWRP, 1974; Moore and Mearns, 1980; Wakefield, 1990) gives more information on fish behavior in the natural environment, but identifications are less accurate and fewer measurements can be taken. SCCWRP (1974) used a cine camera left on the bottom for a 24-hour period and timed to take a 15-second film every half hour to document diel changes in fish activity. A combination of methods would yield the most behavioral and ecological information (M. J. Allen, 1976).

## Trawl Survey Assessments of Soft-Bottom Fauna

### Comparability of Surveys

Although sampling of the soft-bottom fish fauna has been extensive (particularly in California), differences in sampling gear and protocol and differences in types of data gathered in the fisheries surveys of northern and central California and the environmental surveys of the southern California shelf make coastwide comparisons difficult. NMFS surveys use commercial-sized nets (e.g., 27-m headrope, with an actual net spread of 13.4 m), often with roller gear, and towed for 30 minutes at 1.5 m/second (Gunderson and Sample, 1980), whereas environmental surveys use small shrimp trawls (7.6-m headrope, and actual net spread of 4.9 m) towed for 10 min along isobaths at 1 m/second (Mearns and M. J. Allen, 1978). Thus a NMFS trawl sample using a 27-m net collects fish from an area of about 16,800 $m^2$, whereas an environmental trawl survey using a 7.6-m net collects fish from about 2900 $m^2$. Further, the NMFS trawls have larger net mesh (e.g., 8.9-cm body mesh and 3.2-cm cod-end mesh; Dark and Wilkins, 1994) than trawls used in southern California (3.8–5.0-cm body mesh and 1.3-cm cod-end mesh; Mearns and M. J. Allen, 1978). The use of roller gear, which allows trawling on a hard bottom results in an increased proportion of hard-bottom species (e.g., some rockfish species) in the catches, which blurs the distinction between the soft- and hard-bottom fauna. The difference in horizontal sweep and height of net opening, as well as differences in tow duration, body and cod-end mesh size, and presence or absence of roller gear, all but preclude comparisons between northern/central California and southern California trawl surveys of the shelf, except in a very gross manner (e.g., presence/absence of species, relative abundance of species).

These two types of surveys also gather slightly different attributes of the fishes. The NMFS surveys focus on type of species, biomass by species, with information on numbers of individuals for some species, as well as length measurements and otoliths (for aging) of important fisheries species. The environmental surveys in southern California collect information on type of species, numbers and lengths of individuals, biomass by species and assesses anomalies and diseases (e.g., Mearns and M. J. Allen, 1978; M.J. Allen et al., 1998, 2002). Environmental surveys of the inner shelf of northern and central California are comparable with those of southern California, because they used similar gear and protocol.

### Population Characteristics

A number of measures are used to summarize trawl catches across all species sampled, including numbers of individuals (abundance), biomass, species richness (numbers of species), and species diversity (e.g., Shannon-Wiener diversity; Shannon and Weaver, 1949). Abundance and biomass, frequently expressed as catch per unit effort (CPUE), describe the number or biomass of fish per some sampling unit (e.g., unit area; standard tow) (Dark and Wilkins, 1994). In addition to these, length or age frequency distributions are sometimes used to provide information on the population structure of individual species (Dark and Wilkins, 1994; M. J. Allen et al., 1998, 2002).

Based on 2237 otter trawl samples collected in southern California from 1957 to 1975, an average standard 7.6-m headrope otter trawl towed for 10 minutes captured 173 fish representing 11 species, weighing 7 kg, and with a Shannon-Wiener diversity of 1.36 (M.J. Allen and Voglin, 1976). In this area, CPUE is expressed in terms of catch per standard trawl sample, which samples an area of about 2900 $m^2$. In regional surveys of the southern California shelf in 1994 and 1998, an average trawl sample (same dimensions and protocol) collected 156–157 fish representing 10–12 species, weighing 5–6 kg, and with a diversity of 1.57–1.59 (M.J. Allen et al., 1998, 2002). Variation of fish population attributes (abundance, biomass, species richness or number of species, and diversity) have been examined by region and depth in southern California (M.J. Allen and Voglin, 1976; M.J. Allen and Mearns, 1977; M.J. Allen, 1982a; Cross, 1987; Thompson et al., 1987, 1993; M.J. Allen et al., 1998, 2002).

In this region, the best assessment of this variation over a large scale was based on regional surveys of the southern California shelf in July–September 1994 and 1998 using a stratified random survey design for assessing spatial differences (M.J. Allen et al., 1998, 2002). Population attributes vary more significantly by depth than by region within southern California (M.J. Allen and Moore, 1996; M.J. Allen et al., 1998, 2002). Fish abundance, biomass, species richness, and diversity were lowest on the inner shelf; abundance and biomass increased from the middle to the outer shelf. The low population attributes on the inner shelf may be related to a more variable environment (e.g., of temperature, salinity, turbulence, and food availability) (M.J. Allen et al., 1998). High daytime light levels on the inner shelf may make active benthic fishes more susceptible to predation than in deeper water, resulting in less diurnal benthic activity and increased selection for schooling in water-column species. High light levels may also facilitate net avoidance by fishes.

Southern California trawl catches were larger and more diverse on the coastal shelf than on the upper slope (M. J. Allen and Mearns, 1977). Biomass per individual increased on the outer shelf and upper slope (100 to 450 m) due largely to a decrease in the abundance of juveniles. Along the upper slope, significantly more species were taken at 290 m than at deeper stations (Cross, 1987).

Although NMFS surveys provide extensive information on populations of individual fisheries species, they provide less information on the catch as a whole; they lack information on distributions of mean densities, diversity, and species richness per sample (all measures commonly used in environmental analyses). In northern and central California, mean CPUE (kg/km trawled) of all species decreased from the shelf (55–183 m) to upper slope (184–366 m) in the Eureka INPFC area from 1977 to 1986 (Dark and Wilkins, 1994). However, in the Monterey region, this relationship varied by survey year (decreased with depth in 1980 and 1986 and increased with depth in 1977 and 1983).

### Taxonomic Composition of Catches

California trawl surveys collect a large number of species and these represent a diversity of taxa. Three surveys (M. J. Allen, 1982a; M. J. Allen et al., 1998, 2002) in southern California provide information on the general taxonomic composition of southern California regional trawl surveys across depths of 10–200 m. In these surveys, 87–142 species were collected, representing 34–57 families, 12–19 orders, and 3–4 classes. Trawl surveys were overwhelmingly dominated by Actinopterygii (ray-finned fishes), followed by Chondrichthyes (cartilaginous fishes), and Myxini (hagfishes). For example, actinopterygiian fishes comprised 88.1% of the species and 99.8% of total individuals in 1972–1973 (M. J. Allen, 1982a). Scorpaeniform (scorpionfish-like fishes), perciform (perch-like fishes), and pleuronectiform (flatfishes) species comprised 75.4% of the species and 93.5% of total individuals in 1972–1973. Scorpaenidae (scorpionfishes and rockfishes), Pleuronectidae (right-eyed flounders), Cottidae (sculpins), and Paralichthyidae (sand flounders) were the most diverse families (M. J. Allen, 1982a). Typically, 17–24 species occurred in 20% or more of the survey area, 23–26 species comprised 95% of the total catch, and 28–44 species comprised 95% of the total biomass (M. J. Allen, 1982a; M. J. Allen et al., 1998, 2002). The most frequently occurring species were Dover sole (*Microstomus pacificus*) in 1972–1973 and Pacific sanddab (*Citharichthys sordidus*) in 1994 and 1998. The most abundant species was stripetail rockfish (*Sebastes saxicola*) in 1972–1973, Pacific sanddab in 1994, and white croaker (*Genyonemus lineatus*) in 1998 (which included harbors as well as the shelf). The biomass dominant was California halibut (*Paralichthys californicus*) in 1994 and white croaker in 1998. The dominance of white croaker in the latter study was due to inclusion of Los Angeles-Long Beach Harbors (a preferred habitat for this species) in the survey. Pacific sanddab was biomass dominant in 1998 when harbors were excluded from the analysis.

NMFS surveys of the shelf (55–183 m) of central and northern California in 1995 and 1998 (Wilkins, 1998; Wilkins and Shaw, 2000) collected the same four classes as in southern California. Scorpaenidae was the most diverse family with 33 species, followed by Pleuronectidae with 13, and Cottidae with 7. Dominant species by biomass CPUE varied by INPFC areas (Wilkins et al., 1998; Shaw et al., 2000); Pacific hake (*Merluccius productus*) was dominant in the Eureka and Monterey INPFC areas and either spotted ratfish (*Hydrolagus colliei*) or shortbelly rockfish (*Sebastes jordani*) in the Conception INPFC area. Pacific sanddab was generally the dominant obligate soft-bottom species in these trawls in all areas, usually ranking second or third to the dominant species. Other species ranking among the top three in these regions were epipelagic species: Pacific herring (*Clupea pallasii*) (Eureka and Conception) and jack mackerel (*Trachurus symmetricus*; (Monterey and Conception). Important demersal species were English sole (*Parophrys vetulus*), chilipepper (*Sebastes goodei*), and spiny dogfish (*Squalus acanthias*) in the Eureka, Monterey, and Conception areas, respectively.

On the upper slope (200–500 m), the four classes mentioned above occurred with similar abundance and diversity relationships as on the shelf (M. J. Allen and Mearns, 1977; Cross, 1987; SCCWRP, unpublished data). As on the shelf, Scorpaenidae and Pleuronectidae are the most diverse families, but Zoarcidae (eelpouts) ranked third. Although sablefish (*Anoplopoma fimbria*), Dover sole, shortspine thornyhead (*Sebastolobus alascanus*), and splitnose rockfish (*Sebastes diploproa*) were the four most frequent species in both periods, sablefish occurrence decreased by nearly half between the 1970s and 1980s.

Similarly, in NMFS surveys of the central and northern California upper slope (183–500 m) in 1995 and 1998, Scorpaenidae, Pleuronectidae, and Zoarcidae were the most diverse families, with 30, 10, and 7 species, respectively (Wilkins, 1998; Wilkins and Shaw, 2000). Dominant species differ somewhat between the shallower (183–366 m) and deeper (367–500 m) parts of the this depth zone as well as by region. Pacific hake was typically the dominant species in the shallower region and Dover sole in the deeper region. In the Eureka area, three species have the highest biomass CPUE in both years and depths: Pacific hake, Dover sole, and sablefish; Pacific hake dominated the shallower region. In the Monterey Area, Pacific hake and splitnose rockfish dominated the shallow region (with stripetail rockfish or chilipepper third), whereas Dover sole dominated the deeper region (Pacific hake or rex sole, *Glyptocephalus zachirus*, were second or third). In the Conception area, the shallow region was dominated by splitnose rockfish, stripetail rockfish, and Pacific hake, respectively, whereas the deeper region was dominated by Dover sole or Pacific hake (rex sole or splitnose rockfish also was important).

### Assemblages

Soft-bottom fish assemblages have been described on the shelf and upper slope of California, but descriptions are done by different methods, based on different population attributes of the species and for only part of the area. Assemblages described on the shelf and upper slope of northern and central California have used NMFS survey data, species biomass, and cluster analysis (Gabriel, 1980; Jay, 1996). In southern California, statistical assemblage analysis has used environmental and academic survey data. Two types of analyses have been used there. Recurrent group analysis with presence/absence data (SCCWRP, 1973; Mearns, 1974; M.J. Allen, 1982a; M.J. Allen and Moore, 1997; M.J. Allen et al., 1998, 2002) and cluster analysis using species abundance data (L.G. Allen, 1985; M.J. Allen et al., 1998, 2002). Rockfish assemblages in NMFS West Coast trawl surveys were defined by ordination and cluster analysis (Williams and Ralston, 2002).

Recurrent group analysis describes groups of species that occur together frequently (Fager, 1957, 1963) and is based on binary (presence–absence) data. Recurrent group analyses in southern California have generally shown distinct recurrent groups associated with different shelf depth zones (e.g., inner shelf, middle shelf, outer shelf), but some groups with overlapping distributions did occur (e.g., inner shelf–middle shelf; middle shelf–outer shelf) (SCCWRP, 1973; Stephens et al., 1973; Mearns, 1974; M. J. Allen, 1982a; M. J. Allen and Moore, 1997; M. J. Allen et al., 1998, 2002). In the 1998 survey (which included bays, harbors, and islands), bay and harbor groups were identified, but there was no major island recurrent group (M. J. Allen et al., 2002). At the 0.50 affinity level, these studies described 9–11 recurrent groups with 2–7 species per group. Generally, 33–34 species comprised the recurrent groups, and these represented 23–39% of the species taken in a survey. Comparison of recurrent groups from a cold-regime period (1972–1973; M. J. Allen, 1982a), warm-regime period (1994; M. J. Allen et al., 1998), and El Niño period (1998; modified by M. J. Allen et al., 2002) identified core groups of species that occurred together in all three oceanic periods. These included the following: (1) an inner shelf–middle shelf group—California tonguefish (*Symphurus atricaudus*) and hornyhead turbot (*Pleuronichthys verticalis*); (2) a middle shelf–outer shelf group—Pacific sanddab, Dover sole, plainfin midshipman (*Porichthys notatus*), and stripetail rockfish; (3) an outer shelf group associated with fragile sea urchin (*Allocentrotus fragilis*)—slender sole (*Lyopsetta exilis*) and shortspine combfish (*Zaniolepis frenata*); and (4) an outer shelf group associated with northern heart urchin (*Brisaster latifrons*)—rex sole and blacktip poacher (*Xeneretmus latifrons*) (M. J. Allen et al., 2002). Other species co-occurred variably with other species during the three periods.

Site and species assemblages on the shelf and slope of central and northern California have been described in fish biomass data from NMFS surveys (Gabriel, 1980; Jay, 1996). Gabriel (1980) identified three major site groups, with two extending into southern California: (1) an upper slope group extending from Juan de Fuca Canyon, Washington, to Port Hueneme, California at depths of 183–467 m; and (2) a southern midshelf break [southern outer shelf–upper slope] group, extending from Cape Flattery, Washington, to Port Hueneme at depths of 91–267 m. These were divided into subregions along isobaths. Eight species groups were also identified, and two are important in California: a deepwater group of ubiquitous species largely found in the upper slope group and a shallow group concentrated in the southern outer shelf–upper slope site group. Jay (1996) described 23 site assemblages based on the biomass of the 33 dominant species in the NMFS continental shelf and upper slope surveys from the Canada-Washington border to Monterey, California, from 1977 to 1992. Most of the assemblages were dominated by Pacific hake. Of the 23 assemblages, 20 extended into California, with 13 occurring commonly. Of these, three were largely middle shelf assemblages and one was an upper slope assemblage; the remaining nine were predominantly outer shelf assemblages (with some overlapping into the mesobenthal slope). Williams and Ralston (2002) defined four major rockfish assemblages based on NMFS trawl surveys off California and Oregon: (1) a nearshore assemblage at depths less than 150 m; (2) a northern shelf group, from about 150 to 200 m and extending south to Monterey Canyon; (3) a southern shelf group, extending north to Cape Mendocino; and (4) a deepwater slope group, occurring below 200 m.

Although site and species clusters have been described in local assessments of pollution effects in southern California (e.g., CSDOC 1996), regionwide descriptions of fish site and species assemblages for this area were not done until 1994 and 1998 (M. J. Allen et al., 1998, 2002). These identified depth-related assemblages in both years and also identified bay and harbor assemblages in 1998 (when these areas were included in the surveys). Five site assemblages and four species assemblages were described for the mainland shelf in 1994 (M. J. Allen et al., 1998). Site assemblages included inner shelf, inner shelf–middle shelf, middle shelf (two), and outer shelf assemblages. Species clusters included the following dominant species: (1) inner shelf—white croaker, (2) middle shelf—yellowchin sculpin (*Icelinus quadriseriatus*), (3) middle–outer shelf—Pacific sanddab, and (4) outer shelf—slender sole. In 1998, eight site clusters and seven species clusters were defined (M. J. Allen et al., 2002). Although the same five depth-related site clusters of 1994 were defined in 1998, a northern inner shelf- harbor group, a central inner shelf harbor group, and a southern bays group were also defined. Species groups were dominated by the following species: (1) southern bays—round stingray (*Urobatis halleri*), (2) southern inner shelf/harbors—deepbody anchovy (*Anchoa compressa*), (3) central inner shelf/harbor—white croaker, (4) middle shelf–inner shelf—California lizardfish (*Synodus lucioceps*), (5) middle shelf–outer shelf (soft bottom)—Pacific sanddab, (6) middle shelf–outer shelf (island sand-rock)—spotfin sculpin (*Icelinus tenuis*), and (7) outer shelf—slender sole.

## General Characteristics of the Fauna

### What Is a Soft-Bottom Fish?

Although many fish species are caught on the soft-bottom habitat by trawls, only some are characteristic of the habitat. Soft-bottom fishes live on sandy, silty, or muddy bottoms of the sea floor. The true soft-bottom fish fauna of the California and Baja California shelf and slope is regarded here as those species that occur commonly on the soft bottom in at least one of the different life zones and play important ecological roles (generally with regard to feeding) in the community. Frequent occurrence is more important than abundance in this regard because this generally identifies species that are adapted to the soft-bottom habitat. Some taxonomic groups (e.g. Pleuronectiformes, Rajiformes, Ophidiidae [cusk-eels]) have morphologies specifically adapted to the soft-bottom habitat. Others (e.g., Cottidae, Scorpaenidae, Embiotocidae [surfperches]) commonly show fewer morphological adaptations (although some may show color adaptations) for this habitat. Also included here in this study are some near-bottom neritic species which occur frequently across the soft-bottom habitat.

Although a large number of species are taken in trawl surveys in any area, only about half or less are characteristic soft-bottom species. A high proportion of the species on the soft-bottom habitat of the mainland shelf of southern California are either incidental to the habitat or region or are inadequately sampled by trawl. For instance, of 126 fish species collected in the early 1970s at depths of 10 to 200 m on the southern California shelf, 33 (26%) formed recurrent groups, occurred commonly in different life zones of the shelf, and were considered to represent the most characteristic soft-bottom fishes of the region (M. J. Allen, 1982a). These species accounted for 95% of the total fish abundance in this habitat. The remaining 93 species (68% of the total) were considered incidental (i.e., strays from other habitats, biogeographic provinces, or life zones). Similarly, 33 species (including most but not all of the recurrent group species) played important ecological roles as dominant members of different foraging guilds in life zones (M. J. Allen, 1982a). A soft-bottom fish then, is a fish that uses the soft-bottom habitat as its primary or one of its primary habitats and is a foraging guild dominant for this habitat in some part of its range.

### Biotic Zones

#### ZOOGEOGRAPHIC PROVINCES

The distribution of marine organisms varies with latitude along the west coast of North America, usually from regional changes in water temperature (see chapter 1). This results in different regions having fish faunas with different species.

Similar faunas are often found over a large part of the coast, but these faunas may change abruptly at certain locations along the coast (Briggs, 1975; Horn and L G. Allen, 1978; M. J. Allen and Smith, 1988; Briggs, 1995). Along the coasts of California and Baja California are two major zoogeographic provinces: Oregonian and San Diegan (Briggs, 1974, 1995). The cold temperate Oregonian Province extends from Vancouver Island south along the oceanic edge of the Southern California Bight into the nearshore upwelling areas of Northern Baja California. The warm temperate San Diego Province extends from southern California (inside of the California Current) down the Baja California coast to about Bahía Magdalena. In cold periods (e.g., 1950 to 1980) and particularly in the shallowest areas, Point Conception represents the northern limit of this fauna. However, in the past two decades of warm ocean conditions (Smith, 1995), many species in this zone have expanded their ranges farther north to Monterey or beyond. Off Baja California Sur, the San Diego fauna mixes with fishes from the warm temperate Cortez Province of the Gulf of California and the tropical Mexican and Panamanian Provinces (Briggs, 1974, 1995). Most of the Oceanic Region offshore of the Californias lies within the Transition Zone.

During the past two warm decades, many of these species have extended their ranges northward; some reached southern California during the 1997–1998 El Niño (Lea and Rosenblatt, 2000; M. J. Allen and Groce, 2001a,b; Groce et al., 2001a,b). Although some species have ranges typical of the provinces described, others are temperate species, whose distributions of frequent occurrence extend across both Oregonian and San Diego Provinces (e.g., Pacific electric ray, *Torpedo californica*; Pacific hake; M. J. Allen and Smith, 1988). In addition, some are Californian warm-temperate species (found in both San Diego and Cortez Provinces) (e.g., Gulf sanddab, *Citharichthys fragilis*) or warm temperate-tropical, found in San Diego Province as well as in Mexican and Panamanian Provinces (e.g. longfin sanddab, *Citharichthys xanthostigma*).

M. J. Allen and Smith (1988) examined distributions of soft-bottom species in 25,000 trawl samples collected in 30 years from the Arctic Ocean to the U. S.-Mexico border from a zoogeographic perspective. None of the 125 most common species had distributions restricted to a single biogeographic province of Briggs (1974). Because this study focused on the temperate Northeast Pacific, the greatest number of species were Eastern Boreal Pacific (i.e., Aleutian-Oregonian) species. Many of these boreal species extend in abundance into California to about the Mendocino Escarpment, with notable reduction in occurrence and abundance south of there. Examples of these species include Pacific tomcod (*Microgadus proximus*) and butter sole (*Isopsetta isolepis*). Others extend further south to Point Conception with reduced abundance to the south (e.g., big skate, *Raja binoculata*).

A number of soft-bottom species typically have a San Diego Province distribution pattern (Point Conception to Bahía Magdalena) (Eschmeyer et al., 1983). These include thornback (*Platyrhinoidis triseriata*), California skate (*Raja inornata*), California lizardfish (*Synodus lucioceps*), specklefin midshipman (*Porichthys myriaster*), basketweave cusk-eel (*Ophidion scrippsae*), barred sand bass (*Paralabrax nebulifer*), bigmouth sole (*Hippoglossina stomata*), and California tonguefish. A number of species have San Diego-Cortez distributions and are found in both southern California and the Pacific Coast of Baja California and in the Gulf of California (usually the upper Gulf). These include California scorpionfish (*Scorpaena guttata*), stripefin poacher (*Xeneretmus ritteri*), California halibut, fantail sole (*Xystreurys liolepis*), diamond turbot (*Pleuronichthys guttulatus*), and hornyhead turbot.

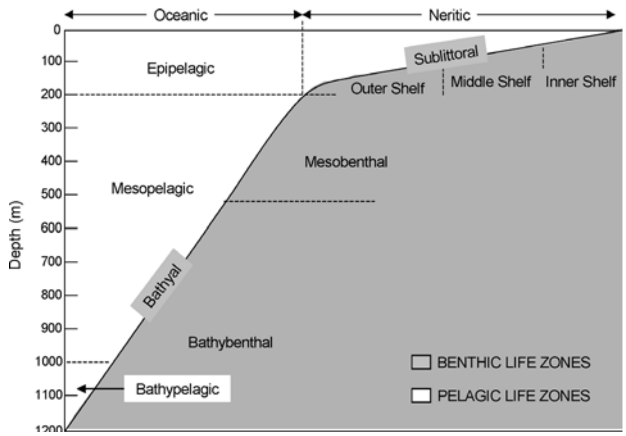



FIGURE 7-2 Pelagic and benthic life zones on the continental shelf and slope of California and Pacific Baja California (modified from M. J. Allen and Smith, 1988).

## LIFE ZONES

Adaptive zones on or over the shelf and upper slope include pelagic and benthic habitats, with subregions of these, and depth-related life zones (Hedgpeth, 1957; M. J. Allen and Smith, 1988) (fig. 7-2). The pelagic region is divided into Oceanic and Neritic Subregions. The Neritic Subregion is that portion of the water column lying over the continental shelf (from the shore to a depth of 200 m), with the Oceanic Region over the slope and basins. Over the study area of this chapter (5 to 500 m), there are two Oceanic Zones: Epipelagic at depths of 0–200 m, and Mesopelagic from 200–1000 m. Hedgpeth (1957) partitioned the benthic region relevant to this chapter into a Sublittoral Zone from shore to depths of 200 m (the continental shelf), a Mesobenthal Zone from 200 to 500 m (the upper slope), and a Bathybenthal Zone from 500 to 1000 m. The Sublittoral Zone was then subdivided into an Inner Sublittoral Zone from 0–100 m and an Outer Sublittoral Zone from 100–200 m.

M. J. Allen (1982a) described three major life zones (inner shelf—0–20 m; outer shelf—20–80 m, and upper slope—80–170 m) for soft-bottom fishes on the continental shelf of southern California, based on shifts in the occurrence of 18 foraging guilds and changes in the dominance of depth-displacing guild species comprising these guilds. Based on recognition that the continental shelf has conventionally been defined as extending to 200 m, regardless of the actual depth of the shelf break, I suggest that the outer shelf zone of M.J. Allen (1982a) be called the middle shelf zone, and the upper slope of that study be the outer shelf. Guild-related depth breaks change somewhat between different oceanic regimes; the inner shelf ranges from 0 to 20–30 m, the middle shelf from 20–30 m to 80–120 m, and the outer shelf from there to 170–200 m (M.J. Allen, 1982a; M.J. Allen et al., 1998, 2002).

M.J. Allen and Smith (1988) used three shelf zones in an atlas of trawl-caught fishes from the Arctic Ocean to the United States-Mexico Border: inner shelf (0–50 m), middle shelf (50–100 m), and outer shelf (100–200 m), with the mesobenthal (upper) slope (200–500 m) and bathybenthal slope (500–1000 m). The greater depth of the inner shelf zone was based on a hydrographic region in the Bering Sea and on inshore limits of most National Marine Fisheries Service (NMFS) surveys along the West Coast. Hecker (1990) defined an upper slope zone from 200–500 m and an upper middle slope zone from 500–1,000 m (the same as Hedgpeth's Mesobenthal and Bathybenthal Zones).

In this chapter, the following definitions are used for these zones: inner shelf (5–30 m); middle shelf (31–100 m); outer shelf (101–200 m); and mesobenthal slope (201–500 m) (fig 7-2). In southern California the inner shelf, middle shelf, and outer shelf comprise about 22%, 54%, and 24% of the mainland shelf, respectively (M. J. Allen, 1982a).

Although conditions vary along the coast, the inner shelf zone has relatively high temperature, oxygen, light, and turbulence with strong seasonal variability; low water pressure; and generally coarser sediments (except in protected areas). The deeper zones have decreasing temperatures, oxygen, and light, with less seasonal variability; low turbulence; and increasing water pressure. Offshore of the inner shelf, benefits from neritic and epipelagic productivity are highest on the middle shelf (which is the broadest shelf zone), decreases on the steeper outer shelf, and is least on the mesobenthal slope.

## Regional Distribution of Families

### DISTRIBUTIONAL DATA SOURCES

Important species of soft-bottom fishes were identified based on information on the frequency of occurrence and abundance from the following sources: northern and central California—inner shelf (California State Water Resources Control Board data, 1973–1977) and middle and outer shelf and mesobenthal slope (Wilkins, 1998; Wilkins and Shaw, 2000); southern California—inner shelf, middle, outer shelf, and mesobenthal slope (M. J. Allen, 1982a; Cross, 1987; SCCWRP historical trawl database from 1969 to 2000 [about 6200 samples]); and Baja California (Scripps Institution of Oceanography, Fish Collection data, 1950–1998; California Department of Fish and Game, CalCOFI cruise data, 1970–1971). These surveys provide widespread information on fish occurrence but differ widely in the size of trawl used; much larger trawls (27-m headrope) were used on the northern and central California middle and outer shelf and Mesobenthal slope; smaller trawls (e.g., 7.6-m) used on the northern and central California inner shelf and southern California shelf and Mesobenthal slope; and 3- to 15-m headrope trawls off the Baja California shelf and Mesobenthal slope. Because of this, small species were not well represented in the northern and central California middle and outer shelf and mesobenthal slope, and large species were poorly represented on the inner shelf of northern and central California, southern California, and Baja California. Nevertheless, these surveys provide relatively comparable information on moderate-sized species across all areas. Few samples were collected on the mesobenthal slope of Baja California, and hence it is is not well characterized in this study.

In comparing the fauna across the California/Baja California shelf and slope, regions are defined as follows: northern California (Oregon-California border to Cape Mendocino); north-central California (Cape Mendocino to San Simeon); south-central California (San Simeon to Point Conception); southern California (Point Conception to the U.S.–Mexico Border); northern Baja California (U.S.–Mexico border to the Baja California–Baja California Sur border); Northern Baja California Sur (Baja California–Baja California Sur border to Magdalena Bay); and southern Baja California Sur (Magdalena Bay to Cabo San Lucas, Baja California Sur) (fig. 7-1).

A large number of species were collected in these surveys, and it is not possible to list all in this chapter. Those listed and considered important in this study (table 7-2) are those that occur frequently within a life zone and a region (based on the distributional information sources listed above) and are likely to be important representatives of a foraging guild there.

### DISTRIBUTION OF IMPORTANT FAMILIES

About 40 families have members that are good representatives of the soft-bottom habitat of the shelf and slope of the Californias (tables 7-2, 7-3). Based on the frequency of occurrence in the above trawl surveys, the most widespread families on the soft-bottom habitat of the Californias were the Paralichthyidae, Pleuronectidae, Batrachoididae (midshipmen), and Ophidiidae, in all regions from northern California through Southern Baja California Sur (table 7-3). Pleuronectidae and Ophidiidae were generally important across the shelf and mesobenthal slope, Paralichthyidae and Batrachoididae on the shelf. Merlucciidae was important in all regions except northern Baja California, predominantly on the middle shelf, outer shelf, and mesobenthal slope.

Of the remaining families, there is a gradual shift in distribution from the north to the south (table 7-3). Of families with northern affinities, Gadidae (cods) are important only in northern California and across the shelf. Osmeridae (smelts) and Squalidae (dogfish sharks) were important from Northern through south-central California on the inner shelf and middle shelf–outer shelf, respectively. Torpedinidae (torpedo electric rays), Anoplomatidae (sablefish), Scyliorhinidae (cat sharks), Liparidae (snailfishes), and Macrouridae (grenadiers) were important from northern California through southern California. Torpedinidae is most important on the outer shelf and the others on the mesobenthal slope. Hexagrammidae (greenlings), Chimaeridae (chimaeras), and Zoarcidae were important from northern California through northern Baja California, the first on the shelf and the last two on the outer shelf–mesobenthal slope. Cottidae, Embiotocidae, Rajidae (skates), Scorpaenidae, and Agonidae, also widespread, were important from northern California through northern Baja California Sur. Cottidae and Embiotocidae were imporant on the shelf, Rajidae and Scorpaenidae on the shelf and mesobenthal slope, and Agonidae on the outer shelf.

Of families with southern affinities, Sciaenidae (drums and croakers) were important from north-central California through northern Baja California on the inner shelf and middle shelf. Cynoglossidae (tonguefishes) were important from north-central California to southern Baja California Sur on the shelf, shifting to deeper zones going south. Platyrhinidae (thornbacks) were important on the inner shelf in southern California and Argentinidae (argentines) on the middle shelf of southern California and northern Baja California. Serranidae (sea basses) and Synodontidae (lizardfishes) were important from southern California to southern Baja California Sur on the shelf; the former are restricted to the inner shelf to the north. Uranoscopidae (stargazers) and Moridae (codlings) were important on the mesobenthal slope in northern Baja California. Balistidae (triggerfishes), Congridae (conger eels), Urolophidae (round stingrays), Achiridae (American soles), Gerreidae (mojarras), Haemulidae (grunts), and Triglidae (searobins) were important on the shelf from northern to southern Baja California Sur, Balistidae and Achiridae are restricted to the inner shelf. Bothidae (lefteye flounders), Rhinobatidae (guitarfishes), Labridae (wrasses), and Callionymidae (dragonets) were important in these trawl data primarily on the outer shelf off southern Baja California Sur.

## DISTRIBUTION OF IMPORTANT FAMILIES AND SPECIES BY REGION WITHIN THE LIFE ZONE

### Inner Shelf

The inner shelf (5–30 m) is the shallowest part of the shelf (fig. 7-2). It is the zone most subject to environmental variability, with seasonally variable changes in water temperature, salinity, productivity, and turbulence; diel variability in light levels; and coastwise variability in sediment type (sandy along exposed coasts and silty along protected coasts).

Important soft-bottom fish families and species in this zone vary regionally from northern California to southern Baja California Sur (table 7-2, fig. 7-3). Note that additional species of some families are important shallower than 10 m (see chapter 6), and some species that occur infrequently in this zone were not considered important. The most widespread families (seven regions from northern California to southern Baja California Sur) are Pleuronectidae and Paralichthyidae. Batrachoididae was imporant in six regions from north-central California to southern Baja California Sur. The next most widespread families (five regions) were Embiotocidae (northern California through northern Baja California) and Ophidiidae (important from northern California through northern Baja California Sur, except in south-central California). Other families that were important both north and south of Point Conception included Rajidae, Sciaenidae, and Cynoglossidae (all occur in four regions). Other families were important over more restricted ranges. Families important only in the north included Gadidae and Liparidae (northern California) and Osmeridae, Hexagrammidae, and Cottidae (northern California to south-central California). Families important only in the south include Platyrhinidae (southern California); Synodontidae and Serranidae (southern California through southern Baja California Sur); and Urolophidae, Gerreidae, Haemulidae, Triglidae, Achiridae, and Balistidae (northern and southern Baja California Sur).

The most widespread species are the shiner perch (*Cymatogaster aggregata*), white seaperch (*Phanerodon furcatus*), speckled sanddab (*Citharichthys stigmaeus*), and English sole that occur commonly from northern California through northern Baja California (five regions) (table 7-2; fig. 7-3). Different patterns are found among species continuously common in four regions. White croaker and California tonguefish are important from north-central California through northern Baja California. Specklefin midshipman and California halibut are important from the southern California Bight to southern Baja California Sur. Other species (table 7-2) are important over more restricted ranges.

### Middle Shelf

The middle shelf (30–100 m) is typically the broadest part of the shelf (figs. 7-1 and 7-2). It is less subject to environmental variability than the inner shelf zone and generally lies below the thermocline (except during El Niño events). Compared with the inner shelf, there is less seasonal variability in water temperature and salinity, although seasonality in productivity in epipelagic waters affects this zone. Also, there is little turbulence, sediments are generally finer, pressure is greater, oxygen and light levels are lower, and diel variability in light levels is less.

Important soft-bottom fish families and species in this zone vary regionally from northern California to southern Baja California Sur (tables 7-2, 7-3; fig. 7-4). The most widespread families (seven regions) were Ophidiidae, Batrachoididae, and Paralichthyidae. Nearly as widespread (six regions) were Rajidae, Scorpaenidae, Cottidae, and Pleuronectidae (northern California through northern Baja California Sur). Families important in five regions were Merlucciidae (northern California through south-central California and northern Baja California Sur), Hexagrammidae (northern California through northern Baja California), and Cynoglossidae (south-central California through southern Baja California Sur). Other families found north and south of Point Conception include Sciaenidae and Embiotocidae (four regions, north-central California through northern Baja California). Families important only in the north include Gadidae (northern California) and Squalidae (three regions; northern through south-central California). Families important only in the south included Argentinidae and Agonidae (two regions; southern California through northern Baja California); Synodontidae (four regions; southern California through southern Baja California Sur); Gerreidae, Haemulidae, and Triglidae (two regions; northern through southern Baja California Sur); and Urolophidae, Congridae, and Bothidae (Baja California Sur). The restricted importance of some families with small species (e.g., Agonidae) from other areas is likely to be a gear-related artifact.

The most widespread species on the middle shelf were stripetail rockfish and English sole, occurring in six regions from northern California through northern Baja California Sur (table 7-2; fig. 7-4). Plainfin midshipman, spotted cusk-eel (*Chilara taylori*), longspine combfish (*Zaniolepis latipinnis*), and roughback sculpin (*Chitonotus pugetensis*) were important in five regions (northern California through northern Baja California). Species important in four regions included Pacific sanddab (northern California through southern California), white croaker, and pink seaperch (*Zalembius rosaceus*) (north-central California through northern Baja California). Other species (table 7–2) are important over more restricted ranges.

### Outer Shelf

The outer shelf (100–200 m) is typically at least partly below the shelf break and hence usually has a steeper slope than the middle shelf (fig. 7-2). In most areas along the coast of the Californias, the outer shelf is narrower than the middle shelf. The water directly over the outer shelf is typically part of the California Counter Current that flows northward. Compared with the outer shelf, sediments are typically finer, and water temperature, oxygen levels, and light levels are lower with virtually no diel variation in ambient light. However, pressure and salinity are higher. Although topographically part of the upper slope where this is below the shelf break, this zone is still strongly influenced by epipelagic productivity.

Important soft-bottom fish families and species in the outer shelf zone vary regionally from northern California through southern Baja California Sur (tables 7-2, 7-3; fig. 7-5). Ophidiidae were important in all seven regions. Rajidae,

TABLE 7-2

Ecologically Important Soft-Bottom Fishes of the Shelf and Mesobenthal Slope of California and Baja California

| *Species* | *Common Name* | *California* | | | | *Baja California* | | |
|---|---|---|---|---|---|---|---|---|
| | | *North* | *N-Cen* | *S-Cen* | *South* | *NBC* | *NBCS* | *SBCS* |
| Chondrichthyes | Cartilaginous Fishes | | | | | | | |
| Chimaeriformes | | | | | | | | |
| Chimaeridae | Shortnose Chimaeras | | | | | | | |
| *Hydrolagus colliei* | Spotted ratfish | OU | OU | OU | OU | O | — | + |
| Squaliformes | | | | | | | | |
| Squalidae | Dogfish Sharks | | | | | | | |
| *Squalus acanthias* | Spiny dogfish | MO | MO | MO | + | + | + | — |
| Carcharhiniformes | | | | | | | | |
| Scyliorhinidae | Cat Sharks | | | | | | | |
| *Apristurus brunneus* | Brown cat shark | U | U | U | U | + | — | — |
| Torpediniformes | | | | | | | | |
| Torpedinidae | Torpedo Electric Rays | | | | | | | |
| *Torpedo californica* | Pacific electric ray | O | O | O | O | + | + | — |
| Rajiformes | | | | | | | | |
| Rhinobatidae | Guitarfishes | | | | | | | |
| *Zapteryx exasperata* | Banded guitarfish | — | — | — | + | + | + | O |
| Platyrhinidae | Thornbacks | | | | | | | |
| *Platyrhinoidis triseriata* | Thornback | — | + | + | I | + | + | + |
| Rajidae | Skates | | | | | | | |
| *Raja binoculata* | Big skate | I-MO | I-MO | I-MO | + | + | + | — |
| *Raja inornata* | California skate | + | + | + | MO | I-MO | MO | + |
| *Raja rhina* | Longnose skate | U | U | U | U | U | + | — |
| Myliobatiformes | | | | | | | | |
| Urolophidae | Round Stingrays | | | | | | | |
| *Urobatis halleri* | Round stingray | + | + | + | + | + | I | I-M |
| Actinopterygii | Ray-finned Fishes | | | | | | | |
| Anguilliformes | | | | | | | | |
| Congridae | Conger Eels | | | | | | | |
| *Chiloconger dentatus* | Thicklip conger | — | — | — | — | — | O | M |
| Argentiniformes | | | | | | | | |
| Argentinidae | Argentines | | | | | | | |
| *Argentina sialis* | Pacific argentine | + | + | + | M | M | + | + |
| Salmoniformes | | | | | | | | |
| Osmeridae | Smelts | | | | | | | |
| *Spirinchus starksi* | Night smelt | I | I | I | — | — | — | — |
| Aulopiformes | | | | | | | | |
| Synodontidae | Lizardfishes | | | | | | | |
| *Synodus evermanni* | Spotted lizardfish | — | — | — | — | — | — | MO |
| *Synodus lucioceps* | California lizardfish | — | + | + | I-MO | I-MO | I-MO | + |
| *Synodus scituliceps* | Lance lizardfish | — | — | — | — | — | — | I |
| Ophidiiformes | | | | | | | | |
| Ophidiidae | Cusk-Eels | | | | | | | |
| *Cherublemma emmelas* | Black brotula | — | — | — | — | — | — | U |
| *Chilara taylori* | Spotted cusk-eel | I-MOU | I-MOU | MOU | MOU | MO | O | — |
| *Lepophidium microlepis* | Finescale cusk-eel | — | — | — | — | — | + | O |
| *Lepophidium stigmatisium* | Mexican cusk-eel | — | — | — | — | — | + | M |
| *Ophidion scrippsae* | Basketweave cusk-eel | — | — | + | I | I | I-M | + |
| Gadiformes | | | | | | | | |
| Macrouridae | Grenadiers | | | | | | | |
| *Nezumia stelgidolepis* | California grenadier | U | U | U | U | + | + | — |
| Moridae | Codlings | | | | | | | |
| *Physiculus rastrelliger* | Hundred-fathom codling | + | + | + | + | U | + | + |
| Merlucciidae | Merlucciid Hakes | | | | | | | |
| *Merluccius angustimanus* | Panama hake | — | — | — | + | + | + | U |
| *Merluccius productus* | Pacific hake | MOU | MOU | MOU | OU | + | MOU | + |
| Gadidae | Cods | | | | | | | |
| *Microgadus proximus* | Pacific tomcod | I-M | + | + | — | — | — | — |

TABLE 7-2 (continued)

| Species | Common Name | California | | | | Baja California | | |
|---|---|---|---|---|---|---|---|---|
| | | North | N-Cen | S-Cen | South | NBC | NBCS | SBCS |
| Batrachoidiformes | | | | | | | | |
| Batrachoididae | Toadfishes | | | | | | | |
| *Porichthys analis* | Darkedge midshipman | — | — | — | — | — | — | M |
| *Porichthys myriaster* | Specklefin midshipman | — | — | — | I | I | I-M | I |
| *Porichthys notatus* | Plainfin midshipman | MO | I-MO | I-MO | MO | MO | O | + |
| Scorpaeniformes | | | | | | | | |
| Scorpaenidae | Scorpionfishes | | | | | | | |
| *Scorpaena guttata* | California scorpionfish | — | + | + | M | M | + | — |
| *Sebastes caurinus* | Copper rockfish | + | M | M | + | + | — | — |
| *Sebastes chlorostictus* | Greenspotted rockfish | + | O | O | + | + | + | — |
| *Sebastes diploproa* | Splitnose rockfish | U | U | U | U | U | + | — |
| *Sebastes jordani* | Shortbelly rockfish | + | + | + | O | + | + | + |
| *Sebastes rosenblatti* | Greenblotched rockfish | — | + | + | O | O | O | — |
| *Sebastes saxicola* | Stripetail rockfish | MO | MO | MO | MO | MO | M | — |
| *Sebastes semicinctus* | Halfbanded rockfish | + | + | + | + | + | O | — |
| *Sebastolobus alascanus* | Shortspine thornyhead | U | U | U | U | + | + | — |
| Triglidae | Searobins | | | | | | | |
| *Bellator gymnostethus* | Nakedbelly searobin | — | — | — | — | — | — | O |
| *Prionotus ruscarius* | Rough searobin | — | — | — | — | — | — | I-O |
| *Prionotus stephanophrys* | Lumptail searobin | + | + | + | + | + | I-M | MO |
| Anoplomatidae | Sablefishes | | | | | | | |
| *Anoplopoma fimbria* | Sablefish | U | U | U | U | + | + | — |
| Hexagrammidae | Greenlings | | | | | | | |
| *Ophiodon elongatus* | Lingcod | I-MO | I-MO | I-MO | + | + | — | — |
| *Zaniolepis frenata* | Shortspine combfish | + | + | O | O | O | + | — |
| *Zaniolepis latipinnis* | Longspine combfish | M | M | M | M | M | + | — |
| Cottidae | Sculpins | | | | | | | |
| *Chitonotus pugetensis* | Roughback sculpin | M | M | M | M | M | — | — |
| *Icelinus filamentosus* | Threadfin sculpin | + | O | O | + | — | — | — |
| *Icelinus quadriseriatus* | Yellowchin sculpin | — | + | + | M | M | M | + |
| *Leptocottus armatus* | Pacific staghorn sculpin | I | I | I | + | + | — | — |
| *Radulinus asprellus* | Slim sculpin | M | M | M | + | + | — | — |
| Agonidae | Poachers | | | | | | | |
| *Agonopsis sterletus* | Southern spearnose poacher | — | — | + | + | + | O | — |
| *Bathyagonus pentacanthus* | Bigeye poacher | + | + | + | U | — | — | — |
| *Odontopyxis trispinosa* | Pygmy poacher | + | + | + | M | M | + | — |
| *Xeneretmus latifrons* | Blacktip poacher | O | O | O | O | O | — | — |
| *Xeneretmus ritteri* | Stripefin poacher | — | — | — | + | U | + | — |
| Liparidae | Snailfishes | | | | | | | |
| *Careproctus melanurus* | Blacktail snailfish | U | U | U | U | — | — | — |
| *Liparis pulchellus* | Showy snailfish | I | + | — | — | — | — | — |
| Perciformes | | | | | | | | |
| Serranidae | Sea Basses and Groupers | | | | | | | |
| *Diplectrum labarum* | Highfin sand perch | — | — | — | — | — | MO | M |
| *Diplectrum pacificum* | Pacific sand perch | — | — | — | — | — | I | I |
| *Paralabrax maculatofasciatus* | Spotted sand bass | — | + | + | + | + | I | I |
| *Paralabrax nebulifer* | Barred sand bass | — | + | + | I | I | + | — |
| *Pronotogrammus multifasciatus* | Threadfin bass | — | — | — | + | + | + | O |
| *Serranus aequidens* | Deepwater serrano | — | — | — | + | + | + | O |
| Gerreidae | Mojarras | | | | | | | |
| *Eucinostomus argenteus* | Spotfin mojarra | — | — | — | + | + | I-M | I-M |
| Haemulidae | Grunts | | | | | | | |
| *Haemulopsis axillaris* | Yellowstripe grunt | — | — | — | — | — | — | I-M |
| *Orthopristis reddingi* | Bronzestriped grunt | — | — | — | — | — | I-M | + |
| *Xenistius californiensis* | Salema | — | + | + | + | + | I | I-M |
| Sciaenidae | Drums and Croakers | | | | | | | |
| *Genyonemus lineatus* | White croaker | + | I-M | I-M | I-M | I-M | + | — |
| *Seriphus politus* | Queenfish | + | + | + | I | I | + | — |
| Embiotocidae | Surfperches | | | | | | | |
| *Cymatogaster aggregata* | Shiner perch | I | I | I | I | I | — | — |
| *Phanerodon furcatus* | White seaperch | I | I | I | I | I | + | — |
| *Zalembius rosaceus* | Pink seaperch | — | MO | MO | MO | MO | O | — |

TABLE 7-2 (continued)

| Species | Common Name | California | | | | Baja California | | |
|---|---|---|---|---|---|---|---|---|
| | | *North* | *N-Cen* | *S-Cen* | *South* | *NBC* | *NBCS* | *SBCS* |
| Labridae | Wrasses | | | | | | | |
| *Polylepium cruentum* | Bleeding wrasse | — | — | — | — | — | — | O |
| Zoarcidae | Eelpouts | | | | | | | |
| *Lycodes cortezianus* | Bigfin eelpout | U | U | U | U | — | — | — |
| *Lycodes pacificus* | Blackbelly eelpout | O | O | O | O | O | — | — |
| *Lyconema barbatum* | Bearded eelpout | + | + | + | + | OU | — | — |
| Uranoscopidae | Stargazers | | | | | | | |
| *Kathetostoma averruncus* | Smooth stargazer | — | — | + | + | U | + | + |
| Callionymidae | Dragonets | | | | | | | |
| *Synchiropus atrilabiatus* | Blacklip dragonet | — | — | — | + | + | + | O |
| Pleuronectiformes | | | | | | | | |
| Bothidae | Lefteye Flounders | | | | | | | |
| *Engyophrys sanctilaurentii* | Speckledtail flounder | — | — | — | + | + | + | M |
| *Perissias taeniopterus* | Flag flounder | — | — | — | — | — | + | O |
| Paralichthyidae | Sand Flounders | | | | | | | |
| *Citharichthys gordae* | Mimic sanddab | — | — | — | — | — | — | O |
| *Citharichthys sordidus* | Pacific sanddab | M | M | M | M | + | + | + |
| *Citharichthys stigmaeus* | Speckled sanddab | I | I | I | I | I | + | + |
| *Citharichthys xanthostigma* | Longfin sanddab | — | + | + | + | M | I-MO | M |
| *Hippoglossina bollmani* | Spotted flounder | — | — | — | — | — | — | M |
| *Hippoglossina stomata* | Bigmouth sole | — | + | + | MO | MO | MO | O |
| *Paralichthys californicus* | California halibut | + | + | + | I | I | I | I |
| *Syacium ovale* | Oval flounder | — | — | — | — | — | — | I |
| *Xystreurys liolepis* | Fantail sole | — | + | + | I | I | + | + |
| Pleuronectidae | Righteye Flounders | | | | | | | |
| *Atheresthes stomias* | Arrowtooth flounder | U | + | — | — | — | — | — |
| *Eopsetta jordani* | Petrale sole | MO | MOU | MOU | U | + | — | — |
| *Glyptocephalus zachirus* | Rex sole | MOU | MOU | MOU | OU | + | + | — |
| *Isopsetta isolepis* | Butter sole | I | + | + | + | — | — | — |
| *Lyopsetta exilis* | Slender sole | OU | OU | OU | OU | OU | + | — |
| *Microstomus pacificus* | Dover sole | MOU | MOU | MOU | OU | O | O | — |
| *Parophrys vetulus* | English sole | I-M | I-M | I-M | I-M | I-M | I-M | — |
| *Pleuronichthys decurrens* | Curlfin sole | + | I | I | + | + | — | — |
| *Pleuronichthys ritteri* | Spotted turbot | — | — | — | + | + | I-M | I |
| *Pleuronichthys verticalis* | Hornyhead turbot | — | + | + | I-M | I-M | + | — |
| *Psettichthys melanostictus* | Sand sole | I | I | I | + | — | — | — |
| Achiridae | American Soles | | | | | | | |
| *Achirus mazatlanus* | Pacific lined sole | — | — | — | — | + | I | I |
| Cynoglossidae | Tonguefishes | | | | | | | |
| *Symphurus atramentatus* | Halfspotted tonguefish | — | — | — | — | — | — | M |
| *Symphurus atricaudus* | California tonguefish | + | I | I-M | I-M | I-M | MO | + |
| *Symphurus oligomerus* | Whitetail tonguefish | — | — | — | — | — | — | O |
| Tetraodontiformes | | | | | | | | |
| Balistidae | Triggerfishes | | | | | | | |
| *Balistes polylepis* | Finescale triggerfish | + | + | + | + | + | I | I |

NOTE: "Ecologically important" species listed here are species that occur frequently on the soft-bottom habitat in a region and which are likely to be the dominant representative of a foraging guild in the region and life zone. Those reported but less important (+) may occur incidentally in trawl catches beyond the area of most importance. In addition, differences in sampling gear between regions (Northern to south-central California, southern California, northern Baja California to Baja California Sur) may affect the occurrence of species in this table. Also note that a typical trawl survey captures many species from adjoining habitats and hence would include many more species. − = not reported; + = reported but less important; North = northern California; N-Cen = north-central California; S-Cen = south-central California; South = southern California; NBC = northern Baja California; NBCS = northern Baja California Sur; SBCS = southern Baja California Sur; I = inner shelf; M = middle shelf; O = outer shelf; U = mesobenthal (upper) slope.

Data from California State Water Resources Control Board data (northern and central California); Southern California Coastal Water Research Project data (southern California); Scripps Institution of Oceanography, fiish collection data; and California Cooperative Oceanic Fisheries Investigations data (Baja California). Taxonomic classifiication, scientifiic names, and common names from Nelson et al. (2004

Batrachoididae, Scorpaenidae, Agonidae, and Pleuronectidae were important in six regions, ranging from northern California through northern Baja California Sur. Chimaeridae, Hexagrammidae, Zoarcidae, Merlucciidae, and Embiotocidae were important in five regions. The first three ranged from northern California through northern Baja California, Merlucciidae from northern California through southern California and in northern Baja California Sur, and Embiotocidae from north-central California through northern Baja California Sur. Families important only in the north

TABLE 7-3

Ecologically Important Soft-Bottom Fish Families of the Shelf and Mesobenthal Slope of California and Baja California

| | *California* | | | | *Baja California* | | |
|---|---|---|---|---|---|---|---|
| *Family* | *North* | *N-Cen* | *S-Cen* | *South* | *NBC* | *NBCS* | *SBCS* |
| Gadidae | I-M | + | + | + | − | − | − |
| Osmeridae | I | I | I | + | − | − | − |
| Squalidae | MO | MO | MO | + | + | + | − |
| Torpedinidae | O | O | O | O | + | + | − |
| Liparidae | I-U | U | U | U | + | + | + |
| Anoplomatidae | U | U | U | U | + | + | − |
| Scyliorhinidae | U | U | U | U | + | + | + |
| Macrouridae | U | U | U | U | + | + | + |
| Hexagrammidae | I-MO | I-MO | I-MO | MO | MO | + | − |
| Chimaeridae | OU | OU | OU | OU | O | + | + |
| Zoarcidae | OU | OU | OU | OU | OU | + | + |
| Cottidae | I-M | I-MO | I-MO | M | M | M | + |
| Embiotocidae | I | I-MO | I-MO | I-MO | I-MO | O | − |
| Rajidae | I-MOU | I-MOU | I-MOU | MOU | I-MOU | MO | + |
| Scorpaenidae | MOU | MOU | MOU | MOU | MOU | MO | + |
| Agonidae | O | O | O | MOU | MOU | O | − |
| Paralichthyidae | I-M | I-M | I-M | I-MO | I-MO | I-MO | I-MO |
| Batrachoididae | MO | I-MO | I-MO | I-MO | I-MO | I-MO | I-M |
| Pleuronectidae | I-MOU | I-MOU | I-MOU | I-MOU | I-MOU | I-MO | I |
| Ophidiidae | I-MOU | I-MOU | MOU | I-MOU | I-MO | I-MO | MOU |
| Merlucciidae | MOU | MOU | MOU | OU | + | MOU | U |
| Sciaenidae | + | I-M | I-M | I-M | I-M | + | + |
| Cynoglossidae | + | I | I-M | I-M | I-M | MO | MO |
| Platyrhinidae | − | + | + | I | + | + | + |
| Argentinidae | + | + | + | M | M | + | + |
| Serranidae | + | + | + | I | I | I-MO | I-MO |
| Synodontidae | − | + | + | I-MO | I-MO | I-MO | I-MO |
| Uranoscopidae | − | + | + | + | U | + | + |
| Moridae | + | + | + | + | U | + | + |
| Balistidae | + | + | + | + | + | I | I |
| Achiridae | − | − | − | − | + | I | I |
| Urolophidae | + | + | + | + | + | I | I-M |
| Gerreidae | − | − | − | + | + | I-M | I-M |
| Haemulidae | − | + | + | + | + | I-M | I-M |
| Triglidae | + | + | + | + | + | I-M | I-MO |
| Congridae | − | − | − | + | + | O | M |
| Bothidae | − | − | − | + | + | + | MO |
| Rhinobatidae | − | + | + | + | + | + | O |
| Labridae | + | + | + | + | + | + | O |
| Callionymidae | − | − | − | + | + | + | O |

NOTE: North = northern California; N-Cen = north-central California; S-Cen = south-central California; South = southern California; NBC = northern Baja California; NBCS = northern Baja California Sur; SBCS = southern Baja California Sur. Based on California State Water Resources Control Board data (Northern and Central California); Southern California Coastal Water Research Project data (southern California); Scripps Institution of Oceanography, fiis collection data; and California Cooperative Oceanic Fisheries Investigations data (Baja California).I = inner shelf; M = middle shelf; O = outer shelf; U = mesobenthal slope; + = family reported from region; − = not reported.

included Squalidae (three regions, northern through south-central California), Torpedinidae (four regions, northern through southern California), and Cottidae (two regions, north-central and south-central California). Those important only in the south included Paralichthyidae and Synodontidae (four regions, southern California through southern Baja California Sur), Serranidae and Cynoglossidae (two regions, northern and southern Baja California Sur); Congridae (northern Baja California Sur); and Rhinobatidae, Labridae, Callionymidae, and Bothidae (all southern Baja California Sur).

The most widespread species on the outer shelf (six regions) were spotted cusk-eel, plainfin midshipman, and Dover sole, ranging from northern California to northern Baja California Sur (table 7-2). Species important in five regions include spotted ratfish, stripetail rockfish, slender sole, blacktip poacher, and blackbelly eelpout (*Lycodes pacificus*) from northern California to northern Baja California; Pacific hake from northern California through southern California and northern Baja California Sur; and pink seaperch from north-central California through northern Baja California Sur. Species important in four regions were Pacific electric ray (northern California through

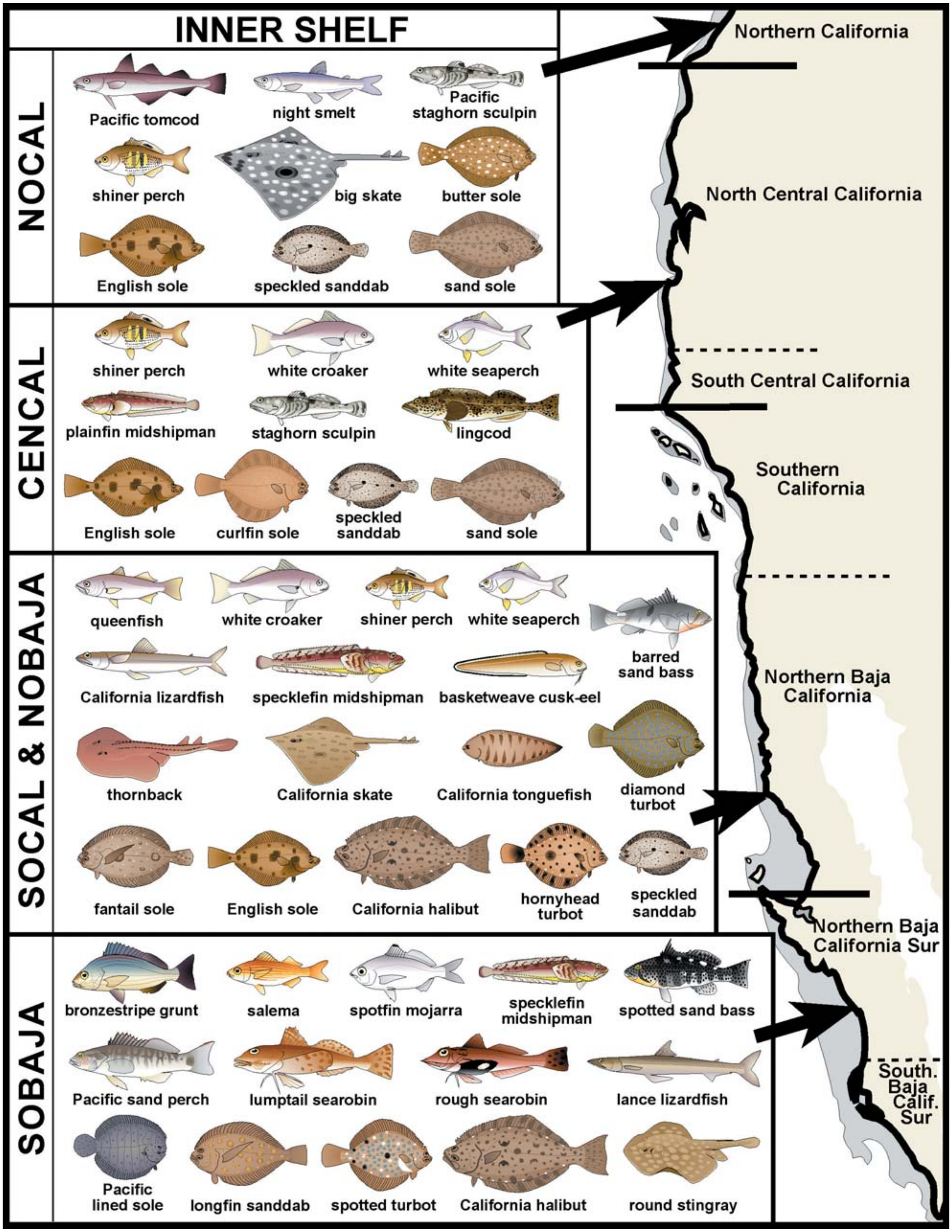



FIGURE 7-3 Soft-bottom fishes representative of the inner shelf in four latitudinal regions off the Californias.

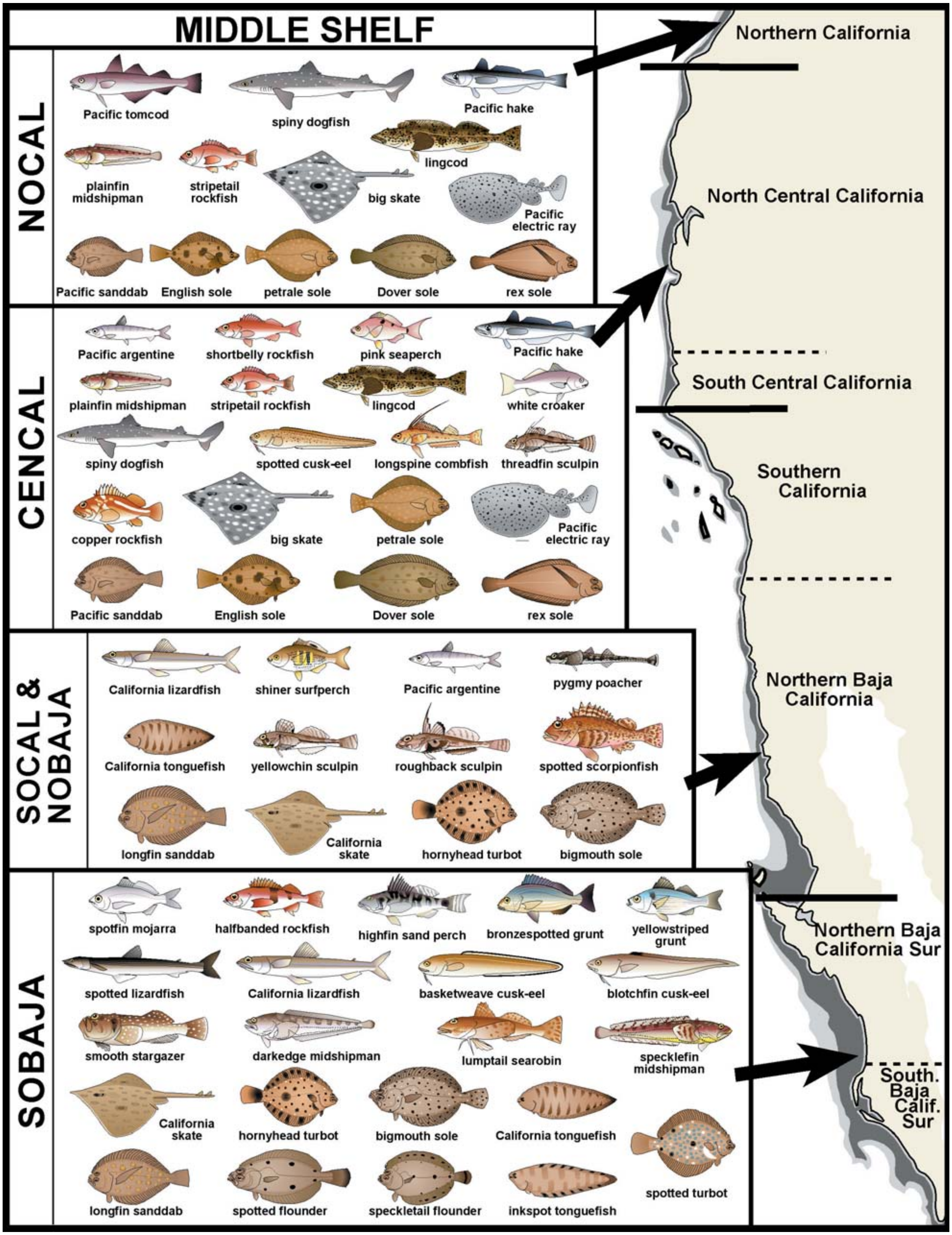



FIGURE 7-4 Soft-bottom fishes representative of the middle shelf in four latitudinal regions off the Californias.

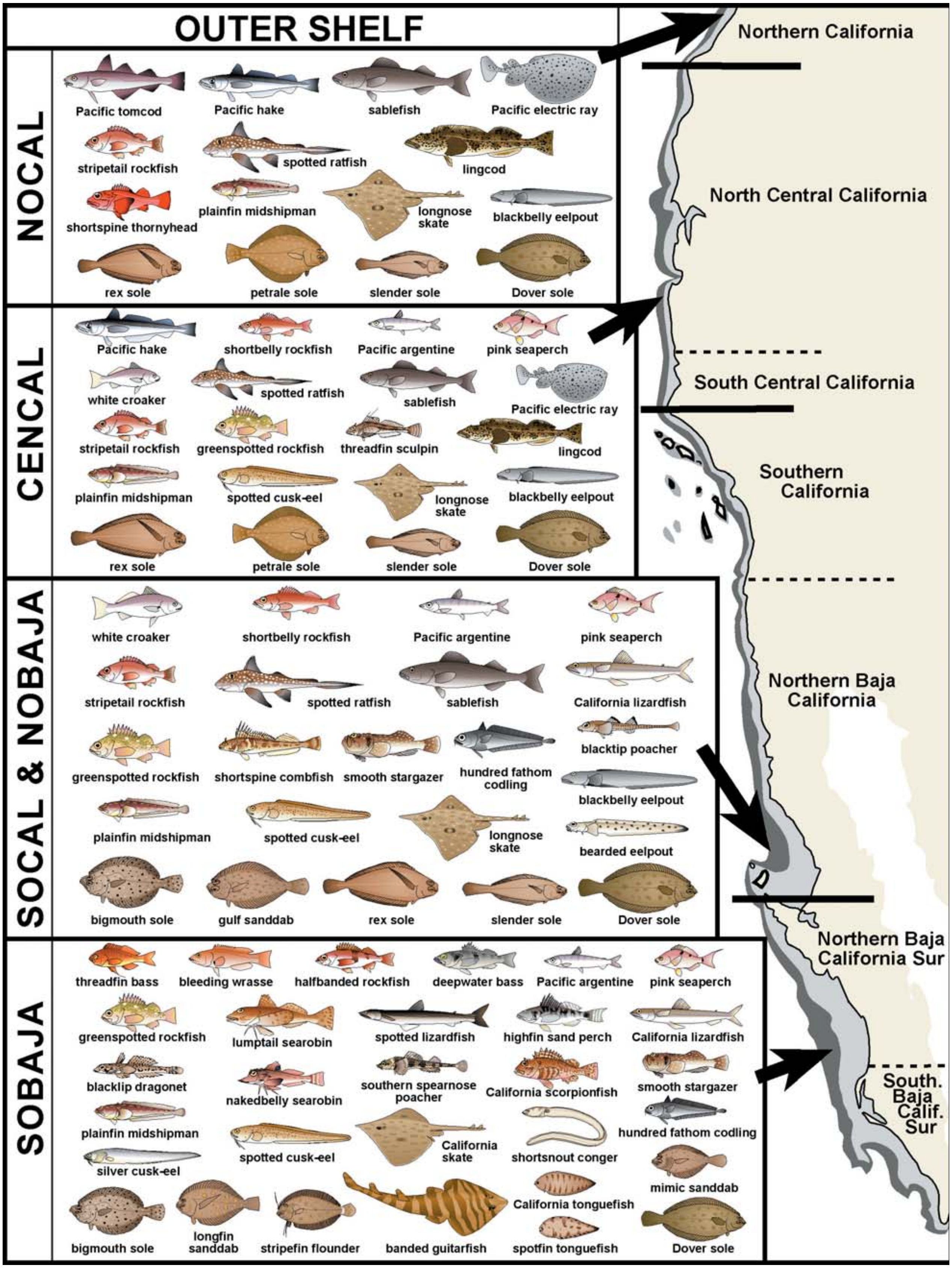



FIGURE 7-5 Soft-bottom fishes representative of the outer shelf in four latitudinal regions off the Californias.

southern California) and bigmouth sole (southern California through southern Baja California Sur).

#### Mesobenthal Slope

The mesobenthal slope (200–500 m) typically has a steep slope with fine sediments (fig. 7-2). In most areas along the coast of the Californias, the mesobenthal slope is narrower, but in southern California, it extends as an elongate peninsula from Point Conception to Cortez Bank (with a small gap north of Tanner Bank) as the Santa Rosa-Cortez Ridge. Another broad area of the mesobenthal slope occurs off Baja California Sur. As with the outer shelf, the water over the mesobenthal slope is exposed to the California Counter Current that flows northward. Compared with the outer shelf, pressure is higher, water temperature is lower, oxygen levels approach the oxygen minimum for this area, and ambient light is virtually nonexistent. In contrast to the outer shelf, this zone is less strongly influenced by epipelagic productivity and has fewer small juvenile fish.

The distribution of families and species in this zone is less well defined in this study because few data are available from the mesobenthal slope of Baja California (table 7-2, 7-3; fig. 7-6). Merlucciidae was the most widespread family (six regions), important from northern California to southern Baja California Sur, except in northern Baja California. Rajidae, Scorpaenidae, and Pleuronectidae were important in five regions from northern California through northern Baja California. Ophidiidae was also important in five regions but from northern California through southern California and off southern Baja California Sur. Chimaeridae, Scyliorhinidae, Macrouridae, Anoplopomatidae, Liparidae, and Zoarcidae range from northern California through at least southern California.

In this limited data set, Pacific hake was important from northern California through southern California and off northern Baja California Sur. Longnose skate (*Raja rhina*), splitnose rockfish, and slender sole were important from northern California through northern Baja California. Species that were important from northern California through at least southern California included brown cat shark (*Apristurus brunneus*), spotted ratfish, California grenadier (*Nezumia stelgidolepis*), spotted cusk-eel, shortspine thornyhead, sablefish, blacktail snailfish (*Careproctus melanurus*), bigfin eelpout (*Lycodes cortezianus*), rex sole, and Dover sole. Other species (table 7-2, fig. 7-6) are important over more restricted ranges.

### Natural History Traits

Soft-bottom fishes are diverse; some species have adaptations specific to the soft-bottom habitat, whereas others have traits that are also found among fishes in other habitats. Some traits are characteristic of taxonomic affiliation rather than specifically of habitat. Examination of the variety of natural history traits found in soft-bottom fishes provides insight into the diversity of lifestyles found in the fauna and their relevance to life in this habitat. Many of these traits are described for individual taxa in taxonomic works (e.g., Jordan and Evermann, 1896–1900, Norman, 1934), life-history compilations (e.g., Hart, 1973; Fitch and Lavenberg, 1968, 1971; Leet et al., 1992, 2001; Love, 1996), and studies on specific species (e.g., Hagerman, 1952; Ford, 1965) or ecological groups of species (e.g., Hobson and Chess, 1976). M. J. Allen (1982a) provides a description of many of these traits of soft-bottom fish communities on the southern California shelf and their relation to community organization. The following sections describe the variation of natural history traits found in soft-bottom fishes of the Californias.

#### MORPHOLOGICAL ATTRIBUTES

The soft-bottom habitat is generally flat and relatively featureless. Although vast areas are flat with no relief, relief occurs in some areas in the form sand ripples, flat rock outcroppings, excavations made by rays, burrows of infaunal or epifaunal invertebrates, protruding tubes of polychaete or tube anemones, protruding sea pens, and large, well-protected echinoderms (sea urchins, sea cucumbers, sand dollars, sea stars), crustaceans (e.g., crabs), gastropods (e.g., sea slugs, snails), and brachiopods.

Benthic fish species adapted for living on this soft-bottom generally can hide in this relatively featureless bottom either by being flat and presenting a profile similar to the bottom or by reducing their visibility (generally during the day) by burrowing in the sediments or living in preexisting fixed burrows. Fishes with flattened bodies are morphologically most specialized for these habitats. There are two basic flattened body morphologies: (1) compressed, laterally asymmetrical species and (2) depressed, laterally symmetrical species.

The compressed, laterally asymmetric morphology occurs entirely within the flatfishes, Pleuronectiformes. Although flatfishes are bilaterally symmetrical as larvae, they are asymmetrical after settling to the bottom as juveniles. The body is laterally compressed and the fish lie on their sides with both eyes on the side of the body away from the sediment. Typically, the eyed side has a color typical of the substrate; some species can change colors to match the substrate. The blind side is typically white. Some species also have other asymmetries (e.g., no lateral line on blind side, smaller or no teeth on the eyed side). This morphology is most specialized for the soft-bottom habitat because none (at least on the coast of the Californias) is found predominantly in either hard-bottom or water-column habitats. With their flat bodies and cryptic coloration, pleuronectiform fishes are hardly noticeable on the bottom and most bury themselves slightly in the sediments with only the eyes (and perhaps mouth, and gill opening) visible when inactive. Paralichthyidae and Pleuronectidae are found along almost the entire coast of California and Pacific Baja California, whereas Cynoglossidae occur largely from central California south, and Bothidae and Achiridae predominantly south of Bahia Magdalena, Baja California Sur, with stragglers to southern California.

Depressed, laterally symmetrical species are dorsoventrally flattened; lateral features are symmetrical in color and form. On the shelf and slope of the Californias, the most extreme forms include Pacific angel shark (*Squatina californica*), rays (Batoidea: Torpediniformes, Rajiformes, and Myliobatiformes), and lophiiform (e.g., Lophiidae [goosefishes]; Ogcocephalidae [batfishes], found predominantly off southern Baja California). Batoid fishes are depressed (flattened dorsoventrally), with flattened heads and bodies; eyes are on the dorsal body, the mouth on the ventral side, and small gill openings (spiracles) on the dorsal side behind the eyes.

Some roundfish species that bury in sediments have flattened dorsal surfaces to match the profile of the soft bottom (Uranoscopidae, Batrachoididae, some Cottidae).

These morphologies are found primarily on soft bottoms. Other morphologies found on soft-bottoms (e.g., eel-like and tadpole-shaped species) are also found in hard-bottom habi-

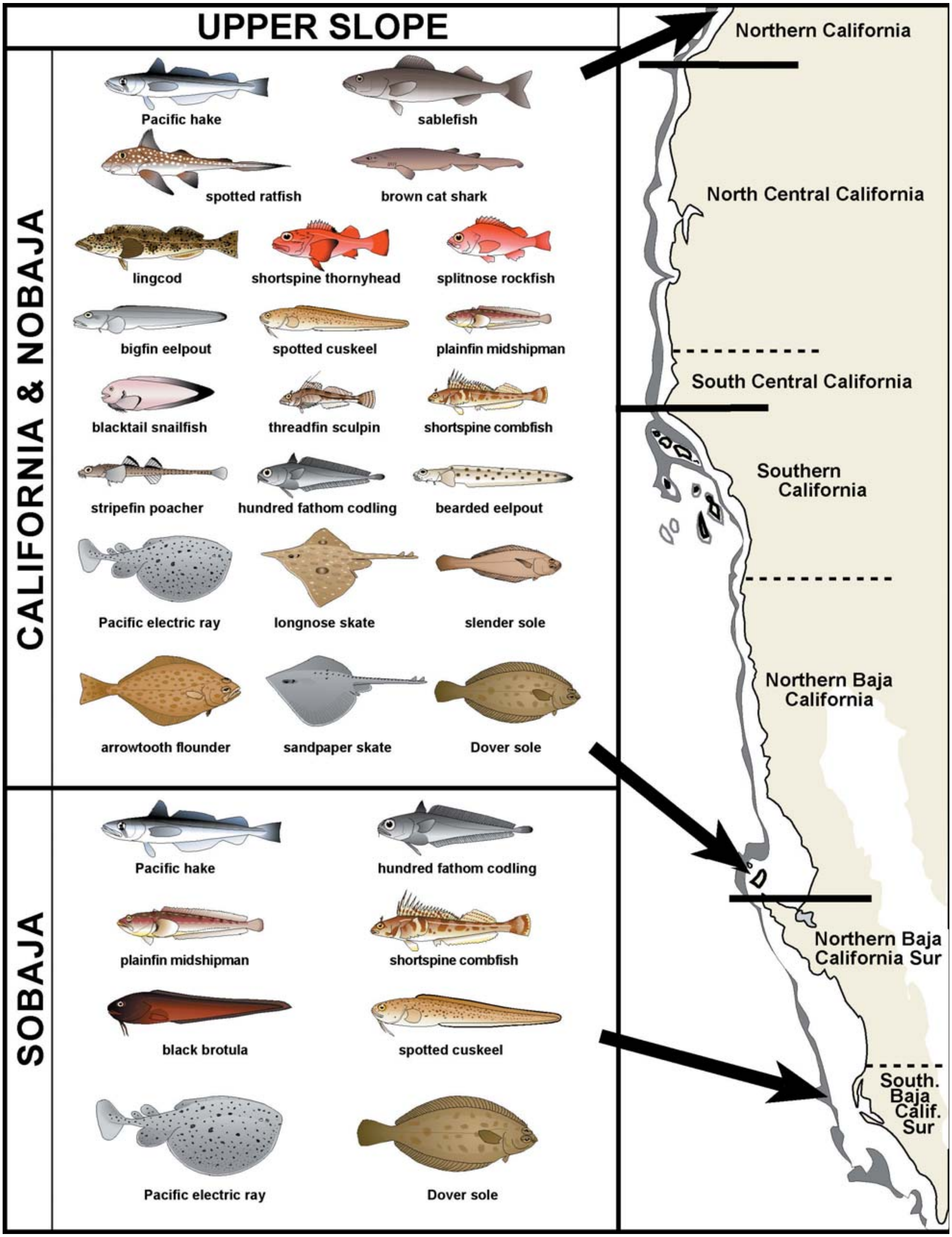



FIGURE 7-6 Soft-bottom fishes representative of the upper (mesobenthal) slope in two latitudinal regions off the Californias.

tats. White body coloration is typical of inner shelf water-column species that live on soft bottoms (e.g., white croaker; queenfish, *Seriphus politus*; shiner perch; and white seaperch. Benthic soft-bottom species typically have rather plain brownish bodies with some spotting.

## REFUGE

Unlike the hard bottom, the soft bottom provides little cover for fishes during their periods of inactivity (at night for diurnal species or during the day for nocturnal species). Major soft-bottom community members on the southern California shelf find refuge in four ways: (1) by burial or burrowing in sediments, (2) exposed on the bottom, (3) in schools, and (4) in crevices where such cover occurs (M. J. Allen, 1982a). Of 40 major species comprising the soft-bottom fish community of the Southern California shelf, 42% burrow into sediments, 38% are exposed on the bottom, 10% are in schools, and 10% are in crevices (M. J. Allen, 1982a).

### Burial or Burrowing

Generalizing beyond M. J. Allen (1982a), which focused on individual species, soft-bottom fishes that bury themselves in the sediments have distinct body shapes adapted to hiding in the sediments. They typically bury themselves by wiggling their bodies until they gradually sink into the sediment. The body shapes of these fishes are often characteristic of families and orders. This group includes (1) flattened fishes, (2) benthic roundfishes with subcircular or triangular cross sections (with dorsal, ventral, or both sides depressed), and (3) eel-like fishes.

Flattened fishes include those that are depressed (dorsoventrally flattened) such as Rajiformes, Pacific angel shark, and lophiids, as well as those that are laterally compressed and lie on their sides (Pleuronectiformes).

Some benthic roundfishes, such as uranoscopids and batrachoidids are dorsally depressed. Others, such as most synodonitids and triglids have partly depressed cross sections. Some small cylindrical fishes hide in fixed burrows of infaunal invertebrates (e.g., bay goby, *Lepidogobius lepidus*; Grossman, 1979) or protruding polychaete tubes (e.g., orangethroat pikeblenny, *Chaenopsis alepidota*; Thomson et al., 2000).

Eel-like fishes found on soft bottoms typically burrow backward into the sediment using their pointed tails (usually the dorsal, caudal, and anal fins are confluent). This group includes Myxinidae (hagfishes), Congridae, Ophichthidae (snake eels), Ophidiidae, and Zoarcidae.

### Exposed in Open

Many species stay in the open when inactive, either relying on spines or armor for protection or are difficult to find at night. Species with spines include the spotted ratfish, combfishes (*Zaniolepis*), nonschooling rockfishes (*Sebastes*), thornyheads (*Sebastolobus*), and scorpionfishes (*Scorpaena*). Some of these taxa, and in particular, the scorpionfishes, have venomous spines. Agonids may get some protection from their armored bodies. Other species, such as soft-bottom embiotocids (e.g., shiner perch, white seaperch, pink seaperch), lie on the bottom in the open at night, although individuals are solitary at this time (Bray and Ebeling, 1975; Ebeling and Bray, 1976; M. J. Allen, 1982a). Shiner perch school during the day when feeding but lie exposed on the bottom at night (Stephens and Zerba, 1981).

### Schooling

Schooling species include those that school as a lifestyle and those that school during part of the day. Many of the coastal pelagic species that occur over soft bottoms of the shelf and slope probably school when feeding or inactive. These include neritic-mesopelagic species such as Pacific hake and neritic-epipelagic species such as northern anchovy (*Engraulis mordax*), as well as neritic species such as shortbelly rockfish. Pacific hake schools can extend continuously for up to 19 km (Quirollo et al., 2001). Some nocturnal species (e.g., white croaker; queenfish; and walleye surfperch, *Hyperprosopon argenteum*) in nearshore soft-bottom areas form standing schools during the day and presumably break up into smaller groups or schools at night (M. J. Allen, 1982a).

### Crevices

Some species caught on soft bottoms may typically find refuge in crevices on hard bottoms. Some of these species may leave the soft bottom at night or may find crevices in a low relief hard bottom or under shells or other objects on a soft bottom. These species are mostly incidental to the soft-bottom habitat but make up a large number of the species taken in trawl surveys. These include many species of Scorpaenidae and Cottidae, as well as occasional Bathymasteridae (ronquils) or Stichaeidae (pricklebacks).

## REPRODUCTIVE MODES, LIFE HISTORY STRATEGIES, AND RECRUITMENT

### Reproductive Modes

The reproductive mode of a species often determines its habitat needs, dispersal abilities, conditions affecting early survival, and recruitment strength (M. J. Allen, 1982a). Differences in reproductive mode are generally associated with differences in higher taxa (Breder and Rosen, 1966; Balon, 1975); species of different families or genera generally have similar strategies. Of particular importance here, are the locations of the zygote and the developing embryo or larva. Zygotes can be either internal or as pelagic or demersal eggs. Developing embryos are maintained internally in some species or are released or hatched as larvae (pelagic, sometimes benthopelagic or benthic). Where maintained internally, the young are released as juveniles. On the southern California shelf, M. J. Allen (1982a) found that 45% of the 40 major community members had pelagic eggs and larvae, 18% (all rockfishes) were ovoviviparous with pelagic larvae, 15% (e.g., combfishes, Cottidae, Agonidae) had demersal eggs and pelagic larvae, 12% (all Embiotocidae) were viviparous (livebearers), and 10% (e.g., Batrachoididae, Zoarcidae) had demersal eggs and larvae. Spotted ratfish and some elasmobranchs (e.g., Scyliorhinidae; Heterodontidae [bullhead sharks]; Rajidae) lay eggs with keratinous shells, which hatch small juveniles. Other sharks and rays are viviparous. Bythitidae (viviparous brotulids), such as red brotula (*Brosmophycis marginata*) and rubynose brotula (*Cataetyx rubrirostris*), are ovoviviparous. Species with pelagic larvae and/or eggs generally have the best dispersal abilities at this stage, whereas those with demersal eggs and larvae or juveniles have the least, and subadults and adults have the best ability to disperse.

### Life-History Strategies

Species differ in their natural life spans and lifetime reproductive output. For a species to survive, its life span and reproductive output must be such that, on average, each individual replaces itself during its lifetime (or a female replaces two individuals). If this rate is maintained, populations remain stable. If more individuals than this survive, the population grows; if fewer, it declines. Thus, it is reasonable to assume that a short-lived species has fewer years to replace itself than a long-lived species, and hence, must have better short-term repopulation capabilities than a long-lived species. For instance, a speckled sanddab that lives for 3 or 4 years has to do this within this time frame, whereas a rockfish, which lives up to 80 years and produces thousands of larvae each year after reaching maturity, is very poor at doing this and needs a long life to get a successful replacement.

Given a narrow shelf off the coast of the Californias and strong upwelling along the central and northern California Coast with offshore transport of surface water, pelagic larvae are likely to be carried offshore and away from a suitable habitat for settlement. Species that settle in relatively shallow water (e.g., California halibut, fantail sole, hornyhead turbot) spend less time in the water column (29 days for California halibut; L. G. Allen, 1988) and settle out at very small sizes (e.g., 10 mm for California halibut) (Kramer, 1990). This strategy reduces the likelihood of drifting offshore of shallow settlement habitat. In contrast, long-lived pelagic larvae which settle more deeply are found among many species common on the outer shelf (e.g., Dover sole, slender sole, rex sole, and some rockfishes; Pearcy et al., 1977; Richardson and Pearcy, 1977; Charter and Moser, 1996b). Dover sole can remain in the water column for up to 2 years before settling (Markle et al., 1992). Some species characteristic of the inner and middle shelf (e.g., speckled sanddab, Pacific sanddab, California tonguefish) tend to settle at intermediate sizes (Kramer, 1990; Moser and Charter, 1996; Charter and Moser, 1996a).

### Recruitment

Species on the edge of their geographic ranges recruit more sporadically than those near the middle of the ranges (Andrewartha and Birch, 1954). Southern California is at the edge of the range of many cool- and warm-water species. Recruitment of small juveniles (young of the year) of southern California demersal fishes is episodic, strong in some years and weak in others, and is species-specific (Mearns, 1979; Mearns et al., 1980). From 1969 to 1978, recruitment was particularly high in 1975 (comprising 50% of the total catch) and represented 20 species; it was particularly low in 1972, 1974, and 1976 (Mearns, 1979). Variability in recruitment of stripetail rockfish and calico rockfish (*Sebastes dallii*) was the main source of variability in rockfish abundance in southern California trawl catches (Mearns et al., 1980). Sherwood and Mearns (1981) found that 15% of the fishes caught by trawl on the soft bottom of the southern California shelf from 1972 to 1977 were less than 60 mm SL. Of these, juveniles of speckled sanddab and stripetail rockfish were most abundant. In contrast, during the warm years of the 1990s, juveniles of both species occurred only in low abundance on the southern California shelf (M. J. Allen et al., 1998, 2002). During the 1997–1998 El Niño, four species of soft-bottom fishes previously not reported north of Baja California Sur were collected in southern California or just south of the border (M. J. Allen and Groce, 2001a,b; Groce et al., 2001a,b).

Most recent studies of settlement and early recruitment have been conducted on the inner part of the inner shelf (< 15 m depth). In the late 1980s, a number of studies assessed settlement of juvenile California halibut in this zone and in enclosed embayments of Southern California using small nets (beam trawls or otter trawls) with fine mesh (L. G. Allen, 1988; L. G. Allen et al., 1990; M. J. Allen and Herbinson, 1990, 1991; Kramer, 1990, 1991; Kramer and SWFSC, 1990; L. G. Allen and Franklin, 1992). M. J. Allen and Kramer (1991) provide a review of the factors influencing the settlement of California halibut. Coastal settlement is more variable than that in bays; interannual variation probably is largely due to oceanic conditions (advection, upwelling) that affect transport and survival of larvae, along with successful spawning and availability of suitable benthic conditions for settling juveniles. M. J. Allen and Herbinson (1991) compared settlement of all fish species collected by fine-mesh (2.5 mm) beam trawls on the inner shelf and embayments in southern California in 1989. In 288 samples, 72 species representing 31 families were collected; these were dominated by newly transformed (10–15 mm) fish. Fish densities were higher in the bays than on the coast, decreased with increasing depth on the coast, and were highest in May. On the inner shelf, speckled sanddab was the most frequent species, but queenfish was most abundant.

## MOBILITY, MOVEMENTS, AND MIGRATIONS

### Mobility

Fish mobility is generally related to size, morphology, and habitat. Larger fishes are more likely to move further than small fishes; those with more fusiform bodies with swimbladders are more likely to move further than those with short depressed bodies without swimbladders. Pelagic species without fixed habitat sites are more likely to move great distances than rocky bottom species which use crevices for refuge. Among soft-bottom fishes, flatfishes and cusk-eels that bury in sediments wherever they need to find refuge are likely to move more than species (e.g., bay goby) that find refuge in fixed burrows.

Soft-bottom fishes vary in mobility, ranging from species that conduct large-scale coastwise migrations, cross-shelf bathymetric migrations, and vertical migrations in the water column to sedentary species that do not move large distances during their postlarval lives. Migrations can be coastwise, bathymetric (along the bottom), or vertical (in the water column). Movements have been most studied for fisheries species; little information on movements exist for most nonfisheries species.

### Coastwise Migrations and Movements

Pelagic or neritic schooling species, as well as large benthopelagic and benthic species, move great distances. Pacific hake, a neritic-mesopelagic species (M. J. Allen and Smith, 1988) migrates up to 1800 km from pelagic spawning areas off southern California to British Columbia during spring and summer, moving along the upper slope and continental shelf of central and northern California (Bailey et al., 1982; Quirollo et al., 2001). Mature fish return to spawning grounds offshore of southern California and Baja California, moving at a rate of 5–11 km per day (Bailey et al., 1982). Sablefish, a benthopelagic species of the shelf and slope, generally moves less than 50 km, but some individuals have moved as far as 4400 km during 6 years from the Bering Sea to San Francisco (Sasaki, 1985).

Dover sole can move up to 680 km (Westerheim and Morgan, 1963).

### Bathymetric Migrations and Movements

Bathymetric movements across the shelf and/or slope occur seasonally in some species and ontogenetically in other species. Seasonal migrations from shelf to slope depths occur in middle and outer shelf species. For example, Dover sole moves inshore to depths of 55 m for feeding during the summer and offshore to depths of 550 m during the winter for spawning (Garrison and Miller, 1982; Hirschberger and Smith, 1983). Ontogenetic movements from shallow to deep water occur for many species; juveniles occur in shallow water and adults in deeper water (e.g., California halibut; sablefish; bocaccio, *Sebastes paucispinis*; English sole). Splitnose rockfish make a distinct ontogenetic migration from surface waters near kelp patties as small juveniles to the outer shelf and mesobenthal slope depths as subadults and adults (Boehlert, 1977). California scorpionfish undertake spawning migrations of up to 42 km to traditional deepwater spawning sites during May through August (Love et al., 1987).

Some species (e.g., Pacific hake; Quirollo et al., 2001) undertake diel vertical migrations, moving higher in the water column at night and lower in the water column during the day. These migrations are usually associated with feeding and are related to similar migrations of prey organisms such as euphausiids. The plainfin midshipman undertakes a similar migration. However, it is buried in the mud during the day (swimbladder deflated), rises into the water column at night after inflating the swimbladder at dusk, and returns to the bottom again, deflating the swimbladder at dawn (Ibara, 1970).

### Local Movements

California halibut, a large benthic species, general moves less than 13 km but can move up to 365 km (Domeier and Chun, 1995). Smaller species are more localized, moving from <100 m to several kilometers in their lives. Very small benthic species (e.g., cottids, agonids, zoarcids, and Gobiidae [gobies]) are likely to be more sedentary due to their size and/or lack of swimbladders, but the mobility of these species is generally not studied because they lack importance to fisheries.

## DIEL BEHAVIOR

As with fishes on other shelf habitats, the diel activity of soft-bottom fishes falls into one of four general types: diurnal, nocturnal, crepuscular (dawn and dusk), or no clear diel behavior (Hobson, 1965, 1968; Hobson and Chess, 1976; Hobson et al., 1981). Diel activity patterns are likely to be better developed at shallow depths, where there is a greater difference in ambient light levels between day and night. With increasing depth, diel differences in ambient light levels decrease to very little by 200 m in coastal waters (Clarke and Denton, 1962), and hence diel behavior may be less well-defined. I have observed spotted cusk-eel, commonly nocturnal in shallow water, actively foraging during the day in deeper waters of the shelf. Further, nocturnally active fishes may be more active in shallow water during the day when conditions are turbid. Bioluminescence in nocturnal, vertically migrating, mesopelagic organisms that move over the shelf at night may nevertheless result in deepwater species that focus on one time period or another.

Nocturnal species often have larger eyes and/or obvious non-visual sense organs (e.g., barbels, enlarged olfactory organs, more elaborate lateral line systems, electroreceptive organs) than diurnal species at the same depth. Hobson and Chess (1976) note that nocturnal planktivores have larger eyes and mouths than diurnal planktivores. Some direct observation of nocturnal activities of pelagic fishes occurring over soft bottoms have also been made (L. G. Allen and DeMartini, 1983) (see chapter 6).

Of 40 major species in soft-bottom fish communities on the Southern California shelf at depths of 10–200m, M. J. Allen (1982a) surmised (based on literature, sensory morphology, diet, and/or some direct observation) that 32% were predominantly or probably diurnal, 25% were predominantly or probably nocturnal, and 42% had no discernible or predictable diel pattern. Species comprising shallow recurrent groups had distinct differences in diel behavior, but those comprising deeper groups generally had some species with no obvious patterns. However, diel differences in behavior extended at least as deep as the outer shelf.

Some families of soft-bottom fishes in this study were characteristically of one type or another. Ophidiidae, Batrachoididae, Sciaenidae, and Cynoglossidae were nocturnally active; Hexagrammidae were diurnally active; Cottidae and Agonidae had no obvious pattern; and Embiotocidae, Scorpaenidae, Paralichthyidae, and Pleuronectidae had species representing more than one pattern.

## FEEDING AND FORAGING

### Diet

Species with commercial or recreational importance often have had extensive studies of stomach analysis sometimes from California waters and sometimes from areas to the north (e.g., Conway, 1967; Jones and Geen, 1977; Kravitz et al., 1977; Pearcy and Hancock, 1978; Gabriel and Pearcy, 1981), but feeding studies of less important species are more limited (e.g., Luckinbill, 1969; Ware, 1979; Murillo et al., 1998). A difficulty in comparing diet studies results from inconsistencies in the way data were analyzed (e.g., number of prey individuals, volume or biomass, frequency of occurrence, index of relative importance). The same set of stomachs of a species can give very different assessments of diet if number of prey, prey volume, or frequency of occurrence are examined alone. The Index of Relative Importance (IRI) (Pinkas et al., 1971) combines the three variables into a single index. Percent IRI provides a useful means of comparing diets of different species (M. J. Allen, 1982a).

Few studies have focused on feeding habits of the soft-bottom fish community as a whole. M. J. Allen (1982a) examined 1018 stomachs of the 40 most common soft-bottom species on the southern California shelf; these contained 461 prey species, representing 218 families, and 31 classes. Crustacea were the most important class of prey and were found in all species. These were followed by Polychaeta and Actinopterygii (ray-finned fishes), both occurring in 65% of the fish species. Of the crustacea, gammaridean amphipods were consumed by all species, calanoid copepods and reptantian decapods (crabs) each occurred in 68% of the species. Noteworthy was the near absence of gastropods and isopods in the diets of these fishes. Most of the prey were species that were active on or just above the sediments but could be found in either location.

Many fishes undergo ontogenetic diet changes. Coastal pelagic and neritic fishes over the soft bottom typically feed on calanoid copepods when small, shift to euphausiids (over the middle shelf to mesobenthal bottom) or mysids (on the inner shelf) at moderate sizes, and to fish and squid when large. Some species never get beyond one of these stages: shiner perch feed primarily on calanoid copepods on the shelf, never growing larger. Stripetail rockfish and shortbelly rockfish (residents of the middle and outer shelf) feed on euphausiids when larger than the calanoid-feeding stage, whereas queenfish feed primarily on mysids at night over the inner shelf. Larger species (e.g., bocaccio, Pacific hake, California halibut) can grow beyond the euphausiid/mysid stage to feed on fish and sometimes squid. Similarly, among larger species feeding on benthopelagic prey (e.g., greenblotched rockfish, *Sebastes rosenblatti*; California scorpionfish), the sequence is typically gammaridean amphipods when small; amphipods and decapod crustaceans (shrimp, crabs) at moderate sizes; and decapods, fish, and octopus when large. This sequence of dietary change also occurs in Rajidae (Orlov, 1998). Small species (e.g., yellowchin sculpin) or small-mouthed species (e.g., pink seaperch, white seaperch) remain at the gammaridean amphipod level. Moderate sized species (white croaker) or small species with moderate sized mouths (e.g., roughback sculpin) feed primarily on amphipods and decapods. Some species (e.g., white croaker, Ware, 1979; benthopelagic rockfishes) feed on calanoid copepods in the water column before making a transition to feeding on gammarideans on the bottom. Infaunal feeders show less of a change in diet to higher taxonomic levels as they grow. Smaller individuals feed on smaller polychaetes, larger individuals on larger polychaetes and small clam siphons, and larger species include larger clam siphons. The size transitions discussed above were noted in fish collected with the small (7.6-m headrope) otter trawls used in southern California. Some species with adaptations for crushing hard shells (e.g., bat ray, *Myliobatis californica*) feed on whole clams. Because small species and smaller individuals of larger species are not so well represented in catches of larger trawls used in NMFS surveys, the general diet patterns are euphausiids to fish and squid for pelagic feeders; decapods, fish, and octopus for benthopelagic feeders; and polychaetes and clams for some infaunal feeders.

### Foraging Behavior

Foraging behavior generally determines what a species eats. Foraging behavior is often reflected in the morphology of a fish because the morphology creates constraints on behavior. M. J. Allen (1982a) examined the morphology and diet of 40 soft-bottom species on the southern California shelf and using additional information from underwater videos or photographs and the literature, described inferred foraging behavior of these species.

Fishes were first classified into roundfishes and flatfishes (M. J. Allen, 1982a). Roundfishes were further divided into those with swimbladders and without, and then further classed by mouth type (superior, terminal, and inferior). Flatfishes were sorted into those with symmetrical mouths (same size and tooth development on eyed and blind side of head) and those with asymmetrical mouths (larger mouth and better tooth development on blind side). Roundfishes with swimbladders could forage either in the water column or more widely over the bottom than fishes without swimbladders. The latter, however, were likely to be able to forage more thoroughly in small areas of the bottom or were ambushers of nektonic prey. Roundfishes with superior mouths fed on pelagic prey (calanoid copepods, euphausiids, mysids) or nektonic benthopelagic prey, presumably capturing them in the water column. Some benthic species with superior mouths (e.g., smooth stargazer, *Kathetostoma averruncus*) ambush nektonic prey swimming near the bottom. Those with terminal mouths generally ate nektonic and benthic prey, whereas those with inferior mouths generally ate benthic prey. Among flatfishes with symmetrical mouths, those with large mouths feed predominantly on nektonic prey and those with medium-sized mouths were generalists, feeding on both nektonic and benthic prey. Flatfishes with asymmetrical mouths feed primarily on infaunal prey (polychaetes and clam siphons).

Sense organ development also provides information on the way a fish forages. Large eyes relative to confamilial species (e.g., among surfperches) indicate nocturnal feeding, whereas small eyes indicate diurnal feeding (M. J. Allen, 1982a). Among the pelagic planktivores of the inner shelf, nocturnal feeders have large eyes and small mouths, whereas diurnal feeders have small eyes and small mouths (Hobson and Chess, 1976). Within the depth range of the shelf and mesobenthal slope, eye size sometimes increases in confamilial species occupying different bathymetric zones. For instance, eye size is small in the pygmy poacher (*Odontopyxis trispinosa*), a resident of the middle shelf, but large in the blacktip poacher, a resident of the outer shelf (M. J. Allen, 1982a), and larger in the bigeye poacher (*Bathyagonus pentacanthus*) of the mesobenthal slope.

Increased development of other sense organs often indicates feeding in low light levels (at night or in deepwater). Midshipmen (*Porichthys* spp.) have well-developed lateral line systems and small eyes; they are nocturnally active and feed on euphausiids or mysids in the water column, which they locate with the lateral line system (Ibara, 1967, 1970; M. J. Allen, 1982a). Rex sole has an enlarged cephalic lateral line system on the blind side of the head, covered by skin and with no lateral line pores. M. J. Allen (1982a) surmised that this may function like a stethoscope for detecting vibrations of burrowing infauna. Interestingly, this species is closely associated with the northern heart urchin (*Brisaster latifrons*), which burrows beneath sediments (M. J. Allen et al., 2002). Ampullae of Lorenzini (electroreceptive organs) allow Rajidae and Rhinobatidae to detect infaunal prey and benthic fishes on the bottom at night. Barbels (fleshy appendages on the snout or lower head) found in some sciaenids, agonids, and zoarcids (e.g., bearded eelpout, *Lyconema barbatum*) and modified fin rays (pelvic in Ophidiidae, pectoral in Triglidae) are used tactilely to locate prey on the bottom at night or, as with Triglidae, buried in the sand during the day. Sometimes, these or other parts of the body likely to be used in foraging on the bottom are covered with taste buds or chemosensory spindle cells. Tonguefishes (Cynoglossidae) have very small eyes but have enlarged olfactory organs, as well as taste buds on the blind side of the head for locating prey on the bottom at night (M. J. Allen, 1982a).

Other aspects of foraging behavior are also related to the morphology of a species. Of species of similar body morphology and size, those with larger mouths generally eat larger prey than those with small mouths. For instance, roughback sculpin often co-occurs with yellowchin sculpin on the soft-bottom middle shelf of Southern California. Although it grows larger than the yellowchin sculpin, it has a larger mouth when the two are the same size, and eats larger prey (M. J. Allen, 1982a).

Four general types of foraging behavior are common among soft-bottom fishes in southern California: (1) ambushers, (2) searchers, (3) pursuers, and (4) stalkers (M. J. Allen, 1982a). Ambushers expend relatively little energy searching for prey, relying on prey passing by their location. Searchers typically expend much effort locating prey, which once found are not likely to escape. Pursuers typically chase prey that enters their field of vision. Stalkers combine searching and ambushing or pursuing behaviors, expending energy searching for prey that once located, is likely to escape.

Soft-bottom fishes have four major behaviors with regard to the degree to which they forage in the water column or on the bottom (M. J. Allen, 1982a). Different species feed (1) entirely in the water-column, (2) mostly in the water column with some benthic foraging, (3) mostly on the bottom with some water column foraging, and (4) entirely on the bottom. The behavior of these species can be inferred from morphological characters and diet. Both water-column species with swim bladders and benthic species without swimbladders have species representing all four of these categories. Species that live in the water column and feed on prey in the water column typically have superior mouths, whereas those doing this from the bottom typically have large symmetrical mouths. Water-column species that feed on the bottom typically have inferior or terminal mouths; benthic species doing this have inferior mouths (roundfishes) or asymmetrical mouths (flatfishes). Species that feed in both areas tend to have generalized terminal mouths.

Prey behavior can also provide insight into the foraging zone of a fish species (M. J. Allen, 1982a). Prey can be classified by its potential for being captured in the water column (e.g., calanoid copepods), on the bottom (crabs), and whether it is sessile (tubicolous polychaetes) or buried (clams). Though some prey, such as those mentioned, are good indicators of the location of prey capture, most crustaceans (e.g., gammaridean amphipods, shrimp, etc.) are not because they can be taken in a variety of locations (e.g., in the water column, on the bottom, buried, or sometimes in tubes). The use of indicator prey along with the morphology of a fish provides good insight into the probable foraging zone of the fish.

### Ecological Segregation

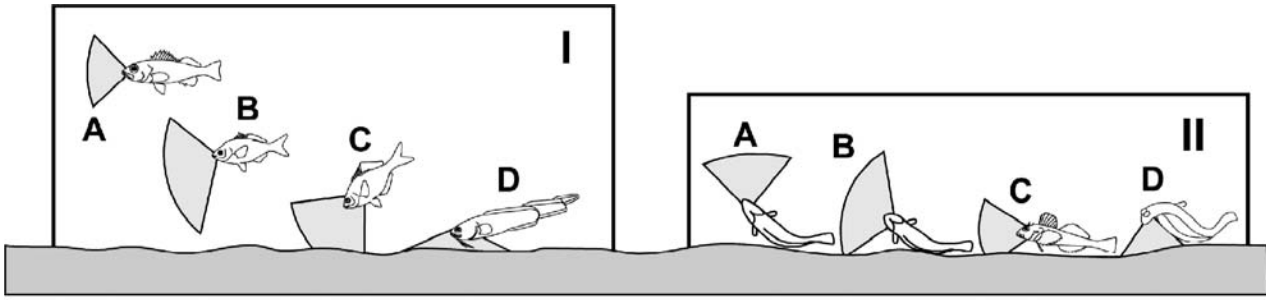
As with other organisms, fish communities can be viewed from a large-scale perspective and a small-scale perspective (M. J. Allen, 1982a,b). The large-scale perspective (biogeographic community) consists of species that live together over a large geographic area and probably represent historical associations. A small-scale perspective (local assemblage) consists of whatever species live together and interact with each other at a given location. It includes some or all of the biogeographic community members plus a number of incidental species with centers of distribution in other biogeographic communities in different biogeographic provinces, life zones, or habitats. Ecological segregation among biogeographic community members is more likely to be the result of coevolution because these species have lived together and have interacted with each other over a large area and a long time. Ecological segregation among species in the local assemblage may in part reflect this among its biogeographic community members; however, differences or lack of difference of many species in the local assemblage may be due to the chance occurrence of species at a given time or location that have evolved in different biogeographic communities in different places. The following discussion of the functional organization of species is based on this biogeographic community concept (i.e., that ecological segregation among species in a biogeographic community is due to coevolution of the species in the community rather than due to chance).

#### FUNCTIONAL ORGANIZATION OF COMMUNITIES ON THE SOUTHERN CALIFORNIA SHELF

M. J. Allen (1982a) used a synthetic approach, beginning with recurrent group analysis and using information on depth distributions, relative abundance, diet and morphological data collected in the study, as well as behavioral information from the literature, to describe the functional organization of the soft-bottom fish communities of the southern California shelf (10–200 m) based on data from 1972–1973. Recurrent groups were generally associated with different depth zones (a major group is in each of the three shelf life zones). Species that were most similar occurred in different recurrent groups at different depths. Recurrent groups contained species that were dissimilar in morphology. Morphological differences were associated with feeding and foraging. The basic difference among species that occurred together most frequently over a large area was orientation to the bottom. Based on this as a point of organization, the 40 most common species were classified into 18 foraging guilds (15 major guilds with one guild divided into four size classes) (fig. 7-7). Fish were classified into water-column and benthic lifestyles, and within these categories, species were classed according to whether they foraged in the water column (pelagivores) or on the bottom (benthivores), with two intermediate foraging zones (mostly water column, some on bottom—pelagobenthivores; mostly bottom, with some in water column—benthopelagivores). All four orientations occurred among both water-column and benthic fishes found near the seafloor on the soft bottom. Some of these orientations were further broken down by refuge mode (e.g., schooling, bottom refuge), sensory differences (e.g., visual, nonvisual), and behavior (e.g., pursuing, ambushing, extracting, excavating). In one guild (benthic ambushing benthopelagivores), ecological segregation appeared to be related to mouth size; up to four different species with nonoverlapping mouth sizes forage similarly on the soft bottom within a given life zone. Species within the same guild were sometimes morphologically similar because they are congeners (e.g., specklefin midshipman, plainfin midshipman), but some were similar due to convergence (e.g., queenfish and shortbelly rockfish or Pacific sanddab and slender sole). Some guilds, however, included species that were not morphologically similar (e.g., bigmouth sole and California lizardfish).

Species comprising a guild were generally segregated by depth; two to four species (depending on the guild) form a depth-displacement series across the shelf (M. J. Allen, 1982a). Depth displacement was best identified by shifts in the relative abundance of guild members with depth. Overlap zones existed where displacing species coexisted.

A set of depth-displacing patterns for each guild was arranged to describe the functional structure and species composition of the communities (fig. 7-8). The functional structure was described in terms of the number and type of feeding guilds at a given depth and the species composition in terms of the dominant species of each guild at a given depth. Dominant species in each guild in 1972–1973 were as follows: (1) schooling (neritic) pelagivores—queenfish (inner shelf)




**I. Water-Column Fishes**
- **A. Pelagivores**
  - **1. Schooling**
  - **2. Bottom-Refuge**
    - **a. Visual**
    - **b. Nonvisual**
- **B. Pelagobenthivores**
- **C. Benthopelagivores (Cruising)**
  - **1. Diurnal**
  - **2. Nocturnal**
- **D. Benthivores (Cruising Nonvisual)**

**II. Bottom-Living Fishes**
- **A. Pelagivores**
- **B. Pelagobenthivores**
- **C. Benthopelagivores**
  - **1. Pursuing**
  - **2. Ambushing**
- **D. Benthivores**
  - **1. Visual**
    - **a. Extracting**
    - **b. Excavating**
  - **2. Nonvisual**

FIGURE 7-7 Foraging guilds of soft-bottom fishes on the southern California shelf (from M. J. Allen, 1982a).

and shortbelly rockfish (middle and outer shelf); (2) bottom-refuge visual pelagivores—stripetail rockfish (middle and outer shelf); (3) bottom-refuge nonvisual pelagivores—specklefin midshipman (inner shelf) and plainfin midshipman (middle and outer shelf); (4) midwater pelagobenthivores—shiner perch (inner and middle shelf); (5) cruising pelagobenthivores—sablefish (outer shelf); (6) cruising diurnal benthopelagivores—white seaperch (inner shelf) and pink seaperch (middle and outer shelf); (7) cruising nocturnal benthopelagivores—white croaker (inner and middle shelf); (8) cruising nonvisual benthivore—spotted cusk-eel (middle and outer shelf) [Note that basketweave cusk-eel should be the inner shelf dominant of this guild, but because of daytime trawling, this nocturnal species was not common in the catches.]; (9) benthic pelagivores—California lizardfish (inner shelf) and bigmouth sole (middle and outer shelf); (10) benthic pelagobenthivores—speckled sanddab (inner shelf), Pacific sanddab (middle shelf), and slender sole (outer shelf); (11) benthic pursuing benthopelagivores—longspine combfish (middle shelf) and shortspine combfish (outer shelf); (12) tiny benthic sedentary benthopelagivores—pygmy poacher (middle shelf) and juvenile blacktip poacher (outer shelf); (13) small benthic sedentary benthopelagivores—yellowchin sculpin (inner and middle shelf) and adult blacktip poacher (outer shelf); (14) medium benthic sedentary benthopelagivores—fantail sole (inner shelf), roughback sculpin (middle shelf), and juvenile greenblotched rockfish (outer shelf); (15) large benthic ambushing benthopelagivores—California scorpionfish (inner and middle shelf) and adult greenblotched rockfish (outer shelf); (16) benthic extracting benthivores—hornyhead turbot (inner shelf), curlfin sole (*Pleuronichthys decurrens*) (northern inner shelf), and Dover sole (middle and outer shelf); (17) benthic excavating benthivores—English sole (inner and middle shelf) and blackbelly eelpout (outer shelf); and (18) benthic nonvisual benthivores — California tonguefish (inner and middle shelf) and rex sole (outer shelf). Depth-displacing members of these guilds are considered ecological counterparts; each performs a similar role within its community relative to other community members.

Examination of the pattern of shifts in dominant guild members and overall occurrence of guilds identified three major faunal breaks within the shelf (M.J. Allen, 1982a). The primary break was at 80 m (roughly the depth of the shelf break along the central shelf of southern California), and 50% of the guilds showed changes there. The next most important break was at 170 m (44% of the guilds showed changes), followed by 20 m (39% showed changes). These breaks separated the shelf into three zones: inner shelf; middle shelf; and outer shelf (the latter two zones were called outer shelf and upper slope in M.J. Allen, 1982a, but as noted above, the terms inner shelf, middle shelf, and outer shelf are more appropriate). In terms of relative abundance, generalists (pelagobenthivores) dominated the community on the inner and middle shelf, and specialists (pelagivores and benthivores) were more important on the outer shelf.

This model of the organization of soft-bottom fish communities of the southern California shelf was examined again in two recent surveys of the southern California shelf (10–200 m): the mainland shelf in 1994 (M. J. Allen et al., 1998) and the mainland shelf and islands in 1998 (M. J. Allen et al., 2002). This provided a perspective on the functional organization of the community in three time periods: (1) cold regime (1972–1973), (2) warm regime (1994), and (3) El Niño (1997–1998) (M.J. Allen et al., 2002). The overall pattern of the guilds and their dominant species were similar, and in particular, the sequence of depth-displacing species within a guild. However, different guilds showed different responses to the warming conditions in later years, particularly in 1998. Minor guilds (e.g., water-column pelagivores) were less widespread. Among dominant members of a guild, some shallow dominant species expanded their depth range into deeper water, but others retreated from shallow water. Some middle shelf species expanded onto the outer

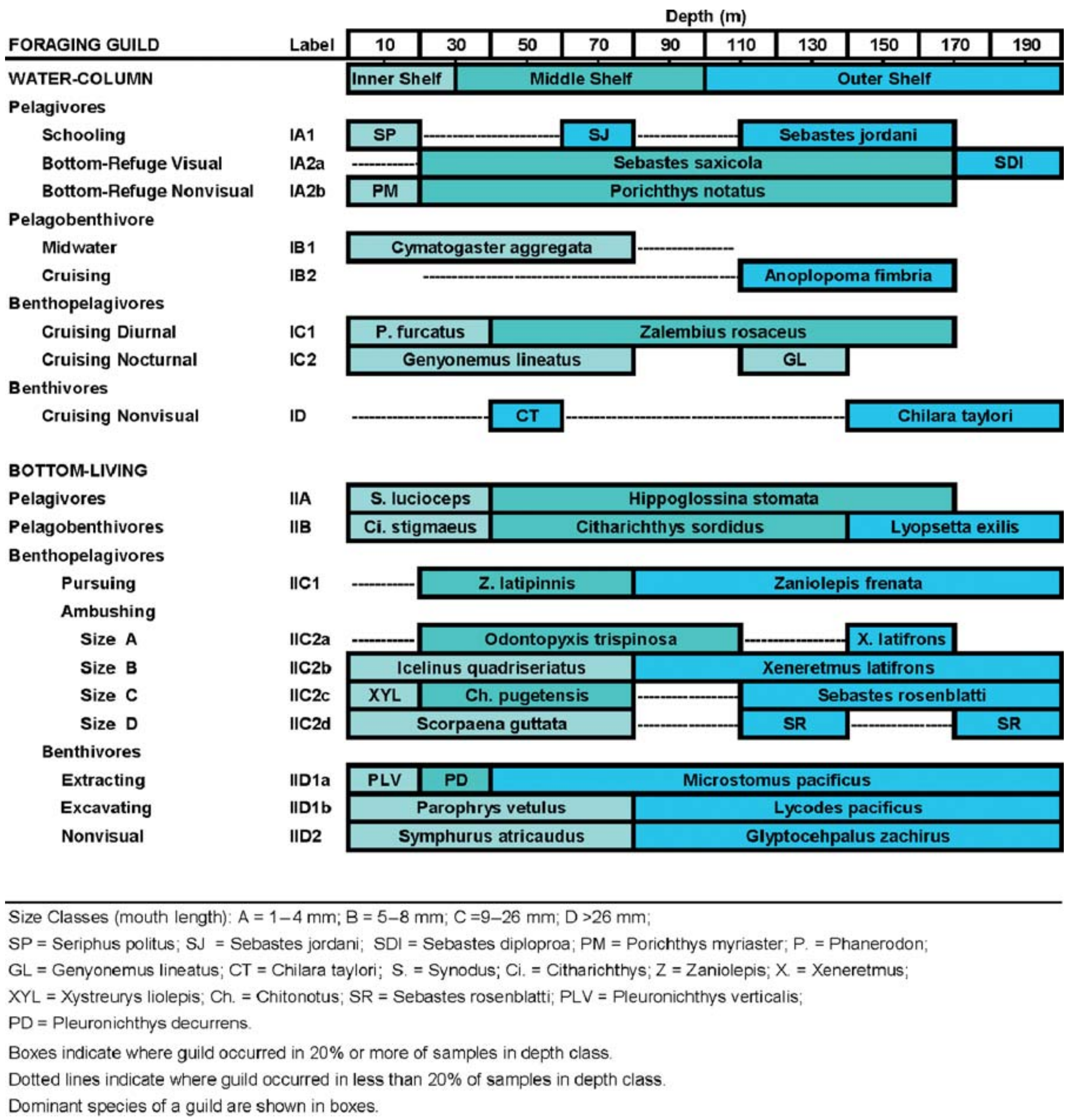



FIGURE 7-8 Functional structure of soft-bottom fish communities of the southern California shelf in 1972–1973 (modified from M. J. Allen, 1982a).

shelf in 1998, and some outer shelf species retreated deeper on the outer shelf to the mesobenthal slope. In some cases, a southerly guild member (not normally a dominant) intruded into the expected depth-displacing series. For example, the bottom-living pelagivore guild typically consisted of the speckled sanddab (inner shelf), Pacific sanddab (middle shelf), and slender sole (outer shelf). In 1998, the longfin sanddab became a dominant in the inner part of the middle shelf between the speckled sanddab and the Pacific sanddab. The Pacific sanddab expanded its zone of dominance to the inner part of the outer shelf. Also, since the 1970s, some cold-water species were replaced by warm-water species across the shelf; however, some guild dominants virtually disappeared during this period but were not replaced, suggesting an open niche.

Bottom-living pelagobenthivores (sanddab guild), bottom-living extracting benthivores (turbot guild), and bottom-living pelagivores (lizardfish/halibut guild) were the most widespread guilds on the mainland shelf in both 1994 and 1998 (M. J. Allen et al., 1998, 2002). In 1994, the sanddab guild occurred in 96% of the samples, the turbot guild in 92%, and the lizardfish/halibut guild in 75%. In 1998, the lizardfish/halibut guild was most widespread (75%) when islands and mainland were combined but was second (87%), following the sanddab guild (93%), but above the turbot guild (80%). Others showed decreasing levels of occurrence, and nonvisual benthivores (tonguefish guild) were next in occurrence. Water column pelagobenthivores and water-column benthivores had the lowest frequency of occurrence in these surveys.

### SPATIAL SEGREGATION OF DOMINANT SPECIES WITHIN SELECTED FORAGING GUILDS ALONG THE SHELF AND MESOBENTHAL SLOPE OF THE CALIFORNIAS

In addition to forming depth-displacement series, guild members can also form biogeographic displacement series. M.J. Allen (1986) examined biogeographic displacement in fusiform gadoids around the coasts of the Americas and Europe. Similarly, M.J. Allen (1990) provided a preliminary depiction of biogeographic displacement series of ecological counterparts of the California halibut along the coasts of the Californias. No description of foraging guilds of soft-bottom fishes exists along the shelf and slope of the Californias, except the depth-displacement model for southern California (M.J. Allen, 1982a). Because of major differences in trawl net size, mesh size, and trawl duration between NMFS surveys on the middle shelf to the mesobenthal slope and small otter trawls used for environmental assessments and museum collections along the inner shelf of the same area and on the shelf and slope of southern California and Baja California, it may seem unreasonable to attempt such an assessment. However, general attributes, such as morphological attributes of the species, information from the literature on feeding and foraging, frequency of occurrence of guilds, and relative abundance of guild members by life zone (using NMFS, SWRCB, SCCWRP, and SIO data, mentioned above) provide the basis for a preliminary description of the spatial segregation of guild dominants along the Californias (figs. 7-9–12). In attempting this description, it became obvious that the NMFS trawls collected larger species, including more elasmobranchs than in the small trawls used from Southern California south. Thus, I have added three guilds (IA2b2, IC2a, and IID2b) to provide some description of the distribution of soft-bottom elasmobranchs. The first is represented by the Pacific electric ray; the second by small benthopelagivore sharks (e.g., brown cat shark); and the last by skates, rays, and guitarfishes. Their generally larger size and use of electroreception are likely to contribute to segregating them ecologically from bony fishes with similar foraging orientation. I have also separated benthic pelagivores into flatfishes (e.g., California halibut, bigmouth sole; IIA1) and roundfishes (e.g., lizardfishes, lingcod; IIA2) because both types occur commonly in the same areas, although they forage similarly.

Many of the guilds form intuitively good geographic displacement series, with ecological counterparts in different regions, as well as across life zones. Bottom-living pelagobenthivores (sanddab guild) represent the most widespread guild on the southern California mainland shelf (M. J. Allen et al., 1998, 2002). Members of this guild are small flatfishes with medium-sized, symmetrical mouths, and they are generalists that feed on nektonic prey near the bottom and on benthic prey. In southern California, this guild consists of a depth-displacement series of speckled sanddab, Pacific sanddab, and slender sole (M. J. Allen, 1982a). Along the coasts of the Californias, speckled sanddab is the dominant member of this guild on the inner shelf from northern California through northern Baja California but is replaced by longfin sanddab from there at least to Magdalena Bay (fig. 7-9). Similarly, Pacific sanddab is the guild dominant on the middle shelf from northern California through southern California but is replaced by longfin sanddab from northern Baja California Sur south to Cabo San Lucas (fig. 7-10). Note that longfin sanddab became a dominant in this guild on the southern and inner part of the middle shelf of southern California during the 1998 El Niño (M. J. Allen et al., 2002). On the outer shelf, slender sole is the dominant from northern California through southern California but is replaced by longfin sanddab and, along the coast of northern Baja California Sur and mimic sanddab (*Citharichthys gordae*) at the southern tip of Baja California on the outer shelf (fig. 7-11). Along the mesobenthal slope, slender sole is the dominant member of this guild from northern California through northern Baja California (fig. 7-12).

The next most widespread foraging guild is the bottom-living extracting benthivores (turbot guild), which consists of flatfishes with small asymmetrical mouths and large eyes, that extract polychaetes from tubes and clip off clam siphons protruding from the sediments. Along the inner shelf of the Californias, the dominant species of this guild off northern California is the butter sole, followed by the curlfin sole in central California (or into southern California during cold periods; M. J Allen, 1982a), the hornyhead turbot in southern California and northern Baja California, and the spotted turbot (*Pleuronichthys ritteri*) along the coasts of Baja California Sur (fig. 7-9). On the middle shelf, Dover sole is the guild dominant from northern California through southern California. Hornyhead turbot is dominant off northern Baja California, spotted turbot off northern Baja California Sur, and speckledtailed flounder (*Engyophrys sanctilaurentii*) off southern Baja California Sur (fig. 7-10). On the outer shelf, Dover sole is dominant from northern California through northern Baja California Sur. Flag flounder (*Perissias taeniopterus*) is a possible replacement in southern Baja California Sur (fig. 7-11). Dover sole is the dominant species along the mesobenthal slope at least from northern California through southern California, and presumably from there through northern Baja California Sur (fig. 7-12). However, there are few trawl samples from this zone off Baja California, and this can be inferred only from its distribution on the outer shelf and its range (M. J. Allen and Smith, 1988).

Interesting patterns also occur among other guilds. Among the cruising nonvisual benthopelagivores on the inner and middle shelf, Pacific tomcod is dominant in northern California, white croaker (also called 'tomcod' by some anglers) from central California to northern Baja California, and other species, such as bronzestriped grunt (*Orthopristis reddingi*) and yellowstripe grunt (*Haemulopsis axillaris*), are possible replacements to the South (figs. 7-9 and 7-10). Among bottom-living pelagivore (ambushing) flatfishes, sand sole (*Psettichthys melanostictus*) is dominant among the inner shelf species in northern and central California but is replaced by California halibut in southern California and off Baja California (fig. 7-9) (M. J. Allen, 1990). On the middle and outer shelf, petrale sole is dominant in northern and central California, and bigmouth sole in southern California and Baja California (figs. 7-10 and 7-11); however, petrale sole grows larger than the bigmouth sole and becomes more piscivorous. Similarly, among elongate roundfishes of this guild, lingcod is dominant in northern and central California, and California lizardfish in southern California and Baja California on the inner, middle, and outer shelves (figs. 7-9–7-11). Among large nonvisual benthivores, big skate is dominant on the inner, middle, and outer shelves of northern and central California, whereas California skate is typically dominant in these zones off southern California and Baja California (although thornback, a platyrhinid, is dominant on the inner shelf in southern California) (figs. 7-9–7-11). Round stingray, typical of shallow bays in southern California, is common on the inner and middle shelves off Baja California Sur (figs. 7-9 and 7-10).

Examination of these patterns (figs. 7-9–7-12) also elucidates biogeographic changes in fauna. Cold temperate Oregonian species are dominant in all life zones off northern and central California, but this fauna is almost exclusively dominant on the mesobenthal slope of California (although there is insufficient data to know how far south off Baja California this is true) (fig. 7-12). Warm-temperate species representing San Diegan fauna

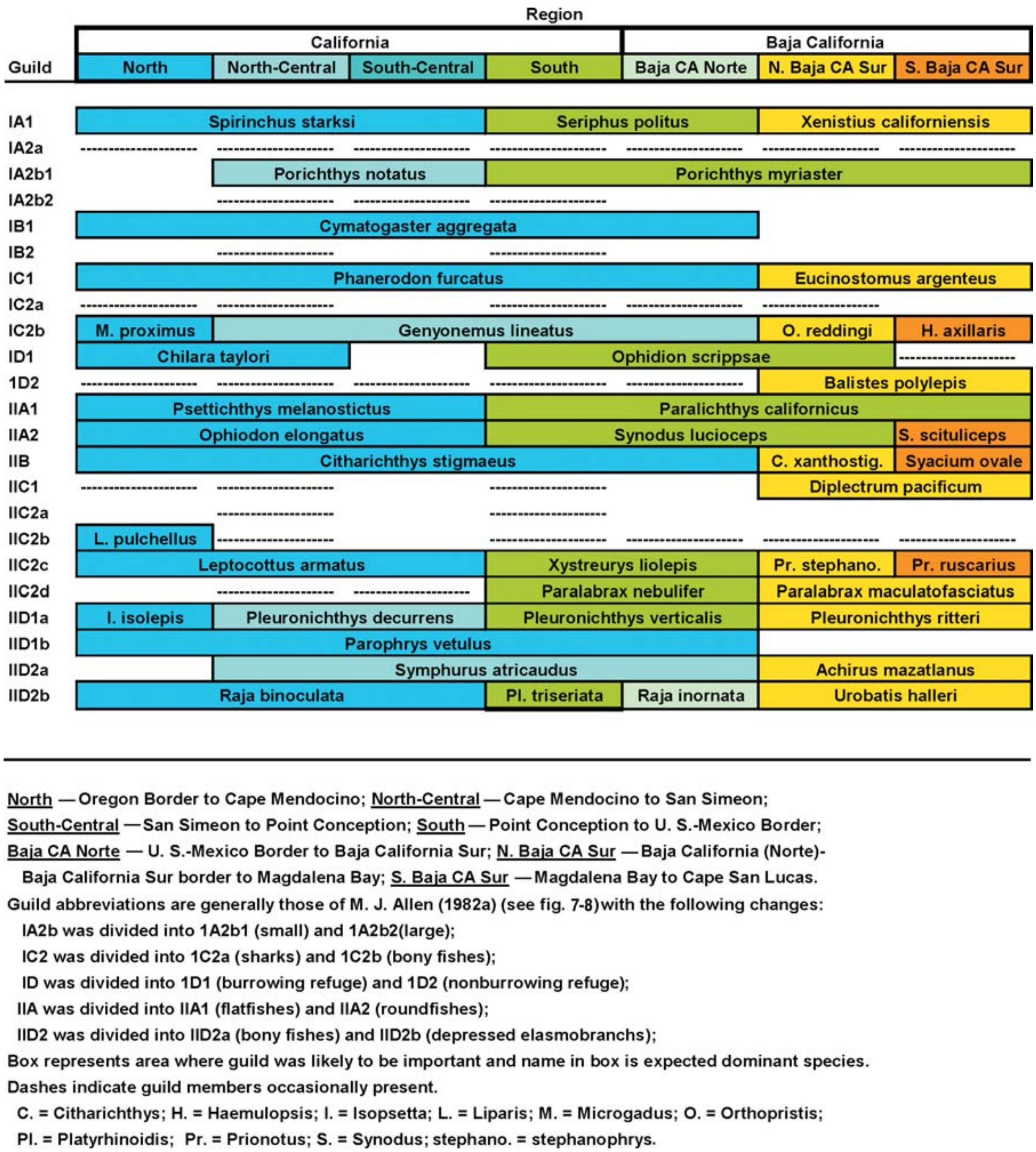



FIGURE 7-9 Generalized functional organization of soft-bottom fish communities on the inner shelf (5–30 m) of California and the Pacific Coast of Baja California.

are distinct in most life zones off southern California and northern Baja California. Along Baja California, there are relatively distinct faunas in northern Baja California (San Diegan fauna), northern Baja California Sur, and southern Baja California Sur (apparently, Mexican and Cortez faunal provinces contribute to different faunas of the Baja California Sur coast). In addition, there are cases of submergence, a shift in species dominance to deeper depths when its range extends into warmer regions. For instance, rex sole is common on the middle shelf in northern and central California but only on the outer shelf and mesobenthal slope in southern California (figs. 7-10–7-12). California tonguefish is the dominant of this guild on the middle shelf of southern California and Baja California. Similarly, spotted cusk-eel is dominant on the inner shelf of northern and central California and on the middle and outer shelves of California and Baja California but is replaced on the inner shelf of southern California and Baja California by the basketweave cusk-eel (figs. 7-9–7-11). The same pattern also occurs with plainfin midshipman and specklefin midshipman. Many species typical of bays of southern California (e.g., spotted sand bass, *Paralabrax maculatofasciatus*; round stingray; banded guitarfish, *Zapteryx exasperata*) are guild dominants on the inner shelf or deeper off southern Baja California (figs. 7-9–7-11). The patterns described here give some preliminary insight into the ecological organization of the soft-bottom fish fauna of the Californias.

## EVOLUTION OF COMMUNITIES

M. J. Allen (1982a,b) examined the geologic age of taxa of soft-bottom fishes in southern California fish communities. Most of the species that co-occurred in communities were

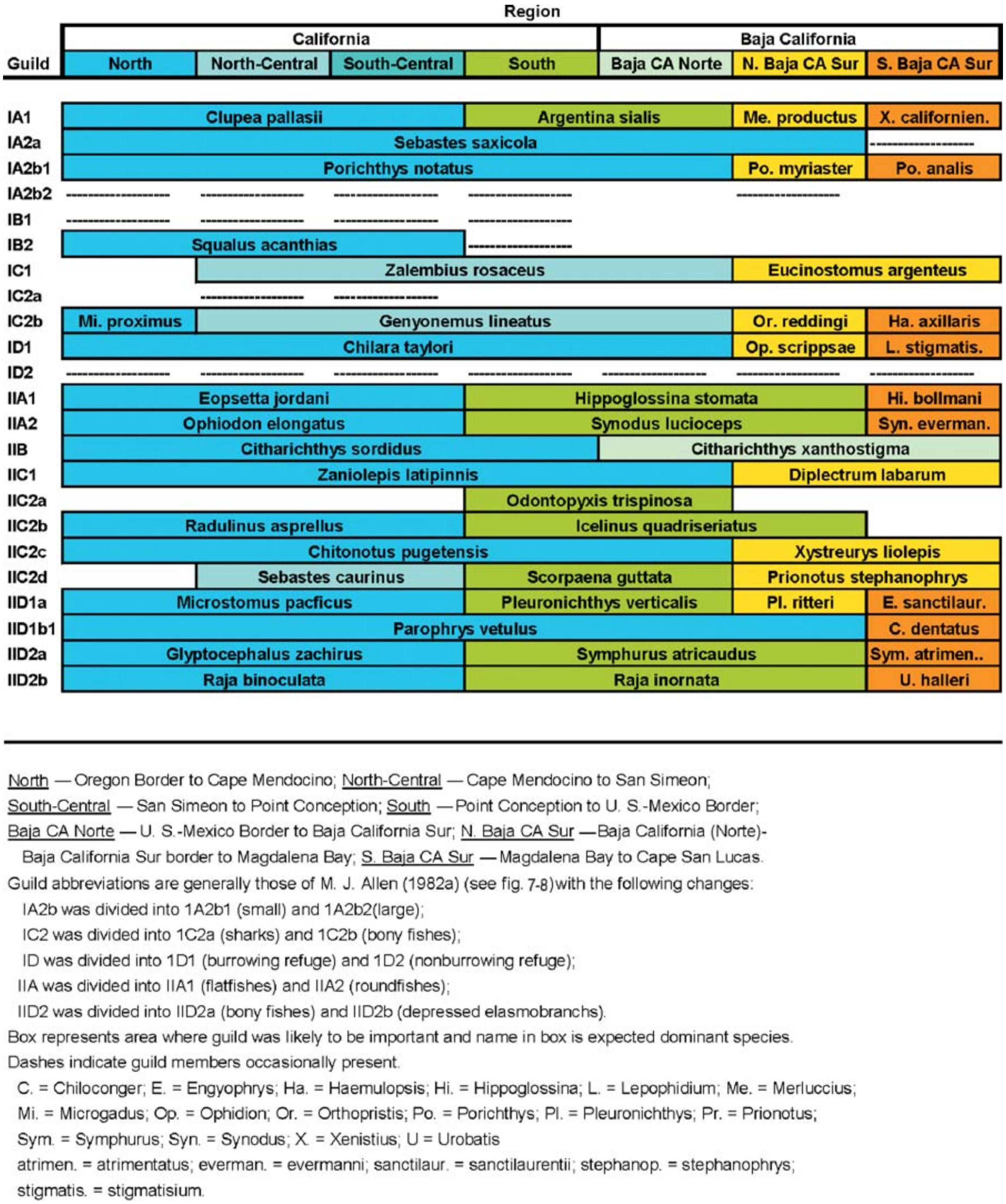



FIGURE 7-10 Generalized functional organization of soft-bottom fish communities on the middle shelf (31–100 m) of California and the Pacific Coast of Baja California.

phylogenetically different; the body form was developed over millions of years of evolution. Of 44 families represented in trawl catches in southern California, 91% were found in the worldwide fossil record (Romer, 1966). Chimaeridae (the earliest) appeared in the Lower Jurassic. About 30% of the families first appeared in the Eocene, and 82% had appeared by the Miocene. All 32 species of demersal species in a Pliocene deposit in southern California exist today. Ecological segregation among phylogenetically different species in the existing fauna is likely to be related to many millions of years of interaction among precursors of existing species and other extinct species and more recently among currently existing species (Allen, 1982a,b). Glacial/interglacial changes in sea level (140 m lower during the maximum of the last ice age) and shifts in isotherms equatorward and poleward, along with isolation of portions of coastal populations in the upper Gulf of California, may have contributed to the recent evolution of the soft-bottom fauna of the Californias (M. J. Allen, 1982a).

### Interactions with Other Organisms

Soft-bottom fishes interact with other organisms in a variety of ways. They prey upon other species (discussed above in the

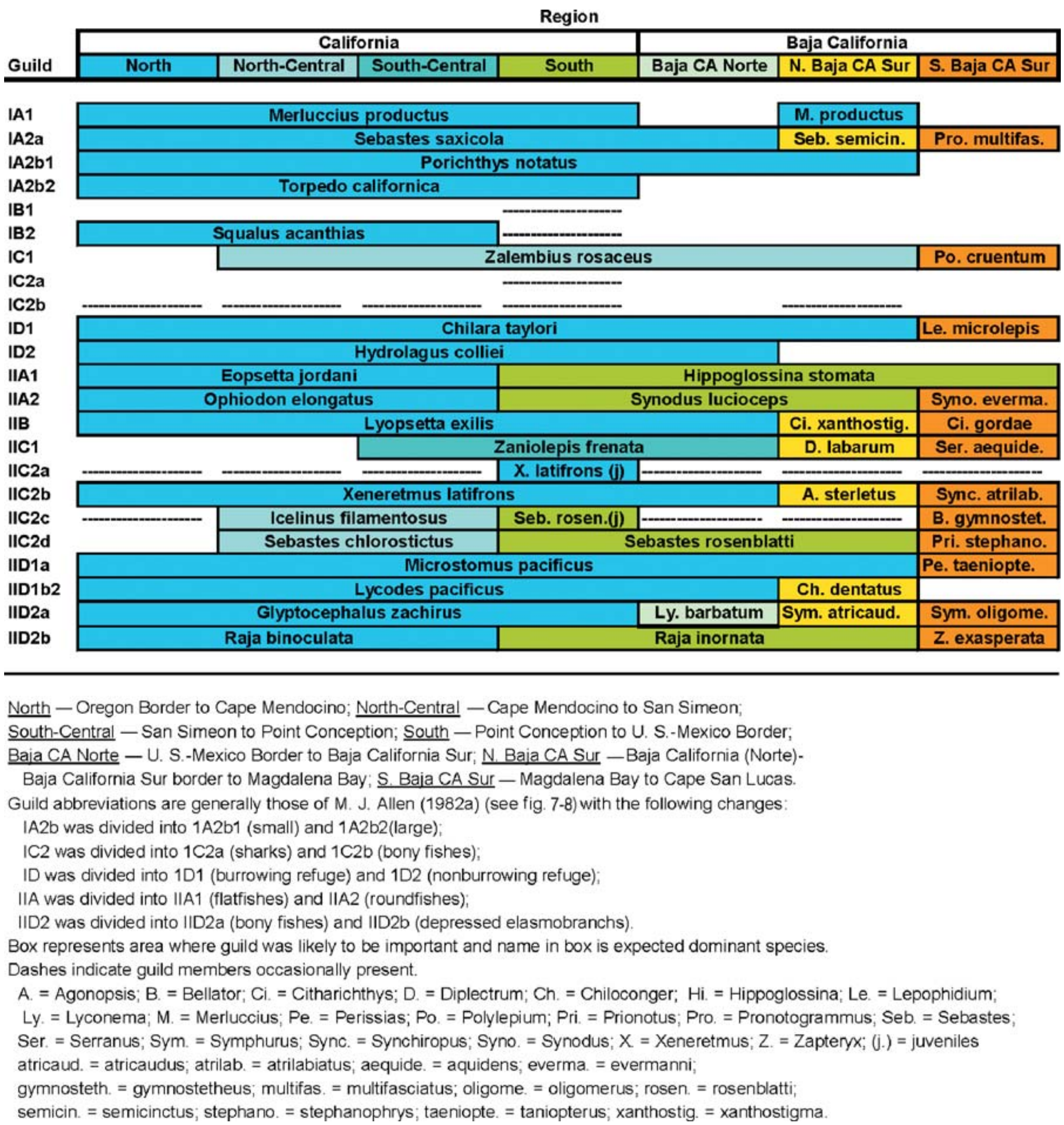



FIGURE 7-11 Generalized functional organization of soft-bottom fish communities on the outer shelf (101–200 m) of California and the Pacific Coast of Baja California.

section on Feeding), compete for food or space (often with species of the same or related guilds), associate with them for refuge, are eaten by predators, or are parasitized. Soft-bottom fishes eat a wide variety of pelagic and benthic invertebrates and also other soft-bottom fishes, including young of their own species. Bay gobies find refuge in burrows made by invertebrates (Grossman, 1979). I have observed small splitnose rockfish moving along under California king crabs (*Paralithodes californiensis*) within the basket formed by their legs in movies made by divers in submersibles in Santa Monica Bay. Some soft-bottom fishes may associate with worm tubes, sea pens, urchins, and sea cucumbers. Predators of soft-bottom fishes often include larger members of the fauna (e.g., Pacific halibut, skates, Pacific angel sharks, benthic feeding sharks) as well as seals and sea lions, dolphins, and some diving seabirds (e.g., cormorants). Sixgill sharks (*Hexanchus griseus*) and northern elephant seals (*Mirounga angustirostris*) may be predators of larger members of the fauna. Soft-bottom fishes are parasitized by a variety of external and internal parasites. External parasites include parasitic copepods, cymothoid isopods, and leeches (Mearns and Sherwood, 1977; Perkins and Gartman, 1997; Kalman, 2001). Among the most obvious external parasites is the eye copepod (*Phrixocephalus cincinnatus*—a pennellid copepod), which attaches to the eye of Pacific sanddab and some other soft-bottom species (Mearns and Sherwood, 1977; Perkins and Gartman, 1997). Internal parasites include (among others) nematodes, digenetic trematodes, and cestodes.

## Comparison of California Fauna to Other Regions

The soft-bottom fish fauna (groundfish) is an important food resource worldwide and hence the focus of extensive surveys by fisheries agencies of many countries. Trawl surveys outside of the Californias to assess North American fisheries stocks

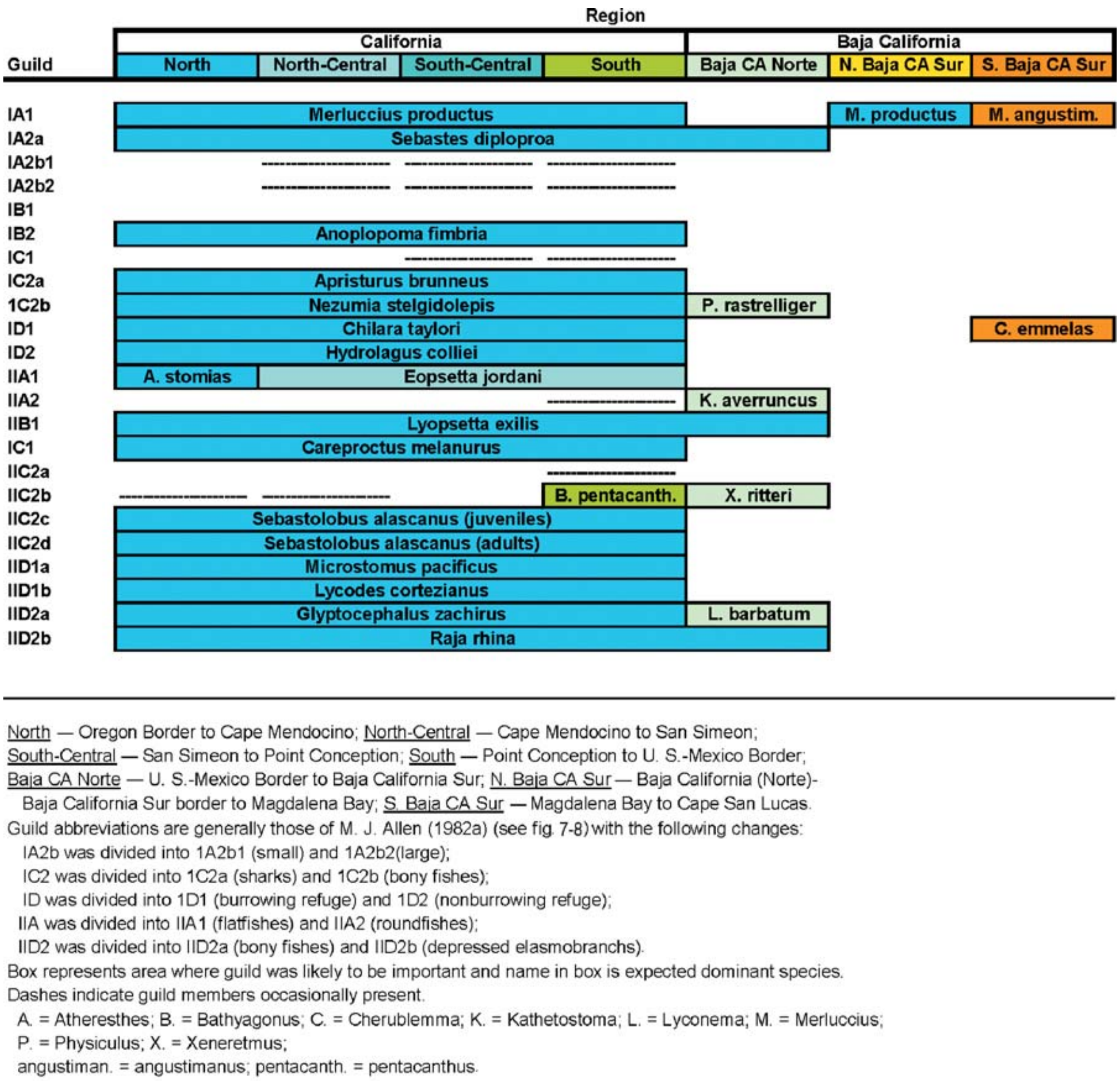



FIGURE 7-12 Generalized functional organization of soft-bottom fish communities on the mesobenthal (upper) slope (201–500 m) of California and the Pacific Coast of Baja California.

extend from Oregon to the Bering Sea on the West Coast and from northeastern Canada south along the Atlantic and Gulf Coasts of the United States. The results of these surveys as well as studies on the biology of commercially important soft-bottom species in these surveys are published extensively in *Fishery Bulletin* and *NOAA Technical Report* and many additional studies are described in the Technical Memoranda series of the NMFS fishery science centers.

Beyond the Californias, soft-bottom fish communities have been described statistically off Oregon (Day and Pearcy, 1968), the Pacific Northwest (Gabriel, 1980; Gabriel and Tyler, 1980; Weinberg, 1994; Jay, 1996), the Caribbean and Pacific Coasts of Central America (Bayer et al., 1970), and from the Atlantic Coast of Africa (Fager and Longhurst, 1968).

M. J. Allen and Smith (1988) examined the geographic and depth distribution of the 125 most common trawl-caught species along the U. S. West Coast from the Arctic Ocean to the U.S.-Mexico international border based on 24,881 trawl samples collected during a 30-year period. The species were classified zoogeographically and by life zone. Most of the species were wide-ranging and hence occurred over more than one zoogeographic province and more than one life zone. The study updates geographic ranges of the species and provides good information on depths of greatest occurrence.

Garrison and Link (2000) examined the diet of 40 species of soft-bottom fishes on the Northeast U. S. continental shelf and identified 14 significant trophic guilds, comprising divisions of six major predator groups. The predator groups included the following: (1) crab eaters, (2) planktivores, (3) amphipod/shrimp eaters, (4) shrimp/small fish eaters, (5) benthivores, and (6) piscivores. This study did not combine dietary information with morphological and distributional information as in M. J. Allen (1982a).

M.J. Allen (1986) described ecological segregation in fusiform gadoid fishes from the Arctic Ocean, along the Eastern Pacific, along the Western Atlantic to the Arctic, and along the Eastern Atlantic, and New Zealand. Pelagivores (including Gadidae and Merlucciidae) formed a geographical displacement series of 25 species. Benthopelagivores (12 species, all Gadidae) were restricted to the North Pacific, Arctic Ocean, and

North Atlantic. Haddock (*Melanogrammus aeglefinus*) was the only benthivore. Comparison of major gadid foraging types in the North Pacific and North Atlantic showed ecological counterparts of two of three guilds in both regions: (1) pelagivores—walleye pollock (*Theragra chalcogramma*) in the Pacific and pollock (*Pollachias virens*) in the Atlantic, (2) benthopelagivores—Pacific cod (*Gadus macrocephalus*) and Atlantic cod (*Gadus morhua*), and (3) benthivores—none in the Pacific and haddock in the Atlantic. Examination of all trawl-caught species in the North Pacific did not reveal a likely ecological counterpart of haddock, suggesting an "open niche" in the North Pacific. Other examples of assemblages of ecological counterparts among gadids were also presented.

## Summary

Soft-bottom fishes occupy the largest benthic habitat of the shelf and upper slope of the Californias and have been important to commercial and recreational fisheries in these areas. They have been extensively surveyed off most of California but only sparsely sampled off the Pacific Coast of Baja California. However, the extensive NMFS surveys in northern and central California and environmental surveys in southern California provide a wealth of information about soft-bottom species in this habitat.

Though the shelf and slope habitat is rather narrow along most of the coast of the Californias, except along the southern Baja California Peninsula, the physical and biological characteristics of the habitat vary greatly with depth, and to a lesser extent geographically. With depth, there are at least four life zones from about 5 to 500 m: inner shelf (5–30 m), middle shelf (31–100 m), outer shelf (101–200 m), and mesobenthal slope (201–500 m). Physical variables, such as temperature, ambient light levels, oxygen levels, and pressure, change dramatically over this depth range, and many species are specifically adapted to one zone or another. Two or three major coastal biogeographic provinces occur along this coast, with major changes in the fauna at Point Conception, California, and Magdalena Bay, Baja California Sur.

Scientific study of this fauna began about 1850 and initially (and largely to this day) was focused on fisheries species, in particular stock assessment and basic biology of species that might affect their abundance and availability. Most scientific fisheries surveys of these fish used commercial trawl gear. These surveys have produced good information on the population status and distribution of fisheries species, with some description of assemblages. In the late 1950s and in particular since 1969, environmental surveys of this fauna have been made to assess pollution effects in southern California and on the inner shelf of northern and central California. These surveys used small otter trawls and focused on all species caught because many of the species were not part of fisheries. These studies have produced good information on fish populations and assemblages, distribution of contaminants in fishes, and distribution of fish diseases. The soft-bottom fish fauna of the shelf and slope of Baja California has largely been sampled intermittently for museum specimens, with little attention to assessment of populations, and for some scientific studies off northern Baja California and Baja California Sur.

Trawl surveys are conducted on soft bottom and typically collect a large number of species. However, only about 30% of these are typical of the soft-bottom habitat in any particular area; many are found primarily in other habitats and only incidentally over the soft bottom. The true soft-bottom fish fauna of the California and Baja California shelf and slope is regarded here as those species that occur commonly on the soft bottom in at least one of the different life zones and play important ecological roles (generally with regard to feeding) in the community. Frequent occurrence is more important than abundance in determining their importance, and this generally identifies species adapted to the habitat. Because the soft-bottom is relatively flat with little relief, the species best adapted are those with flat bodies (e.g., skates, rays, flatfishes) or those that burrow (e.g., cusk-eels). Nevertheless, some species of families apparently best adapted to hard bottoms (e.g., sculpins, rockfishes, and surfperches) live primarily in this habitat.

At least 40 families of fishes have species that are soft-bottom species. The most widespread families are Paralichthyidae, Pleuronectidae, Batrachoididae, and Ophidiidae, which occur in all regions from northern California to southern Baja California Sur on or over the soft bottom. Other families have either a northern or southern occurrence to different degrees. The most widespread species in the shelf life zones occurred commonly from northern California through northern Baja California. The most widespread species by life zone were the following: inner shelf—shiner perch, white seaperch, speckled sanddab, and English sole; middle shelf—stripetail rockfish and English sole; and outer shelf—plainfin midshipman, spotted cusk-eel, and Dover sole. The most widespread species on the mesobenthal slope was Pacific hake; it occurs from northern California through southern California and in northern Baja California Sur. The mesobenthal slope was not well sampled off Baja California.

Soft-bottom fishes have a variety of life-history traits that allow them to live on the soft bottom. Species that live on soft bottoms find refuge by burrowing or burial, being exposed in the open, schooling over the bottom, or occasionally finding crevices in low relief rocky bottoms or objects on the bottom (these latter are likely to be hard-bottom species). In southern California, most of the species were oviparous with pelagic eggs and larvae, the remaining species are divided among three additional categories. Soft-bottom fish vary in their life-history strategies; some are long-lived with poor replacement capabilities and some short-lived with good replacement. For species with pelagic larvae, the narrow shelf and offshore drift in upwelling areas may result in loss of many larvae. Inner shelf species often have larvae that spend little time in the plankton and outer shelf, and mesobenthal species may have larvae that spend several months in the plankton. Recruitment varies as a result of oceanic factors (currents, productivity), as well as spawning success.

Some species, such as Pacific hake, undertake long coastwise migrations, whereas others show only local movements. Bathymetric migrations include seasonal migrations, ontogenetic movements of many species from shallow to deep water, and diel vertical migrations. Diel differences among species within a life zone are greater on the inner shelf than in deeper water, largely due to greater diel differences in ambient light on the inner shelf than on the outer shelf. Bioluminescence becomes an important light source on the outer shelf and upper slope.

In southern California, soft-bottom fishes caught by small otter trawls feed largely on crustaceans, followed by polychaetes and ray-finned fishes. Of the crustacea, gammaridean amphipods were consumed by all 40 species examined, followed by calanoid copepods and crabs. The diet of species (neritic or benthic) that feed on nektonic prey changes with growth from copepods, to euphausiids and mysids, to nektonic fish or squid. Benthopelagic feeders shift from gammaridean amphipods, to shrimp, to fish and octopus with growth. Small species of these two groups stop before reaching one of the next levels. Polychaete-feeders focus on polychaetes and clam siphons.

The foraging behavior of soft-bottom fishes differs in orientation with respect to the bottom; foraging zone (water-column, benthic, or both); and depending on the species, diel activities, strategy, and specialized behavior. Some water-column and some benthic species feed in the water column, on the bottom, or both. Foraging guilds, groups of species that forage in the same way, consist of a series of two to four species that displace each other with depth in Southern California (and presumably elsewhere). A set of the depth-displacement patterns of 18 foraging guilds was arranged to describe the functional organization of soft-bottom fish communities in southern California (M. J. Allen, 1982a). Foraging guilds also show biogeographic displacement series, indicating that similar patterns with different species occur along the entire coast.

Soft-bottom fishes are affected by a variety of other organisms (including predators and parasites, as well as prey abundance) and anthropogenic activities, including commercial and recreational fishing, habitat alteration, and pollution.

## Prospectus for Research

Although the soft-bottom fish fauna of the California shelf has been extensively surveyed in most areas, with many survey reports and studies on biological information on important fisheries species, there are still plenty of opportunities to do significant work on the soft-bottom fish fauna off California and Baja California. The following are some suggestions for future research on this fauna:

1. Conduct comparable trawl surveys in different areas.
2. Conduct baseline surveys off Pacific Baja California.
3. Assess small individuals and species on the middle and outer shelves of Northern and Central California shelf and slope.
4. Conduct comparative studies of catches from small and large trawl gear used in different areas.
5. Make better use of fish caught in scientific trawl surveys to enhance our understanding of soft-bottom fishes.
6. Make better use of life-history information to assess potentially threatened species.
7. Maintain time series surveys, where possible, to understand natural and anthropogenic factors that affect fish populations.
8. Collect more information on the behavior of soft-bottom species on the shelf and slope using basic and innovative techniques.

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Edited by

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