p. 320-341. In: The Ecology of Marine Fishes: California and Adjacent Waters. 2006.
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CHAPTER 12

Surface Waters

LARRY G. ALLEN AND JEFFREY N. CROSS

The Pelagic Zone

The epipelagic realm technically encompasses the upper 200 m of the ocean beyond the continental shelf, world-wide (Parin, 1968; Helfman et al., 1997). It is easily the largest habitat off California and the home of 40% of the species and 50% of the families of fishes. The water column that overlies the continental shelf comprises what we will call the coastal pelagic (neritic) realm (fig. 12-1). Because the continental shelf off most of California and Baja California is narrow, the fish assemblages of the epipelagic zone and those of the coastal pelagic realm overlap and interact on a seasonal basis (see Chapter 5). In fact, unlike most coastal areas, the highly productive waters of the major upwelling region off California are dominated by coastal pelagic species that spread into the open ocean environment well offshore (up to 300–400 km). The waters below the epipelagic zone include the Mesopelagic (approximately 200–800 m) and the bathypelagic zones (>800–1000 m). These deep sea habitats are the main subjects of chapter 13 of this volume.

About 200 species (70 families) have been collected in the California Current (Berry and Perkins, 1966), 79 species (30 families) have been collected in the coastal waters (Horn, 1974), and 124 species have been collected in the mesopelagic and bathypelagic zones (Lavenberg and Ebeling, 1967). Epipelagic fishes are relatively large, active, fast-growing, and long-lived fishes that reproduce early and repeatedly (Childress et al., 1980). Mesopelagic fishes are relatively small, slow-growing, and long-lived fishes that reproduce early and repeatedly. Bathypelagic fishes are relatively large, sluggish, rapid-growing, and slightly short-lived fishes that reproduce late and maybe only once (Childress et al., 1980).

Light penetration, water temperature, and water mass structure define vertical zonation. The epipelagic zone is euphotic, and temperatures fluctuate diurnally and seasonally. It is approximately 50m deep in turbid nearshore waters and expands offshore in clear oceanic waters. The mesopelagic zone is characterized by steep environmental gradients. This zone extends from the permanent thermocline, below the compensation depth, to the 6°C isotherm between 500–1000 m depending on location. The bathypelagic zone is characterized by uniformity and extends nearly to the bottom. It is absent or restricted in the nearshore basins off of southern California and expands offshore (Lavenberg and Ebeling, 1967).

Physical and biological variability in the epipelagic zone are closely linked to oceanographic processes. Wind-driven, coastal upwelling is a prominent feature of the California Current system. Movement of water from nearshore to offshore as driven by Ekman transport causes intense, periodic upwelling, particularly off northern and central California. Such upwelling brings cold, nutrient-rich water to the surface, which promotes the bloom of phytoplankton. These blooms then set up a trophic cascade upon which pelagic fishes depend. Cold, upwelled water adjacent to the coast is swept far offshore in large eddies and plume-like structures of up to several hundred kilometers wide (fig. 12-2). Temperature fronts where cold surface water is adjacent to relatively warm surface are produced and maintained over large distances. These fronts concentrate large numbers of fishes in this otherwise featureless world. Upwelling is not only responsible for high primary productivity, but is also produces an unpredictable distribution and availability of food in the habitat (Parrish et al., 1981).

The California Current is one of only four major eastern boundary currents of the world. These boundary currents occur over narrow continental shelves in temperate areas and are characterized by surface flow toward the equator, coastal upwelling, and high primary productivity. The other boundary currents are the Peru Current off the west coast of South America, the Canary Current off the west coast of southern Europe and northern Africa, and the Benguela Current off the west coast of southern Africa. All four boundary currents are physically similar and are dominated by a small number of closely related, temperate pelagic fishes that can reach large population sizes including anchovy (*Engraulis*), sardine (*Sardinops* or *Sardina*), jack mackerel (*Trachurus*), hake (*Merluccius*), mackerel (*Scomber*), and bonito (*Sarda*) (Parrish et al., 1983).

Prominent Epipelagic Fish Groups World-Wide

Elasmobranch and acanthomorph (spiny-finned) fishes dominate the epipelagic zone throughout the world's oceans. Prominent elasmobranch groups include the carcharhinid and lamnid sharks (e.g., blue shark, pelagic white tip, shortfin

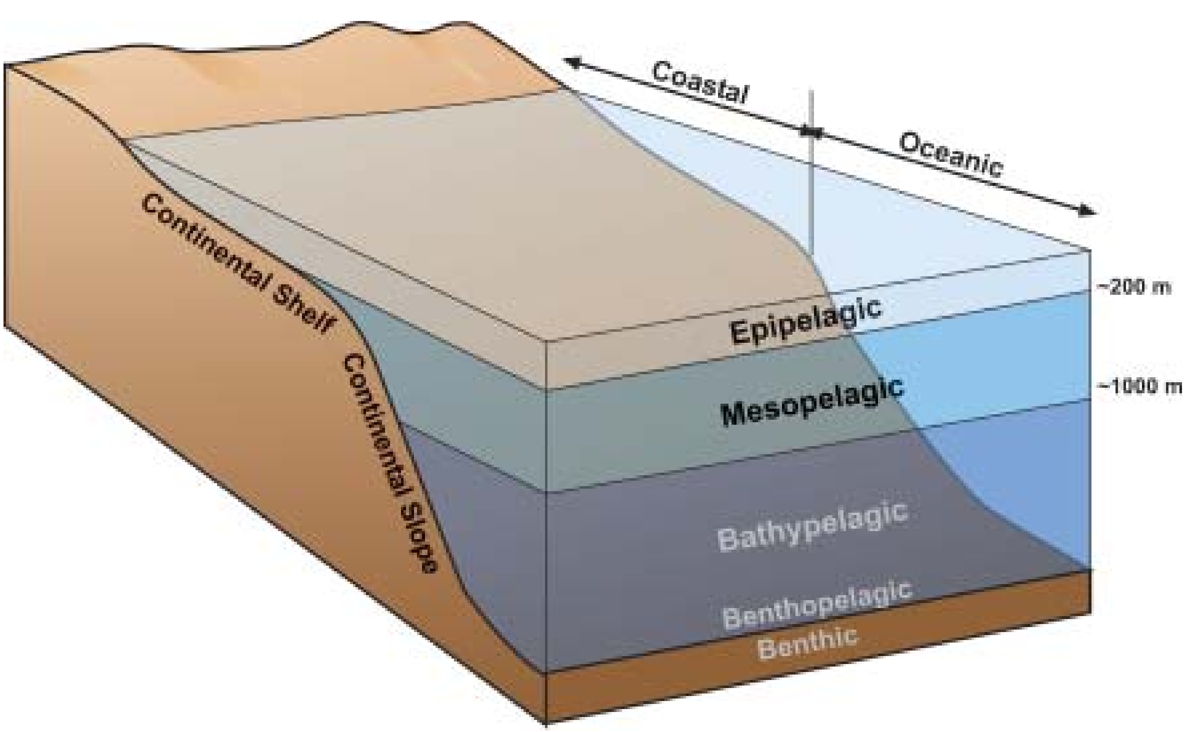

FIGURE 12-1 A classification of pelagic habitats or "life zones". The top 100–200 m constitutes the epipelagic zone covered in the present chapter. The meso-, bathy-, benthopelagic and deep benthic realms are covered in Chapter 13.

mako, and salmon shark). The Atherinomorpha, an important acanthomorph group, includes halfbeaks, needlefish, flying fishes, and sauries, which are typically the smaller, low-level carnivores of the open ocean. Another acanthomorphan superorder, the Percomorpha, is also well-represented, especially among the active swimmers of the surface waters. Large, active fishes belong mainly to the perciform suborders: Scombroidei (mackerels, tunas, and billfishes), Stromateioidei (driftfishes and medusafishes), and Percoidei (jacks and dolphinfishes). Finally, the Lampridiomorpha is well-represented, particularly in the lower portions of the epipelagic zone, by the highly specialized ribbonfishes, oarfishes and opahs (Parin, 1968).

In nearshore and boundary current areas, the surface waters are dominated by Clupeomorph fishes, such as anchovies, herrings, sardines, menhadens, and pilchards (Smith et al., 1983; Helfman et al., 1997).

Adaptations to Epipelagic Existence

Epipelagic fishes live in a three-dimensional world that is virtually devoid of physical structure to use as visual reference points. The fishes that inhabit this unique realm range widely in size from the two largest fishes in the world, the whale shark and the basking shark, to the various small species of halfbeaks, sauries and stromateioids. In general, pelagic fishes are counter-shaded and silvery, round or slightly compressed laterally, and streamlined with forked or lunate caudal fins. They typically: 1) posses large eyes for visual predation, 2) have efficient respiration and food conversion capabilities, 3) have a high percentage of red muscle tissue and lipids. 4) form schools, and 5) undertake long migrations. Finally, all known examples of fish endothermy occur in this habitat (Carey et al., 1971; Helfman et al., 1997). Species that are associated with rare substrata, such as floating kelps including *Sargassum*, are often cryptically colored and not counter-shaded (Parin, 1968).

Locomotory Adaptations

Foremost among the adaptations to the epipelagic zone are the notable locomotory adaptations in many of the fishes that inhabit it. Locomotion among epipelagic fishes evolved along two main paths. The first and most evident path involves active, continuous swimming using caudal propulsion, which is often associated with long distance migrations. A number of less active species have evolved or retained locomotory modes that enable them to hover and move with a lower expenditure of energy. This second, less evident path often involves either the retention of anguilliform locomotory patterns using undulation of the entire body or elongate fins (snake mackerels, and ribbon and oarfishes) (fig. 12-3) or by oscillation of various fins (Parin, 1968; Webb, 1993). Oscillation of fins is best represented by the pelagic members of the Tetraodontiformes (ocean sunfish and oceanic puffers) that use modified dorsal and anal fins, but also includes the opah, a lampridiform fish, that primarily uses its pectoral fins in a labriform-type of locomotory pattern.

Many disparate groups of fishes have converged on the active, continuous swimming mode using caudal propulsion. Most of these undergo long distance feeding and reproductive migrations during their life cycles. Various species of large, oceanic sharks, salmon, tunas, and billfishes migrate thousands

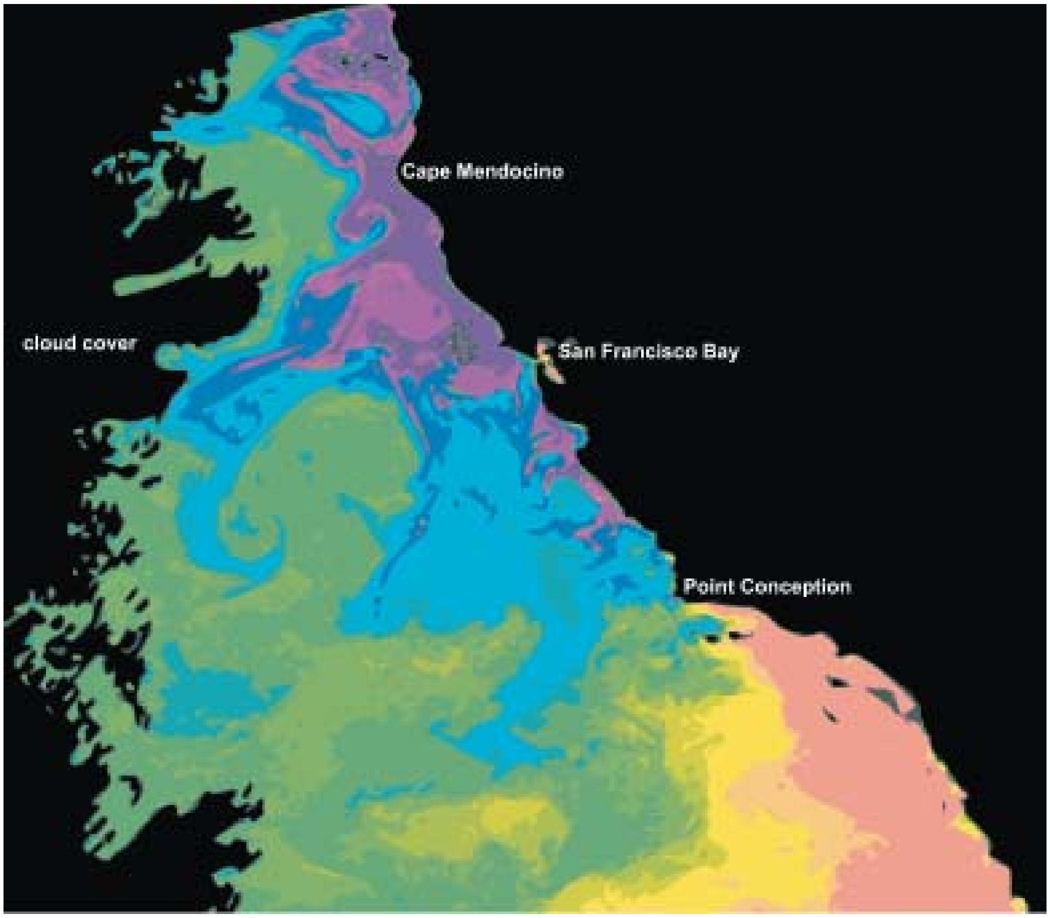

FIGURE 12-2 This infrared satellite image shows summer upwelling along the California coast. Surface water temperatures are color coded with red indicating warm water and blue-violet cold (after Castro and Huber, 2000).

of kilometers each year. Even smaller, coastal pelagic species such as herrings, sardines, and jacks migrate 100s to 1000s of kilometers annually in some parts of the world. Continuous swimming during long-distance migrations requires that these species have very large proportions of red muscle, which operates aerobically and does not fatigue easily. In most fishes, red muscle is superficial to the deeper white muscle masses and occurs in a lateral band along the body. In the highly derived tunas (*Thunnus*), however, the red muscle mass is more extensive and occurs deeper in the body musculature and is kept warm by counter-current heat exchangers promoting endothermy. Similar structures have evolved by convergence in the epipelagic mackerel sharks (Lamnidae) (see chapter 20, Fish Movements and Activity Patterns).

Besides red muscle, highly derived epipelagic fishes, such as tunas, have evolved a number of other important adaptations that promote rapid swimming, including: fusiform (streamlined) bodies, stiff fins that fit into grooves in the body, scale corselets, finlets, keels, lunate caudal fins, and ram gill ventilation (Marshall 1971; Magnuson 1973, 1978). Fusiform body shapes, which greatly minimize drag, have the maximum circumference of the body two-fifths of the way back from the head. Smaller, stiff fins aid in maneuvering, but create drag when swimming straight ahead. At such times, tunas and their relatives depress these fins into depressions or grooves in the body, greatly reducing drag. Tunas have added a corselet of large, bony scales around the area of maximum girth, which also serves to reduce drag and promote laminar water

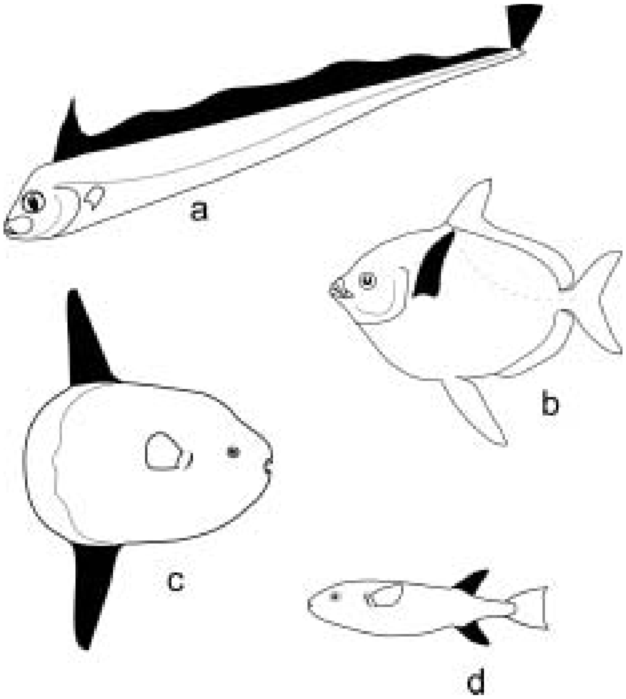

FIGURE 12-3 Epipelagic fishes that move by means of undulating or oscillating fins: a) king-of-the-salmon (anguilliform and/or amiiform); b) opah (labriform); c) ocean sunfish (tetraodontiformd); d) and oceanic puffer (tetraodontiform) (after Parin, 1968).

flow over the posterior half of the body. Many high-speed fishes, such as mackerels and tunas, possess small finlets that occur between the dorsal and anal fins and the caudal fin. These structures have long been thought to prevent eddies from forming, allowing the stiff, lunate caudal to thrust against less turbulence (Helfman et al., 1997). Recent evidence from studies of mackerel indicate that finlets vary greatly in flexure during a caudal fin stroke and that the most posterior finlet is oriented to redirect flow into the developing tail vortex. This action may increase thrust produced by the tail of the swimming mackerel (Nauen and Lauder, 2001). The small second dorsal and anal fins of mackerel sharks, billfishes, and swordfishes are thought to have similar functions to those of finlets. Two kinds of keels have evolved in rapidly swimming fishes, caudal and peduncular keels. Sharks, many jacks, mackerels, tunas, billfishes, and swordfishes all have single or multiple keels near their tails. Tunas have both a singular keel on the caudal peduncle and a pair of caudal keels that angle toward one another front to back. Single peduncular keels reduce drag and act as cut-waters as the narrow peduncle rapidly oscillates through the water with the caudal fin as well as providing hydrodynamic lift to the posterior portion of the fish (Magnuson, 1973, 1978; Pelster, 1997). Paired caudal keels are believed to act as nozzle that accelerates water moving across the tail fin (Collette, 1978). Lunate caudal fins represent a great advantage because they possess very high aspect ratios and produce maximum thrust with a minimum of drag (Magnuson, 1978).

Finally, the high level of activity in pelagic fishes comes with a high oxygen demand that requires a very efficient respiratory system. Continuous swimming provides a means of gill ventilation that does not require the substantial energy expenditure necessary for buccal pumping of water over the gills (estimated at 15% of total energy expenditure by fish). Continuous swimmers need only to open their mouths while swimming to have water flow over their gills. This mode is termed ram gill ventilation and requires fusion of gill lamellae in some fishes to prevent damage. The downside of ram gill ventilation is that many fishes relying on it, such as pelagic sharks, tunas, and billfishes, have lost the ability to pump water over the gills and must swim continuously to breathe (Roberts, 1978).

Two striking adaptations related to locomotion and predatory behavior are well represented in epipelagic fishes. The first is the "flying" behavior of flyingfishes and their relatives. The other is the use of bills as spears in billfishes for prey capture. Evading the pursuit of a predator in surface waters requires maneuverability. Small fishes are at a distinct speed disadvantage because larger predatory fishes are faster. One way to outmaneuver and out-distance predators is to become airborne. This tactic is seen in many members of the Atheriniformes (e.g., sauries, halfbeaks, needlefishes, and flyingfishes) that are common in the surface waters of the world's temperate and tropical seas. By leaping out of the water, a flyingfish can double its speed (36 km/hr to 72 km/hr) as a result of the significant reduction in drag (Davenport, 1994).

In part, because of the speed and maneuverability of most epipelagic prey, the large predatory billfishes have evolved spears for impaling prey. Bills are elongated extensions of the upper jaws of two groups of billfishes, the marlins, sailfishes, and spearfishes (Istiophoridae), and the swordfish (Xiphiidae). Marlins and relatives possess rough bills that are round in cross-section while swordfish bills are flattened and smooth (broadbills in the vernacular).

Recent direct and indirect evidence points to the inescapable fact that both of these bills are indeed used in foraging. A fortuitous, albeit hair-raising observation, made by two spearfisherman off Durbin, South Africa offered convincing confirmation of this fact (van der Elst and Roxburgh, 1981). One of the free-divers speared an amberjack (*Seriola lalandi*) weighing about 15 kg. The following observations were then made:

> The fish pulled off the spear and dashed straight for Roxburgh (at the surface) who simultaneously observed a 3–4 m marlin (probably a black marlin, *Makaira indica*) making a direct charge for the amberjack which was now hiding behind him. At the last moment the marlin halted and Roxburgh was able to push the bill aside after which the marlin circled (the) diver and amberjack several times. Seconds later the amberjack dashed off at great speed to the bottom, closely followed by the highly agitated marlin. Within an estimated 5 sec the marlin had reached its prey and impaled it on its bill. The marlin then shook the amberjack free and swallowed it. Duration of the entire incident was an estimated 30–50 sec (van der Elst and Roxburgh, 1981, p. 215).

Swordfish appear to use their broadbill like a broad sword. They use it to decapitate cephalopod prey and slash them into swallowable pieces. Like marlins, swordfish are also known to slash schooling prey with their bills and return to pick up maimed fish on subsequent passes (Wisner, 1958; Ellis, 1989).

Schooling

Schooling is major characteristic of fishes inhabiting the epipelagic zone world-wide (Smith, 1981) and this is certainly true for pelagic fishes off California. School structure and behavior of several of the common species off California (northern anchovy, in particular) have received a great deal of attention in the past. Within a species, schooling can vary from well-defined, compact aggregations to widespread, scattering layers (Mais, 1974). Commercial fishermen recognize more than a dozen different school types among eastern Pacific tunas (Scott, 1969; Scott and Flittner, 1972). The formation of schools among clupeioids depends largely on vision, but the maintenance of school structure depends on vision and lateral line stimuli (Blaxter and Hunter, 1982; Partridge, 1982; Parrish, 1989a,b). The formation and maintenance of schools is also affected by light level. Schooling fish are randomly distributed in darkness; they join groups that form and disperse as light levels rise, then form compact schools as light levels rise still further (Hunter, 1968; Hunter and Nicholl, 1985). Schooling increases intraspecific competition for food, but the disadvantages must be outweighed by reduction in predation and by facilitation of reproduction (Smith, 1978a; Blaxter and Hunter, 1982).

Smith (1978a) defined four spatial scales for pelagic schooling fishes: behavioral (scale of aggregation caused by individual behavior, that is, the fish school); hydrographic (scale that attracts and keeps fish in a small geographic area, e.g., upwelling and zooplankton blooms); physiological (distribution of a species determined by its physiological limits); and external (scale at which food or predators enter the environment of a species from outside its area of distribution). Individual epipelagic fish schools aggregate into school groups that occupy areas on the order of 10 km (Smith, 1978a, b). The distribution of school groups is often patchy and nonrandom (Mais, 1974, 1977). There may be 3,500 schools in an area

10 km in diameter; for anchovies, this represents about 1% of the biomass of the total stock. The school group comprises a wider range of anchovy sizes and ages than an individual school. The hydrographic features that control this scale of aggregation have not been strictly identified (Smith, 1978a), but the importance of biological factors such as vision (Hunter and Coyne, 1982; Hunter and Nicholl, 1985), predation (Butler and Pickett, 1988), prey acquisition (Nonacs et al., 1994), and distribution of pre-recruits (Smith et al., 2001) have received attention.

Finally, school distribution and formation often change over the course of a day. During the day, northern anchovy occur in small, low-density schools near the surface and in large, loosely compacted schools in deep water (110–220 m). Schools rise to the surface at night and disperse into thin scattering layers. Between midnight and dawn, the fish condense into schools and return to deep water (Messersmith et al., 1969; Mais, 1974, 1977). Schools of jack mackerel remain near the bottom or under kelp canopies in shallow rocky areas during the day, then venture into deeper surrounding areas at night (Mais, 1974). Laboratory experiments suggest that light is sufficient for jack mackerel to maintain schools near the surface on clear, moonless nights and to feed effectively near the surface on full, moonlight nights (Hunter, 1968).

Global Classification of Epipelagic Fishes

A surprisingly heterogeneous assemblage of fishes inhabits the epipelagic zone on a global scale. Joining the fishes that normally occupy this seemingly featureless, three-dimensional habitat are species that associate with various rare substrata, those that spend only a portion of their life history in the open ocean, and those that sporadically penetrate into the surface layers beyond the shelf. Parin (1968) provided a thorough classification of the world's epipelagic fish fauna based on the degree of association with the epipelagic realm. He recognized three main types of epipelagic fishes, holoepipelagic, meroepipelagic and xenoepipelagic (table 12-1; fig. 12-4), as described in the following paragraphs.

Holoepipelagic Fishes

This group of fishes includes those that are normally associated with the oceanic epipelagic zone worldwide. These holoepipelagic (*holos*—all, entire) species are the permanent inhabitants of the oceanic epipelagic and occur there in all life history stages. Holoepipelagic fishes can be divided into two main groups, those that are active swimmers and those that are associated with various animate and inanimate substrata.

The active swimmers of the water column include many pelagic sharks, such as oceanic whitetips, porbeagles, makos, basking sharks, and blue sharks. Prominent among the active swimming bony fishes include flyingfishes, sauries, tunas, marlins, swordfish, opah, pomfrets, and ocean sunfishes (fig. 12-5). Parin (1968) stated that most of these holoepipelagic fishes are limited to the isothermic, surface layer and are mainly encountered in tropical waters where a permanent thermocline exists. These species penetrate into temperate and higher latitudes mainly during the summer when seasonal thermoclines develop.

The holoepipelagic species noted above normally inhabit only the uppermost layer of the epipelagic to depths of 20–30 m. Other active species occur mainly in the deep layers of the oceanic epipelagic zone, adjacent to the mesopelagic zone, and rarely appear near the surface. This lower epipelagic group includes megamouth sharks, lancetfishes, oarfishes, ribbonfishes, crestfishes, opahs, and pomfrets, as well as several species of cutlassfishes and snake mackerels (fig. 12-6). Finally, some large, predatory fishes such as tunas, marlins, and swordfish feed throughout the epipelagic and may even penetrate into the upper horizons of the main thermocline (Parin, 1968).

Species that associate with substrata compose a special group of holoepipelagic fishes. The most specialized and geographically localized of these species include the forms that have evolved to live in association with the floating *Sargassum* algae of the western portion of the North Atlantic Ocean (Sargasso Sea) (Parin, 1968). The sargassum fish (which is actually an anglerfish, *Histrio histrio*) and the sargassum pipefish (*Syngnathus pelagicus*) are the most recognized among these cryptic taxa, although the juveniles of dolphinfish, flyingfish, and many coastal species (halfbeaks, jacks, blennies, triggerfishes, and filefishes) associate with floating *Sargassum* beds (Parin, 1968).

The other, more widespread group of substrate-associated fishes usually lives in symbiosis with other pelagic animals. Members of the bony fish suborder Stromateioidei commonly associate with either inanimate drift or large gelatinous zooplankton including scyphomedusae (sea jellies), siphonophores, and salps (fig. 12-7). In primarily tropical waters, juveniles of the Man-O-War fish (*Nomeus gronovii*) have an obligatory commensal relationship with the highly venomous siphonphore, Portuguese Man-O-War (*Physalia* spp.). Juveniles of the centrolophid genera of *Centrolophus, Icichthys*, and *Schedophilus* are often found in association with medusae or siphonophores while those of squaretails (*Tetragonurus*) are sometimes found within the cylindrical colonies of the salp, *Pyrosoma* (Parin, 1968; Haedrich, 1965; Horn, 1975).

Another interesting association occurs between the pilotfish (*Naucrates ductor*) and a number of large pelagic sharks including the oceanic whitetip and the blue shark (fig. 12-7). Pilotfish are jacks that swim with large, mobile pelagic animals apparently to facilitate locomotion. Several authors (c.f. Parin, 1968) have noted that a small species such as the pilotfish may minimize energy expenditure by swimming in the friction layer encompassing the body of the host. This idea is supported by the observation of other pelagic species such as dolphinfish (*Coryphaena hippurus*) and rainbow runners (*Elegatis bipinnulatus*) practicing the same behavior with oceanic whitetip sharks (Parin, 1968).

Lastly, a most interesting symbiotic relationship exists between remoras (Echeneidae) and various species of marine vertebrates including sharks (fig. 12-8). This association relies on contact attachment between the remora, also known as suckerfish, and its host by way of a highly evolved sucker disk. This disk is actually a modified, spinous dorsal fin that allows the suckerfish to be carried along with the host with no net expenditure of energy. This contact attachment behavior may have evolved from piloting behavior similar to that seen in *Naucrates* spp. The various genera and species of suckerfishes exhibit preferences for certain hosts. The slender sucker (*Phtheirichthys lineatus*) is either free-living or found on sharks. The sharksucker (*Echeneis naucrates*) is usually found on sharks, but also has been found on sea turtles. The whalesucker (*Remilegia australis*) is found only on whales and dolphins while remora (*Remora remora*) is usually found on sharks

TABLE 12-1

A Classification of Epipelagic Fishes of the World

I. Holoepipelagic (*Grk*—entire) fishes inhabiting the isothermic surface layer of the ocean at all stages of life history.
  A. Actively swimming fishes of the upper epipelagic;
  B. Actively swimming fishes of the lower epipelagic;
  C. Actively swimming fishes populating all depths of the epipelagic;
  D. Fishes associated with substrate.
    1. Fishes of permanent floating *Sargassum* beds;
    2. Fishes associated with gelatinous zooplankton
    3. Fishes associated with large marine vertebrates
II. Meroepipelagic (*Grk*—part) fishes, occurring in the epipelagic at certain stages in life history.
  A. Epheboepipelagic (*Grk*—adult) fishes inhabiting the upper layers of the ocean pelagic in the adult stage but spawn nearshore or in freshwater;
  B. Brephoepipelagic (*Grk*—babe) fishes, going through the early stages of their life history in the upper layers of the open ocean but inhabiting coastal pelagic or benthic areas as adults;
  C. Nyctoepipelagic (*Grk*—nocturnal) fishes, in the adult stage undergoing regular vertical migrations between the epipelagic and mesopelagics, occupying the surface layers at night.
III. Xenoepipelagic (*Grk*—foreign) fishes, permanently occurring in coastal waters but sporadically penetrating into the epipelagic.
  A. Coastal pelagic fishes
  B. Coastal benthic fishes
  C. Algophilic fishes associating with floating algae (kelp paddies).

NOTE: After Parin, 1968.

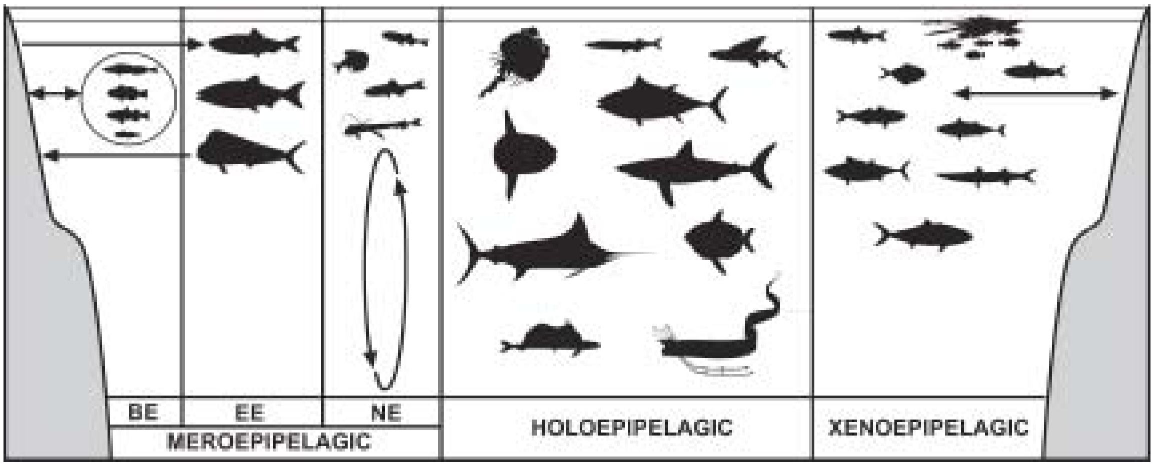

FIGURE 12-4 Parin's classification of the main groups of epipelagic fishes (after Parin 1968) (BE = rephoepipelagic, EE = epheboepipelagic, and NE = nyctoepipelagic, see text for explanation).

and sea turtles. Gray (*Remora brachyptera)* and hardfin (*Rhombochirus osteochir*) marlinsuckers are found on marlins, sailfishes, and swordfish. Lastly, the white suckerfish (*Remorina albescens*) occurs mainly in the gill cavity of manta rays (Parin, 1968; Miller and Lea, 1972).

Meroepipelagic Fishes

The second major group of epipelagic fishes includes those species that occur in the epipelagic zone only during a portion of their life history. Parin (1968) referred to these as meroepipelagic fishes because they spend part (*mero*-) of their lives as epipelagic forms. Meroepipelagic forms are biologically diverse and have been classified into three types (Parin, 1968). First, those species that spend their adult lives in the epipelagic, but migrate into coastal waters or freshwater to spawn are termed Epheboepipelagic (*ephebos*—adult). Second, those species that spend the early stages of their life history in the upper layers of the epipelagic and their adult stages in coastal waters are categorized as Brephoepipelagic fishes (*brephicos*—babe). Finally, Parin viewed those fishes that inhabit deeper, mesopelagic waters during the day and migrate vertically into the surface waters at night to constitute a special type of epipelagic fish group, termed Nyctoepipelagic (*nyctios*—nocturnal).

EPHEBOEPIPELAGIC GROUP

The most familiar forms of epheboepipelagic fishes are the salmons of the genera *Salmo* and *Oncorhynchus* that originally inhabited the cold temperate and boreal waters of the north Atlantic and Pacific oceans. The spawning migrations of salmons into their natal streams are well known and equally well documented (cf. Quinn and Dittman, 1990). Oceanic herring (*Clupea harengus*) belong to the group and exhibit northern distributions much like salmon. The lower latitude forms in this group include the whale shark (*Rhincodon typus*), dolphinfish

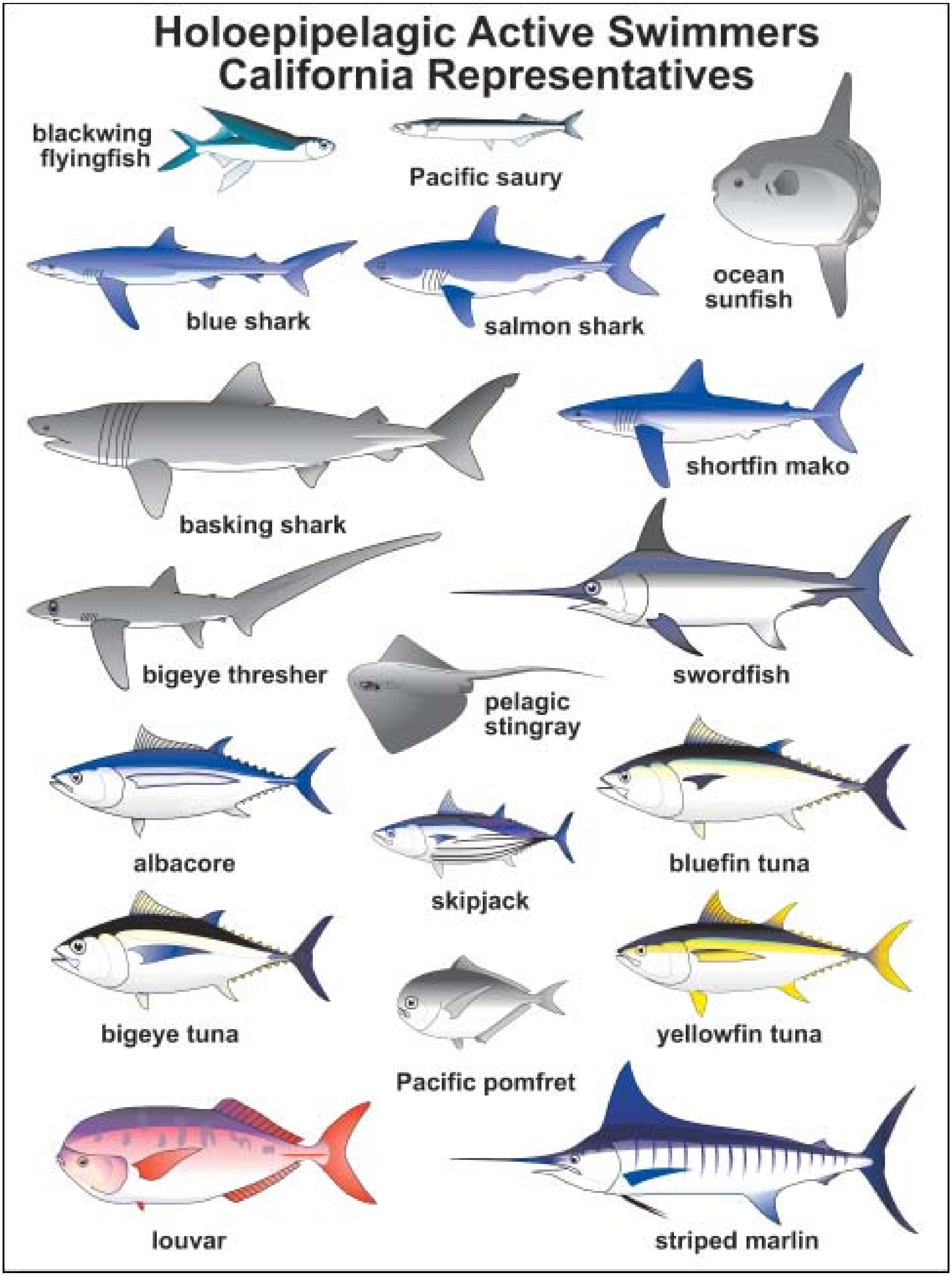

FIGURE 12-5 California representatives of actively-swimming, surface-dwelling holoepipelagic fishes.

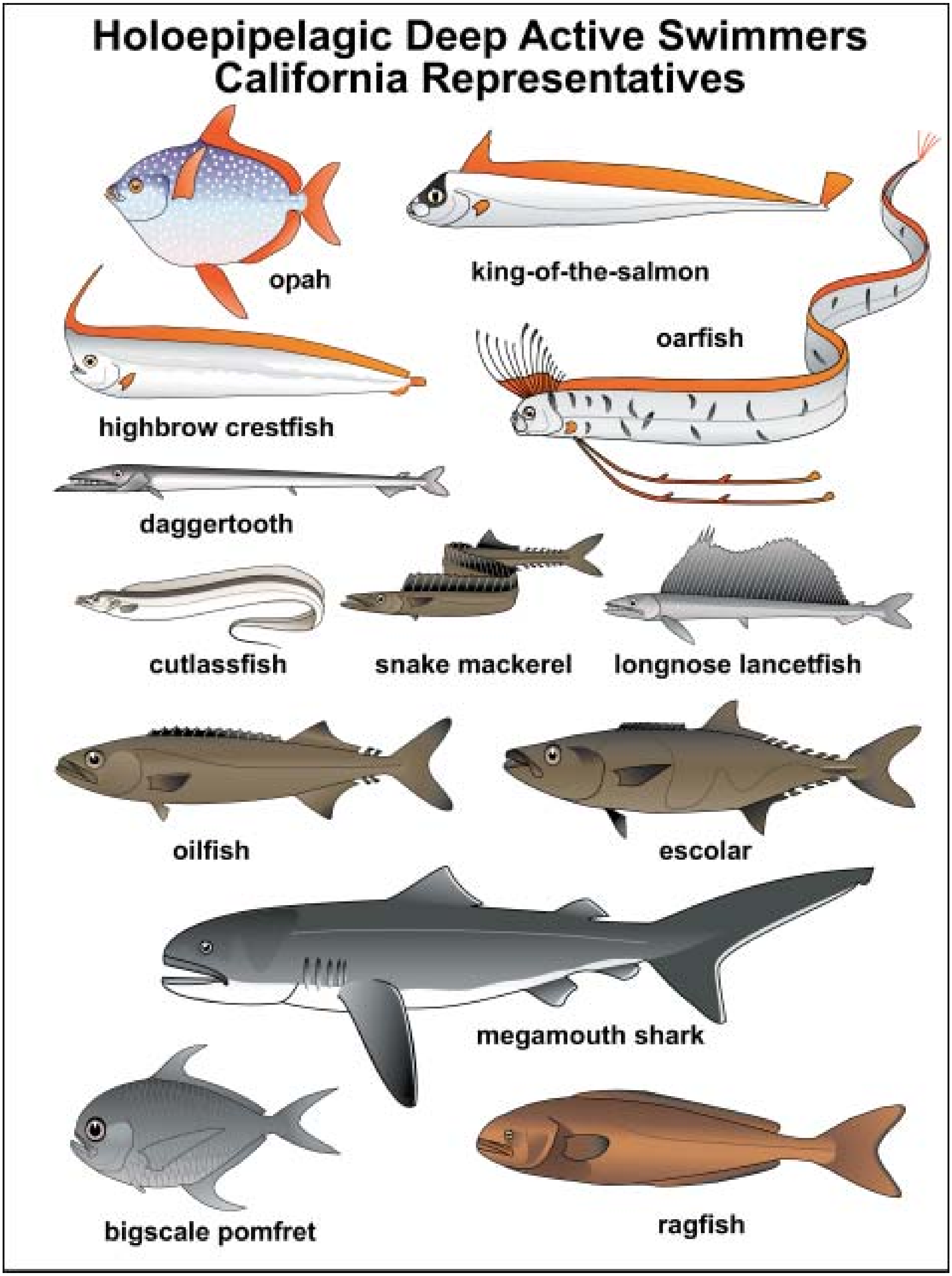

FIGURE 12-6 California representatives of actively-swimming, deep-dwelling holoepipelagic fishes.

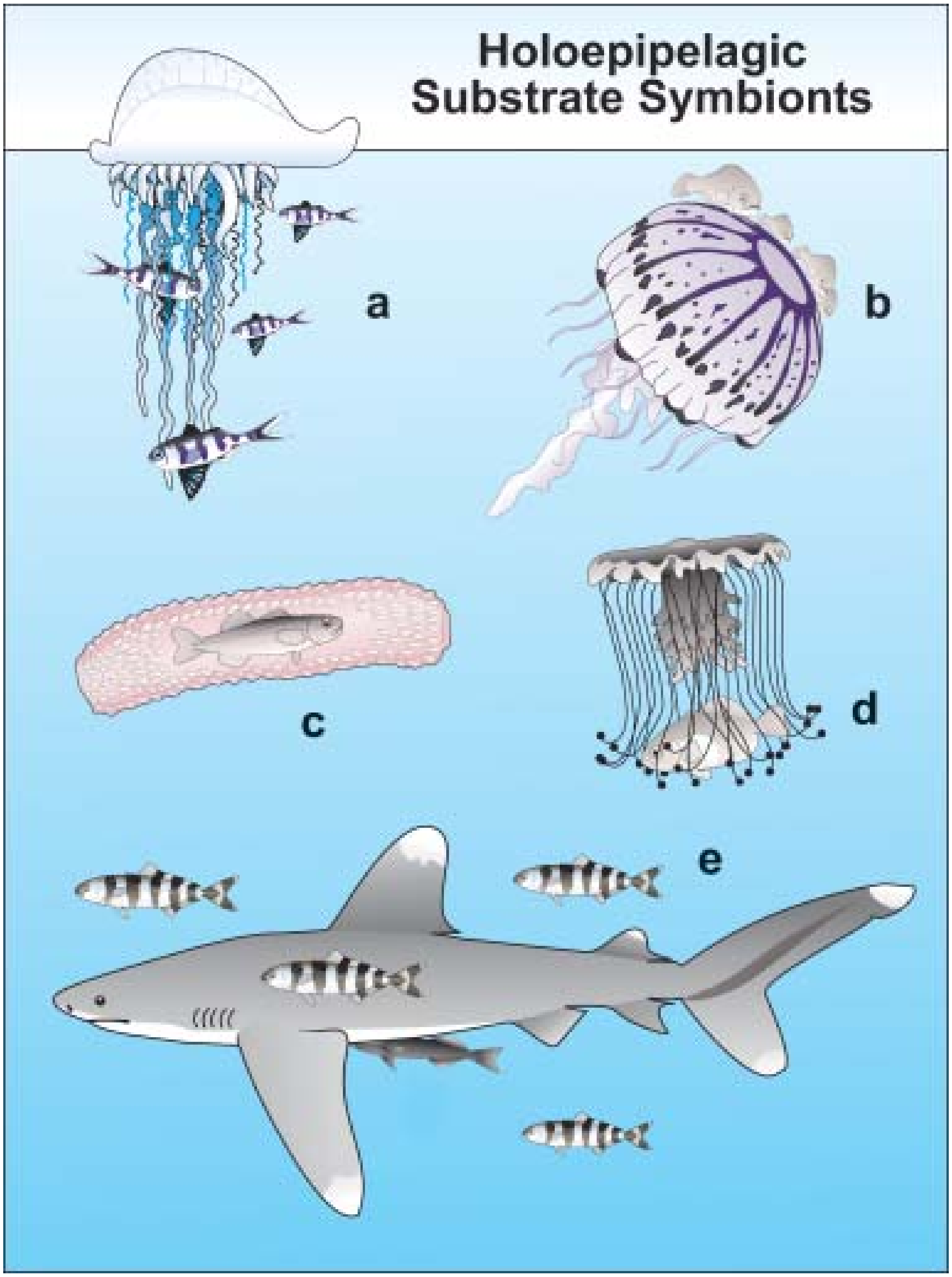

FIGURE 12-7 Examples of holoepipelagic substrate symbionts. A. Man-O-War fish (*Nomeus gronovii*) and host siphonophore (*Physalia* sp., does not occur off California); B. California medusafish (*Icichthys lockingtoni*) and Purple striped sea jelly (*Pelagia* sp.); C. Juvenile smalleye squaretail (*Tetragonurus cuvieri*) in lumen of colonial salp (*Pyrosoma* sp.); D. Driftfish (*Psenes pellucidus*) under the scyphomedusa (*Cyanea* sp.); and E. Pilotfish (*Naucrates doctor*) and remora (*Remora remora*) accompanying an oceanic whitetip shark (*Carcharhinus longimanus*). Examples B–E are known to occur off California.

(*Coryphaena hippurus*), and several species of flyingfishes and halfbeaks. Most of the species above lay eggs in nearshore waters. Whale sharks are ovoviviparious, giving birth in shallow waters. Dolphinfish spawn pelagic eggs where as herrings, halfbeaks, and flyingfishes lay their eggs in floating or attached algae. Typically, the juvenile stages of epheboepipelagic species inhabit the productive, coastal waters and move offshore as they reach maturity.

BREPHOEPIPELAGIC GROUP

These fishes display a life history strategy that is the opposite of epheboepipelagic species (Parin, 1968). Brephoepipelagic species spend the main part of the life history in coastal waters, but produce larval, post-larval, and juvenile forms that spend a significant amount of time in the oceanic surface waters. Worldwide, certain families of fishes tend to

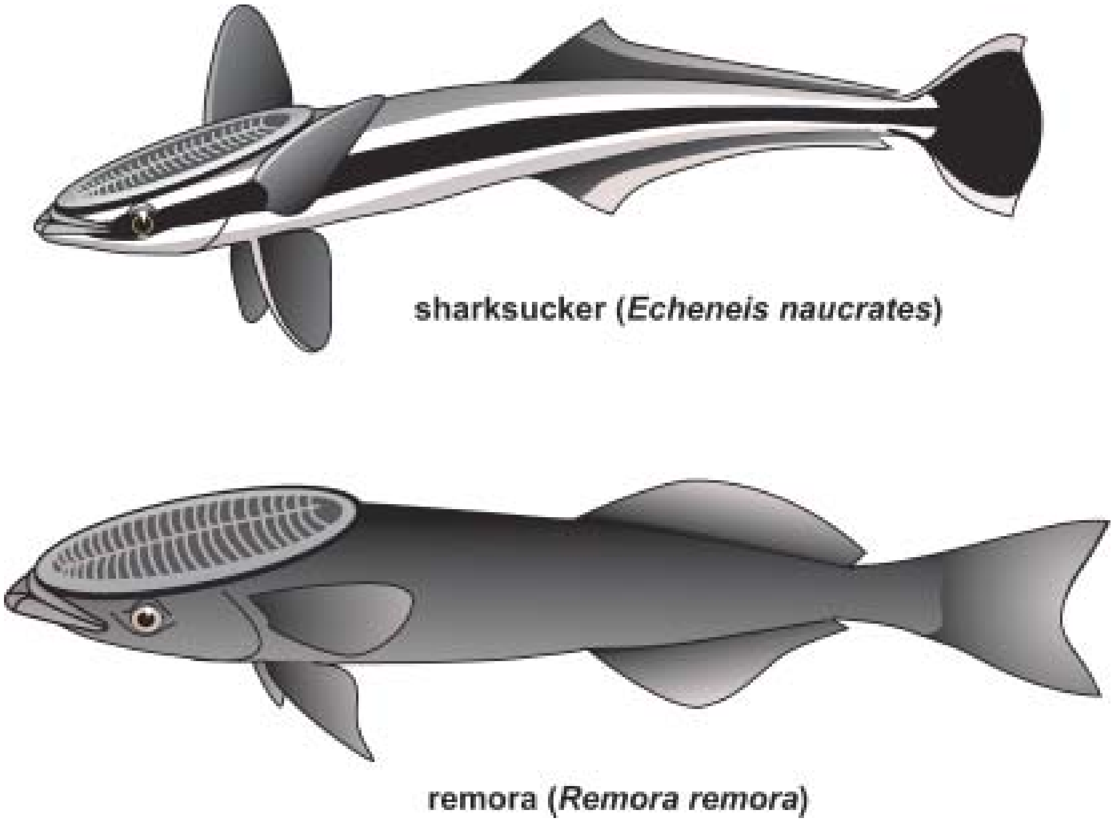

FIGURE 12-8 Examples of two members of the sharksucker family (Echeneidae)

show this strategy, which undoubtedly leads to long distance dispersal in most cases. Parin (1968) noted that greenlings (Hexagrammidae), goatfishes (Mullidae), and soldierfishes (Holocentridae) have extended epipelagic stages. He also included in this group members of the 1) primarily coastal pelagic families, Atherinidae (old world silversides), Scombridae (mackerels), and Carangidae (jacks); 2) coastal benthic families: Synodontidae (lizardfishes), Stichaeidae (pricklebacks), Scorpaenidae (scorpionfishes and rockfishes), Cottidae (sculpins), Acanthuridae (surgeonfishes), Bothidae (left-eye flounders); Cynoglossidae (tonguefishes), and Pleuronectidae (right-eye flounders; and even 3) brackish and freshwater families: Anguillidae (Freshwater eels) and Mugillidae (mullets).

NYCTOEPIPELAGIC

These vertical migrators are best represented by members of the families: Myctophidae (lanternfishes), Gonostomatidae (bristlemouths), Dalatiidae (dwarf sharks), Stomiidae (dragonfishes), and Gempylidae (snake mackerels). Although Parin (1968) considered this group of fishes to be nocturnal epipelagics, the vast majority of classification schemes of marine fishes consider these to be mesopelagic forms (see Chapter 13 for detailed discussion).

Xenoepipelagic Fishes

The third and last major group of epipelagic fishes in Parin's (1968) scheme includes those species that sporadically penetrate into the epipelagic realm from another habitat. Such fishes are termed xenoepipelagic (*xenos*—foreign). Parin recognized two main groups of xenoepipelagic fishes: 1) coastal pelagic species, that migrate offshore into pelagic waters on an irregular basis and 2) algophilic species, which associate with floating algae (kelp paddies). Coastal pelagic species that often occur very far offshore, particularly in upwelling areas, include anchovies (Engraulidae), sardines, herrings (Clupeidae), jacks (Carangidae), and some species of flyingfishes (Exocoetidae).

Algophilic species from coastal waters often become associated with floating algae either through displacement with the algae from shallow water or by recruiting from the plankton to the floating paddy. Such species include pipefishes (Syngnathidae), triggerfishes (Balistidae), porcupinefishes (Diodontidae), and juveniles of many nearshore species (e.g., Kyphosidae, Carangidae, and Scorpaenidae).

Epipelagic Fishes of the Californias

The holoepipelagic fish fauna off the coast of the Californias reflects the diverse nature of the water masses converging on this vast area of the northeastern Pacific Ocean (see fig. 12-11, chapter 11). The California Current dominates the northern portion of the region, transporting cold surface water south over much of this range. This transport results in an epipelagic fauna dominated by boreal and temperate forms over much of the year. The warm water species are normally restricted to the southernmost portion of this region (central to southern Baja California). Each summer, however, tropical forms move northward with the warming surface waters to

TABLE 12-2

Characteristic Species of Epipelagic Fishes in the Main Biogeographical Regions of the Eastern North Pacific

Eastern North Pacific	Characteristic Species		
	Holoepipelagic	*Meroepipelagic*	*Xenoepipelagic*
Boreal	Salmon shark, daggertooth, longnose lancetfish, ragfish	chinook salmon, coho salmon, Pacific herring	—
Temperate	Basking shark, blue shark, Pacific saury, opah, bigscale pomfret, escolar, bluefin tuna, albacore, swordfish, medusafish, smalleye squaretail, ocean sunfish	California flyingfish	Northern anchovy, Pacific sardine, Pacific butterfish, chub mackerel, Pacific bonito, jack mackerel, California barracuda, Yellowtail
Tropical	Shortfin mako, oceanic whitetip, pygmy shark, pelagic stingray, Pacific saury, darkwing flyingfish, opah, oarfish, snake mackerel, oilfish, skipjack, yellowfin tuna, bigeye tuna, striped marlin, blue marlin, swordfish, louvar, cigarfish, Pacific squaretail, man-o-war fish, oceanic puffer, ocean sunfish, slender mola	Whale shark, dolphinfish, ribbon halfbeak	Manta ray, sailfish, black marlin, wahoo

NOTE: After Parin, 1968.

feed or reproduce. This northward migration intensifies during ENSO events resulting in tropical forms penetrating into much higher latitudes than is seen in more neutral years (see chapter 1).

Boreal Region

The holoepipelagic ichthyofauna of the boreal region of the northeastern Pacific is fairly depauperate commonly including only four species (table 12-2). The salmon shark (*Lamna ditropis*) is joined by three, predatory species that are normally associated with the deep epipelagic realm in more southerly latitudes. These three species, daggertooth (*Anotopterus pharao*), longnose lancetfish (*Alepisaurus ferox*), and ragfish (*Icosteus aenigmaticus*), normally occur with the salmon shark off northern California, but can extend farther south during cold water years. The meroepipelagic group dominates the fish fauna of the boreal region off California and northward and includes chinook (*Oncorhynchus tyshawytscha*) and coho (*O. kisutch*) salmon and Pacific herring (fig. 12-9).

Temperate Region

The epipelagic ichthyofauna off California has been characterized historically as temperate in character (table 12-2). Furthermore, it is numerically dominated by several low trophic-level species that are common to the coastal pelagic (xenoepipelagic) realm. Because the waters off central and northern California represent a major upwelling area, many of these coastal pelagic species may occur far offshore (see chapters 3 and 4, and California Current section at end of the current chapter). Chief among these species are northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*), which have alternated as the most abundant fishes of the coastal pelagic zone off California throughout recent history and are among the best studied of all California species because of their commercial importance (Mais, 1974; Squire, 1983) (fig. 12-10). In addition, Pacific pompano (*Peprilus simillimus*), chub mackerel (*Scomber japonicus*) and jack mackerel (*Trachurus symmetricus*) are abundant, low-level carnivores that often occur in open ocean waters far from shore. This group also includes three piscivorous species, California barracuda (*Sphyraena argentea*), Pacific bonito (*Sarda chiliensis*), and yellowtail (*Seriola lalandi*) which are common in waters off of Baja California and enter southern California during the spring and summer months of most years (fig. 12-11).

True holoepipelagic species (fig. 12-5) of the uppermost portions of the offshore water column include blue shark (*Prionace glauca*), basking shark (*Cetorhinus maximus*), and Pacific saury (*Cololabis saira*). Active swimmers of the deeper regions of the temperate epipelagic include opah (*Lampris regius*), bigscale pomfret (*Taractes longipinnis*), and escolar (*Lepidocybium flavobrunneum*). Large, active swimmers of depths throughout the epipelagic zone include albacore (*Thunnus alalunga*), bluefin tuna (*T. thynnus*), and swordfish (*Xiphias gladius*). Research on the daily activities of ocean sunfish (*Mola mola*) indicate that this species makes regular vertical migrations between the surface and lowest portions of the epipelagic zone, and is best placed in the same ecological group as the tunas and swordfish (Cartamil and Lowe, 2004). The medusa fish (*Icichthys lockington*), blackrag (*Psenes pellucidus*), smalleye squaretail (*Tetragonurus cuvieri*) are all cooler water, stromateioid fishes that associate with

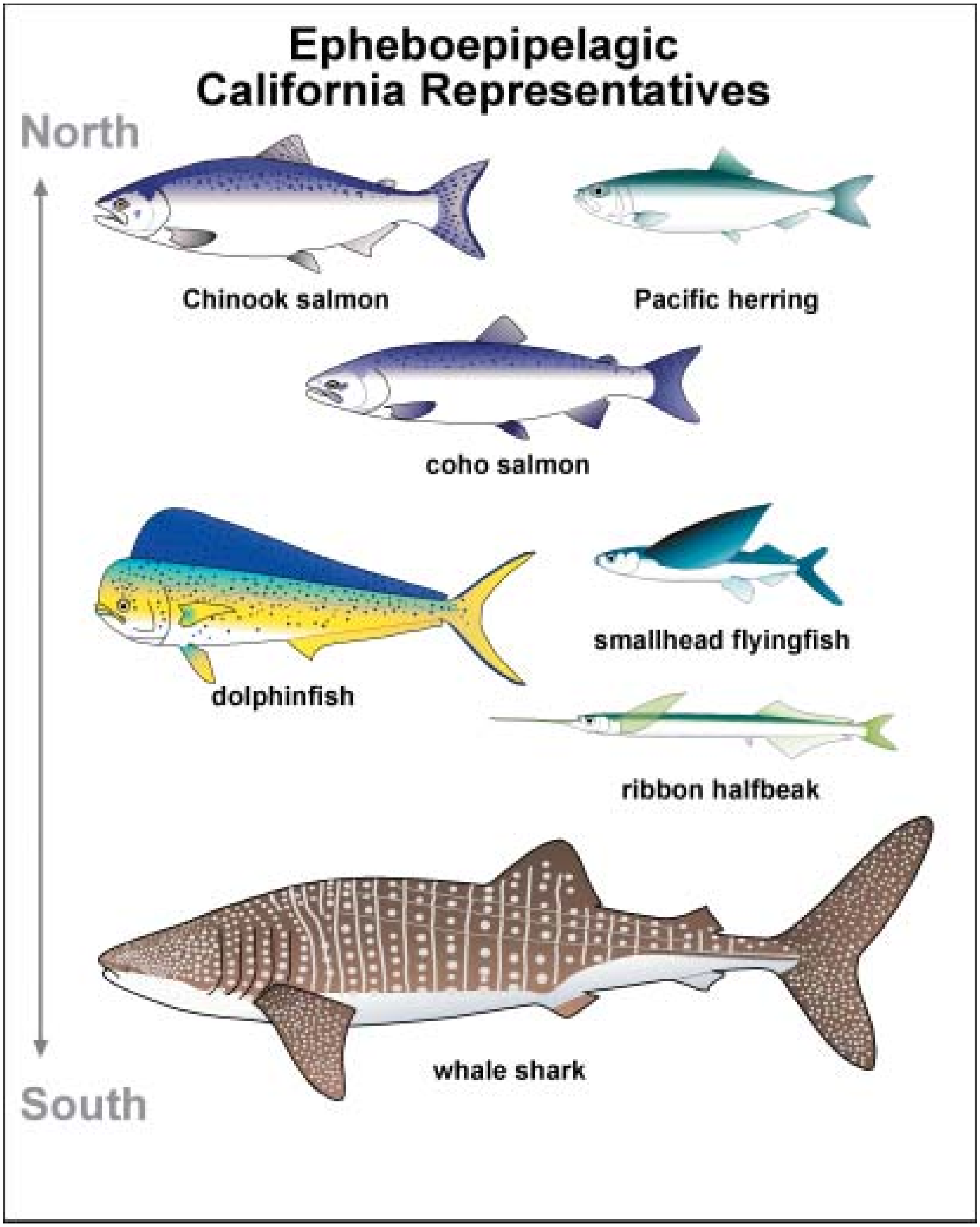

FIGURE 12-9 California representatives of epheboepipelagic fishes (epipelagic adults that breed nearshore or in freshwater) arranged from north to south in occurrence.

medusa and salps as juveniles and become holoepipelagic as adults.

Tropical Region

Parin (1968) noted that the majority of truly holoepipelagic forms are restricted to the isothermic surface layer that occurs mainly in the tropics because of the permanent thermocline that exists there. This restriction is certainly true for the tropical waters of the northeastern Pacific, where the greatest diversity of holoepipelagic forms has been recorded. This fauna normally exists in the waters to the south of the Californias, but regularly enters the southern region off Baja and southern California in the summer months (Bedford and Hagerman, 1983; Cailliet and Bedford, 1983; Cross and Allen, 1993).

This tropical fauna includes shortfin mako (*Isurus oxyrhynchus*), oceanic whitetip (*Carcharhinus longimanus*), pelagic stingray (*Dasyatis violacea*) and the small, deeper dwelling, pygmy shark (*Euprotomicrus bispinatus*). Representative bony fishes of the surface layers include Pacific saury, several species of flyingfishes, including darkwing flyingfish (*Hirundichthys rondeletii*), and skipjack tuna (*Katsuwonus pelamis*). Several other

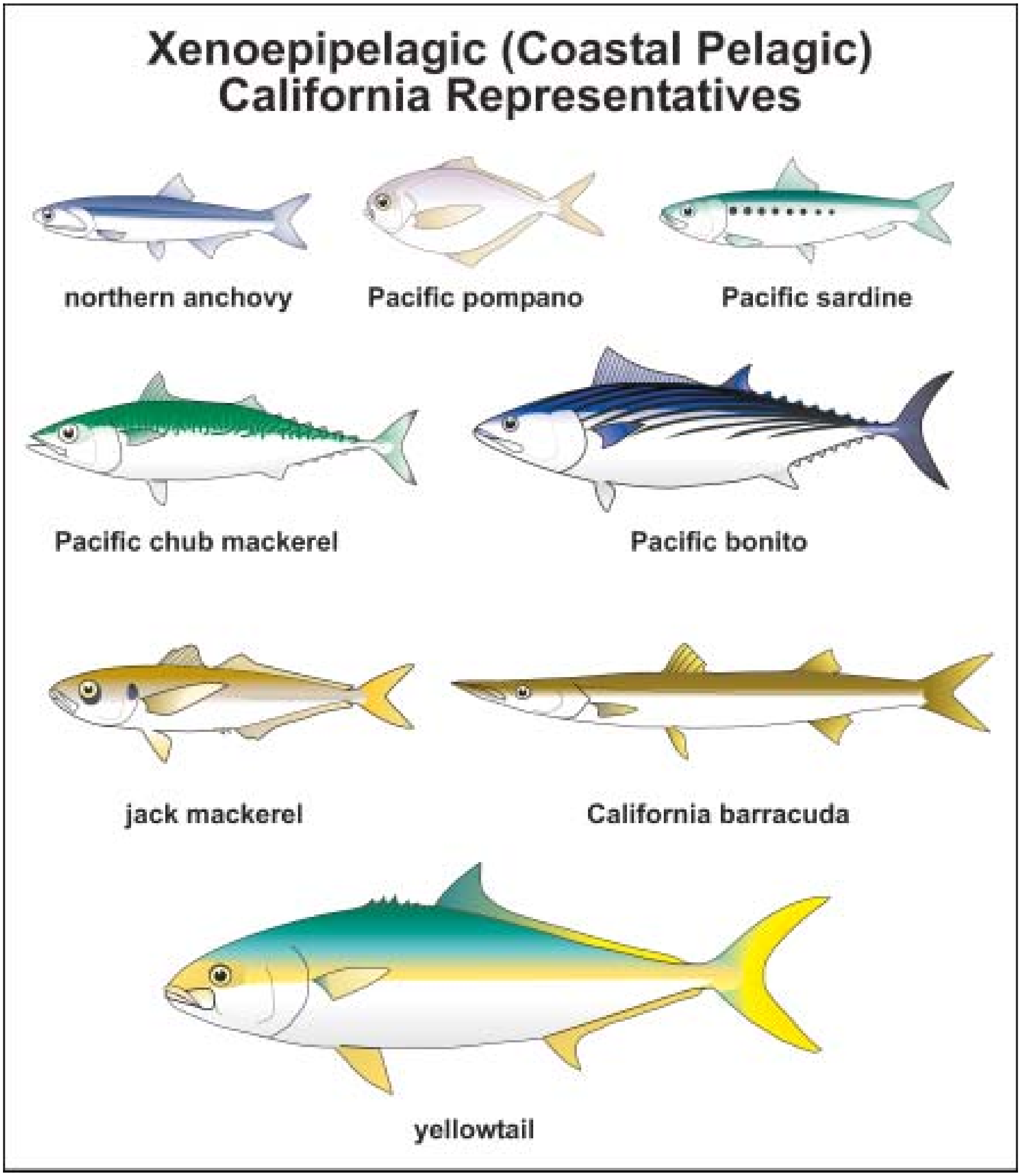

FIGURE 12-10 California representatives of xenoepipelagic fishes (coastal pelagic).

relatively rare, tropical species have been recorded in small numbers off California including: slender snipefish (*Macrorhamphosus gracilis*), oceanic puffer (*Lagocephalus lagocephalus*), and slender mola (*Ranzania laevis*). Dolphinfish (*Coryphaena hippurus*) is also an abundant meroepipelagic fish in the surface layers, particularly around floating objects (Mitchell and Hunter, 1970; Kingsford and Defries, 1999).

Tropical waters also support a diverse group of deep epipelagic forms that penetrate into the upper regions of the mesopelagic zone and are rarely seen at the surface. These species are sometimes found in the temperate zone and include: opah, escolar, and other rare, specialized forms such as ribbon-like lampridiform fishes (oarfish, *Regalaceus glesne*; highbrow crestfish, *Lophotus cristatus*; and king-of-the-salmon, *Trachipterus altivelis*), gempylids (snake mackerel, *Gempylus serpens* and oilfish, *Ruvettus pretiosus*), cutlassfish (Pacific cutlassfish, *Trichiurus nitens*), and louvar (*Louvaris imperalis*), an oceanic acanthuroid (surgeonfish) (Fig. 12-5 and 12-6).

Large tropical tunas, (yellowfin, *Thunnus albacares*; and bigeye, *T. obesus*), marlins (striped, *Tetrapterus audax*; and blue, *Makaira nigricans*), swordfish, and ocean sunfish inhabit a broad depth range within epipelagic zone. These large, holoepipelagic fishes are encountered at all depths within the epipelagic zone and often make feeding excursions into the main thermocline.

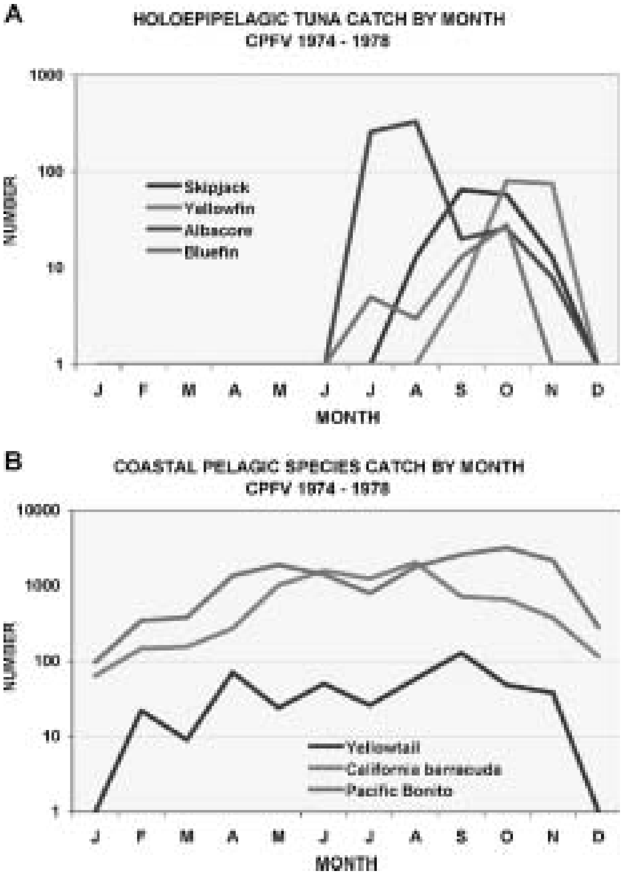

FIGURE 12-11 Commercial Passenger Fishing Vessel (CPFV) monthly catches of four species of tunas (top) and three species of coastal pelagic fishes in California from 1974 to 1978.

Stromateioid fishes are also well represented in the tropical epipelagic realm and are usually associated with floating objects, including medusae, siphonophores, and salps. Various species of cigarfish (*Cubiceps* spp.), squaretails (*Tetragonurus* spp), driftfishes (*Psenes* spp.) all associate with flotsam or gelatinous zooplankton on the high seas and have been variously recorded off the Californias (Miller and Lea, 1976; Fitch and Lavenberg, 1968). The Man-O-War fish, *Nomeus gronovii*, inhabits the surface layers of the tropical regions of the eastern north Pacific in association with the siphonophore *Physalia* sp. (Allen and Robertson, 1994). The occurrence of *Nomeus* off southern Baja California is probably associated only with ENSO events.

Prominent meroepipelagic (epheboepipelgic) fishes of the tropical province of the eastern north Pacific that have been recorded off California include the aforementioned dolphinfish, whale shark (*Rhincodon typus*), the largest living fish, and ribbon halfbeak (*Euleptorhamphus viridis*). Manta (*Manta birostris*), sailfish (*Istiophorus platypterus*), black marlin (*Makaira indica*), and wahoo (*Acanthocybium solandri*) are probably better classified as xenoepipelagic because they sporadically occur far from shore in the epipelagic realm (table 12-2).

The surface waters off the Californias also support an important group of fishes that occupy the epipelagic zone only during their early life history stages (see also chapter 10—Ichthyoplankton). This brephoepipelagic group (Parin, 1968) includes a diverse array of species that have extended pelagic juvenile stages (fig. 12-12). In higher latitudes, many scorpaenifiorm fishes qualify as brephoepipelagic species. Greenlings, most notably lingcod (*Ophiodon elongates*) and kelp greenling (*Hexagrammus decagrammus*), have pelagic juvenile stages and recruit to shallow, benthic nursery areas at relatively large sizes. Cabezon (*Scorpaenichthys marmoratus*), the largest cottid, and many scorpaenids (including genera, *Scorpaena, Sebastes,* and *Sebastolobus*) also produce pelagic juveniles that remain in the epipelagic zone for extended periods and attain lengths between 30–50 mm SL (O'Connell, 1953; Ambrose, 1996a, Ambrose, 1996b; Moser, 1996; Love et al., 2002). These scorpaenids are loosely aggregating, benthic fishes that live on mud from 60–600 m depth (M. J. Allen, 1982; Cross, 1987). In the south, prejuveniles (10–14 mm SL) of splitnose rockfish (*Sebastes diploproa*) congregate in surface waters under drifting objects, such as kelp patties (Mitchell and Hunter, 1970) from August through December. Juveniles at 40–50 mm SL emigrate from the surface waters in April and May (Boehlert, 1977), descend to 200–250 m depth, and migrate horizontally until they contact the bottom (Moser and Ahlstrom, 1978). The two scorpaenid genera, *Sebastes* and *Sebastolobus*, are represented in fig. 12-12 by the boccacio and longspine thornyhead.

Pleuronectids (right-eyed flatfish), such as the Dover sole (*Microstomus pacificus*) (fig. 12-12) and rex sole (*Erres zachirus*) have large, leaf-like larval/juvenile phases that are transparent and can remain pelagic for up to a year (Charter and Moser, 1996). Off southern and Baja California, striped mullet (*Mugil cephalus*) and several species of blennies (*Hypsoblennius spp.*) are brephoepipelagic with the latter having an extended neustonic phase (Sandknop and Watson, 1996; Watson, 1996).

The productive California Current system is actually dominated by coastal pelagic fishes that are more properly considered xenoepipelagic forms in Parin's classification and are discussed in the following section.

The California Current System

Species Composition and Abundance

The fish fauna of the California Current system is dominated by small, planktivorous schooling fishes such as: northern anchovy, Pacific sardine, jack mackerel and chub mackerel (Mais, 1974, 1977; Parrish et al., 1981; Squire, 1983b). The population ecology and biology of the pelagic planktivores is well known (table 12-3) because they have supported important commercial fisheries in the past; far less is known about the large predatory fishes, such as albacore, bluefin tuna, and opah.

Parrish et al. (1981) emphasized that pelagic fishes that spawn throughout the California Current region during the more productive upwelling periods usually suffer a great loss of larvae via offshore surface transport. Northern anchovy, Pacific sardine, jack mackerel, chub mackerel, and Pacific hake are residents of this system, and their reproductive strategies are adapted to its flow characteristics (Parrish et al., 1981; Cross and Allen, 1993).

Parrish et al. (1981) separated the California Current system into four distinct units based on fisheries data, surface transport characteristics, and reproductive characteristics of fish populations: 1) the Pacific Northwest region from Vancouver Island south to Cape Blanco, 2) the region of maximum upwelling between Cape Blanco and Point Conception, 3) the Southern California Bight from Pt. Conception south to Pt. Eugenia, and 4) the southern Baja California Region. Coastal fishes with pelagic larvae in the Pacific Northwest region tend

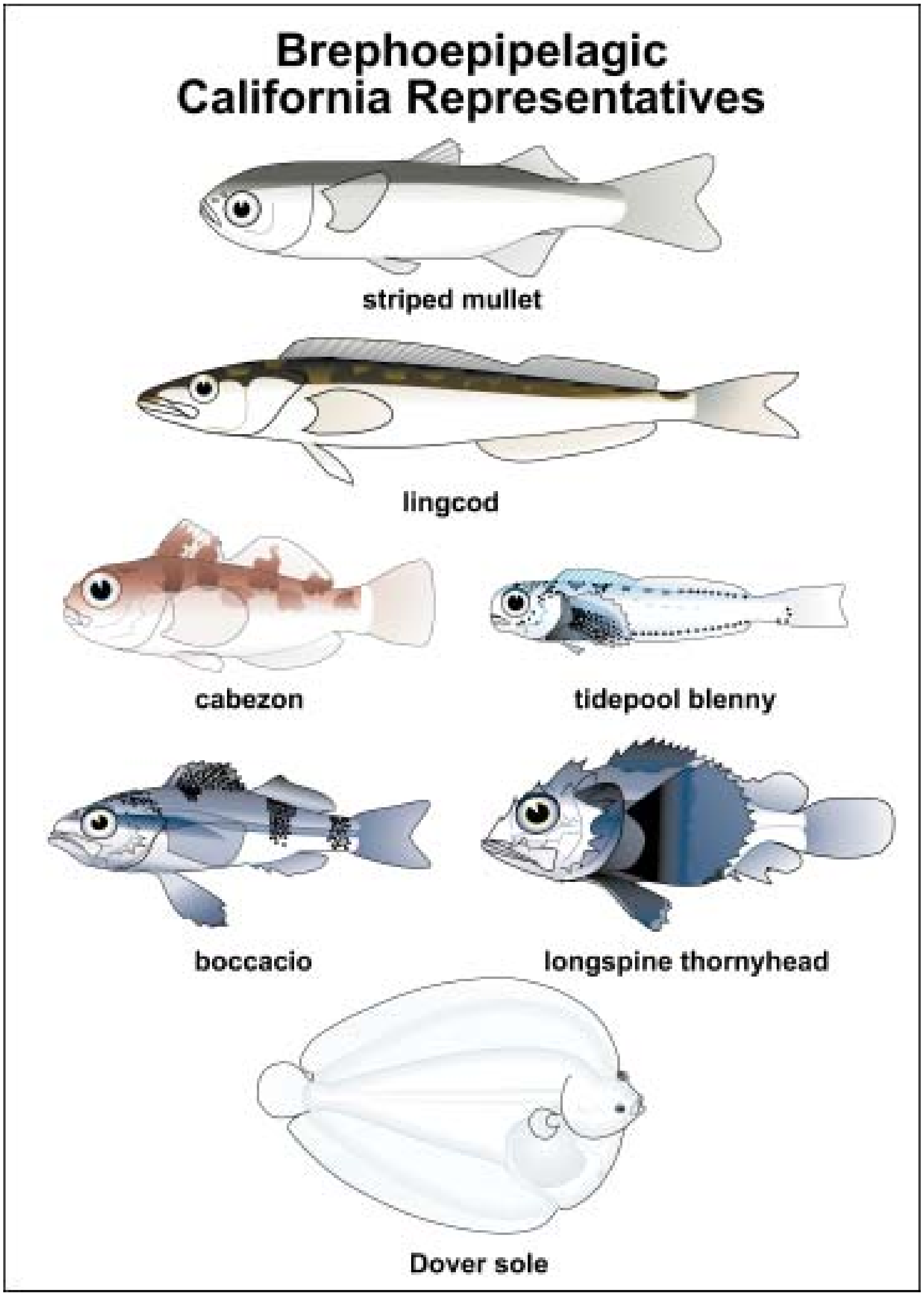

FIGURE 12-12 California representatives of brephoepipelagic fishes (coastal adults that have pelagic juvenile stages).

to spawn in the winter when the wind drift of surface waters is directed toward the coast. The region of vigorous upwelling between Cape Blanco and Pt. Conception (northern and central California), where offshore transport occurs year-round, has few locally spawning fishes. Instead, the region is dominated by large stocks of migratory planktivorous fishes (e.g., northern anchovy, Pacific sardine, jack mackerel, and chub mackerel) that spawn in the more favorable wind drift conditions found farther south in the Southern California Bight and off southern Baja. The closed gyral circulations that characterize these regions foster favorable conditions for spawning that have lead to more-or-less distinct subpopulations of these coastal pelagic species. The reliance of spawning success upon surface drift conditions in the California Current is probably responsible for the wide, year-to-year fluctuations in population size that is characteristic of these important fisheries species. Anomalies in the surface transport caused by ENSO and other climatic events have dramatic impacts on such populations.

Large-scale, fisheries-independent assessments of California pelagic fish populations where juvenile and adult fishes were physically captured are largely limited to two midwater trawl studies conducted from 1950 to 1951 (Radovich, 1952) and from 1966 to 1971 (Mais, 1974) (table 12-4). In the earlier

TABLE 12.3

Research Conducted on the Biology of Economically Important Pelagic Species Off California

Pelagic Species	*References*
Northern anchovy (*Engraulis mordax*)	Bagarinao and Hunter (1983), Booman et al. (1991), Butler (1990), Butler and Pickett (1988), Checkley et al. (2000), Coyer and Hall (1993), Folkvord and Hunter (1986), Hunter (1972), Hunter (1976), Hunter (1977), Hunter (1985), Hunter and Coyne (1982), Hunter and Dorr (1982), Hunter and Goldberg (1980), Hunter and Kimbrell (1980), Hunter and Leong (1981), Hunter and Macewicz (1980), Hunter and Macewicz (1985a), Hunter and Macewicz (1985b), Hunter and Nicholl (1985), Hunter and Sanchez (1977), Hunter and Thomas (1974), Hunter et al. (1981), Hunter et al. (1979), Hunter et al. (1985), Jacobson et al. (1994), Kaupp and Hunter (1981), Moser and Pommeranz (1999), Nonacs et al. (1994), Nonacs et al. (1998), Nonacs et al. (1998), Owen et al. (1990), Santander et al. (1984), Smith (1972), Smith (1980), Smith et al. (1983), Smith et al. (1985), Smith et al. (1989), Vetter et al. (1999), Vlymen (1977), Vrooman and Smith (1971)
Pacific sardine (*Sardinops sagax*)	Arenas et al. (1996), Alvarez and Butler (1992), Arenas et al. (1996), Brewer and Smith (1982), Butler (1991), Butler and Pickett (1988), Butler and de Mendiola (1985), Butler et al. (1993), Butler et al. (1996), Castillo et al. (1985), Checkley et al. (2000), de la Campa et al. (1976), Jacobson and MacCall (1995), Kramer and Smith (1971), Lasker (1970), Lo et al. (1995), Lo et al. (2001), Logerwell (2001), Logerwell and Smith (2001), MacCall (1979), Macewicz et al. (1996), Mallicoate and Parrish (1981), Schwartzlose and Smith (1989), Silliman (1943), Smith (1973), Smith (1990), Smith et al. (2001), Smith et al. (1983), Smith et al. (1989), Smith et al. (1992), Wada and Jacobson (1998), Wolf and Smith (1985), Wolf and Smith (1986), Wolf et al. (1987)
Jack mackerel (*Trachurus symmetricus*)	Hunter (1968), Hunter (1969), Hunter (1971), Hunter and Zweifel (1971), Kramer and Smith (1970), Macewicz and Hunter (1993), Mallicoate and Parrish (1981), Mason (1991), Pritchard et al. (1971)
Pacific chub mackerel (*Scomber japonicus*)	Dickerson et al. (1992), Hunter and Kimbrell (1980), Knaggs and Parrish (1973), MacCall et al. (1985), Mallicoate and Parrish (1981), Parrish and MacCall (1978)
Tunas (*Thunnus, Katsuwonus*)	Bertignac et al. (1999), Bayliff (2001), Dotson and Graves (1984), Dotson et al. (1984), Dotson et al. (1989), Dotson (1976), Dotson (1978), Dotson (1980), Finneran et al. (2000), Hunter et al. (1986), Laurs and Dotson (1983), Laurs and Lynn (1991), Laurs et al. (1981), Laurs et al. (1982), Laurs (1989), Pinkas et al. (1971), Schaefer and Oliver (2000), Sharp and Dotson (1977)
Billfishes (*Makaira, Xiphias*)	Barrett et al. (1998), Hinton (2001), Hinton et al. (2002)

study, which occurred prior to the collapse of the California sardine fishery, the catch was dominated nearly equally by northern anchovy (35.8%) and Pacific sardine (35.2%), followed by jack mackerel (22.2%) and chub mackerel (6.7%). By the 1960s, the northern anchovy (68.1%) dominated the catch in midwater trawls. Jack mackerel ranked second (18.3%) and Pacific hake (10.5%) ranked third (Mais, 1974).

Another fisheries-independent study involved an aerial monitoring program from 1962 to 1978, covering much of California and Baja California coastline (Squirre, 1983). This study reported sightings and estimated abundances of schools of small planktivorous and larger predatory fish species that were observed near the surface from low flying aircraft (table 12-5). Over the 16 years of aerial observations, northern anchovy and jack mackerel were the most abundant species spotted off central California and a number of basking sharks were also observed. Northern anchovy and jack mackerel dominated sightings off southern California, followed by bluefin tuna and chub mackerel. Pacific bonito and albacore tuna constituted a lesser, but important portion of the estimated abundance. Off northern Baja, aerial sightings were dominated by tunas and their relatives, including bluefin, Pacific bonito, and albacore followed by northern anchovy and chub mackerel.

In the decades of the 1970s and 1980s, northern anchovy dominated the catch of all smaller-scale sampling programs that use round-haul nets. Commercial purse seine hauls made at night in the surface waters of Monterey Bay contained 99.9% northern anchovies, which is not surprising because anchovies were the targeted species (Cailliet et al., 1979). In addition to anchovies, seine hauls collected a mixed group of both coastal pelagic and benthic species. Pacific herring were captured in lower abundance along with night smelt (*Spirinchus starksi*) and Pacific sauries. Largely benthic species, such as plainfin midshipman (*Porichthys notatus*) and Pacific electric ray (*Torpedo californica*), composed a surprisingly large portion of the remaining catch in these night-time hauls supporting the hypothesis that they rise into the water column at night to feed.

Another type of round-haul net, a lampara net, was used to assess the populations of coastal pelagic fishes off of San Onofre (Allen and DeMartini, 1982—see chapter 6). Again, northern anchovies dominated the catches, particularly in the offshore sets. In addition to anchovies, southern, coastal pelagic species, including chub mackerel, jack mackerel, Pacific bonito, and California barracuda, were all well represented in the catches.

Beginning in the late 1970s through to the present time, most fisheries-independent, population assessments of California Current fishes (primarily northern anchovy and Pacific sardine) have been indirect in nature. Fisheries-related studies have focused on distribution and biomass estimation

TABLE 12-4

Relative Abundance of Epipelagic Fishes by Region off California Determined by Midwater Trawl Survey

	Midwater Trawls	
Species	*Radovich (1952) 1950–51*	*Mais (1974) 1966–71*
Northern anchovy	35.8	68.1
Jack mackerel	22.2	18.3
Pacific sardine	35.3	1.7
Pacific hake		10.5
Chub mackerel	6.7	0.9
Pacific saury		0.5

NOTE: Surveys from 1950 to 1952 (Radovich 1952) and 1966 to 1971 (Mais, 1973).

TABLE 12-5

Mean Abundance of Epipelagic Fishes by Region off California Determined by Air Born Fish Monitoring

1962–1978		*Region*	
Species	*Cencal*	*Socal*	*Nobaja*
Northern anchovy	39.1	31.4	9.3
Bluefin tuna	0.0	20.2	45.1
Jack mackerel	30.3	25.2	1.3
Pacific bonito	2.3	5.5	21.1
Albacore tuna	0.00	2.2	17.8
Basking shark	17.2	1.4	0.0
Chub mackerel	0.6	10.5	4.8
White seabass	6.4	1.4	0.0
Pacific sardine	3.8	1.7	0.3
Yellowtail	0.1	0.2	0.1
California barracuda	0.1	0.1	0.1

NOTE: Program from 1963 to 1978 (Squire, 1983).

based on: 1) egg and larval densities (Smith et al., 1985; Wolf and Smith, 1985; Wolf and Smith, 1986; Wolf et al., 1987; Butler, 1991; Arenas et al., 1996; Moser and Pommeranz, 1999; Checkley et al., 2000; Lo et al., 2001; Smith et al., 2001) and 2) hydroacoustic (sonar) surveys (Mais, 1977; Smith, 1978; Hewitt and Smith, 1979; Holiday and Larson, 1979); 3), lidar (airborne laser) surveys (Churnside and Hunter, 1996; Lo et al., 1999); and 4) computer modeling (Jacobson et al., 1994; Jacobson and MacCall, 1995; Lo et al. 1995).

Published assessments of the populations of large predatory fishes of the epipelagic realm off the Californias are rare. Hanan et al. (1993) compiled the catch data (landings) from the commercial drift net fishery operating offshore from northern to southern California from 1981 to 1991. This fishery used large mesh nets and targeted swordfish, thresher sharks, and shortfin makos, that constituted the bulk of the catch, but captured a wide variety of other epipelagic fishes (table 12-6). All five major tuna species (bluefin, albacore, yellowfin, bigeye, and skipjack) were well-represented in the catch along with ten species of shark (common thresher, shortfin mako, bigeye thresher, soupfin, hammerhead, blue, pelagic thresher, salmon, white, and dusky) and two oceanic bony fishes (opah and louvar). The remainder of the catch was composed largely of coastal pelagic species (e.g. white seabass (*Atractoscion nobilis*), Pacific bonito, California barracuda, and chub mackerel). More recently, catch data from the Oregon-California drift net fleet from 1990 to 2002 has become available (table 12-7). These data were collected by onboard observers of the National Marine Fisheries Service and included several, non-fisheries species that are captured, but not normally brought back to landings. One such species, the ocean sunfish ranked first in the catch over the 13-year period. Obviously, ocean sunfish are much more common in the surface waters off California than had been reported from previous, fishery-dependent data.

Fisheries-dependent assessments continue to dominate as indicators of population status for fisheries management purposes. Commercial landings over the past 70 years document large fluctuations in northern anchovy, Pacific sardine, and chub mackerel biomass that are attributable largely to fluctuations in recruitment. Anchovy biomass was high in the early 1970s because of favorable environmental conditions, low adult mortality, and above average recruitment (Methot, 1982). The subsequent decline in northern anchovy abundance was attributed to a return to more normal environmental conditions, increased fishing pressure, predation by an expanding chub mackerel population (Mais, 1981; MacCall et al., 1985), and possible interspecific competition with an expanding Pacific sardine population (Wolf et al., 1987; Butler, 1991; Smith et al., 2001; Jacobson et al., 1994). After almost four decades of depressed population levels, the Pacific sardine had once again returned to prominence in the California Current with commercial catches exceeding those of northern anchovies by an order of magnitude by 1999 (Wolf and Smith, 2001). Long-term changes in the fisheries of these two, numerically dominate species are discussed in detail in chapter 25.

Recruitment success in chub mackerel has also been roughly cyclical since the 1930s (MacCall et al., 1985). The total biomass of chub mackerel, one of the most thoroughly studied and variable fisheries in the world, exploded three-times in the last 70 years (MacCall et al., 1985; Prager and MacCall, 1988; Konno and Wolf, 2001) and at least once in the 1800s (Soutar and lsaacs, 1974). Reproductive success of chub mackerel in 1976 at the beginning of the most recent population increase was about 750 times reproductive success in 1983 (Parrish and MacCall, 1978).

Future Research

We hesitate before recommending future directions of research because studies of this expansive habitat and its fishes will undoubtedly require large-scale efforts from commercial and research vessels and equally large budgets. At present, the limited funding for oceanographic and fisheries research off California does not bode well for such endeavors. Never-theless, we believe the following avenues of study would yield valuable information.

1. Fisheries independent quantitative studies should be undertaken to estimate the standing stocks of epipelagic organisms including fishes at the various trophic levels. If the formidable logistic hurdles can be overcome, such an investigation would yield critical

TABLE 12-6

Total Catch of Large Epipelagic Fishes off of California Taken by Commercial Drift Nets from 1981 to 1991

Species	*Catch (kg)*	*% Wt*
Swordfish	9,334,408	55.6
Common thresher	4,687,869	27.9
Shortfin mako	1,190,495	7.1
Opah	524,990	3.1
Albacore	452,789	2.7
Bigeye thresher	178,089	1.1
White seabass	54,444	0.3
Yellowfin tuna	53,729	0.3
Pacific bonita	49,635	0.3
Soupfin shark	36,795	0.3
Louvar	30,608	0.3
Bigeye tuna	28,473	0.3
Bluefin tuna	23,251	0.1
Skipjack tuna	22,851	0.1
Hammerhead shark	21,976	0.1
Yellowtail	19,565	0.1
Blue shark	19,340	0.1
California barracuda	19,001	0.1
Pelagic thresher	12,757	0.1
Chub mackerel	7,849	<0.1
Jack mackerel	2,043	<0.1
Salmon shark	1,714	<0.1
Dolphinfish	581	<0.1
White shark	554	<0.1
Pacific butterfish	198	<0.1
Pacific sardine	143	<0.1
Dusky shark	79	<0.1
Wahoo	64	<0.1
TOTAL	16,774,291	

NOTE: Hanan et al., 1993.

TABLE 12-7

Summary of All Fish Observed Caught in the California/Oregon Drift Gillnet Fishery from 1990 to 2002

Species	*Total*	*% Total*
Common Mola	34,704	29.18
Blue Shark	19,978	16.80
Albacore	15,564	13.09
Swordfish	13,205	11.10
Skipjack Tuna	7,270	6.11
Shortfin Mako Shark	5,170	4.35
Pacific Mackerel	4,834	4.06
Common Thresher Shark	4,688	3.94
Opah	3,406	2.86
Bluefin Tuna	3,255	2.74
Bullet Mackerel	2,962	2.49
Louvar	607	0.51
Yellowfin Tuna	463	0.39
Pacific Pomfret	453	0.38
Bigeye Thresher Shark	413	0.35
Pacific Bonito	357	0.30
Striped Marlin	322	0.27
Pacific Hake	255	0.21
Pelagic Stingray	253	0.21
Jack Mackerel	141	0.12
Remora	101	0.08
Salmon Shark	99	0.08
Pelagic Thresher Shark	77	0.06
Yellowtail	51	0.04
Blue Marlin	49	0.04
Smooth Hammerhead Shark	42	0.04
Pacific Sardine	40	0.03
Pacific Electric Ray	33	0.03
California Barracuda	29	0.02
Bigeye Tuna	20	0.02
Manta	14	0.01
Bat Ray	9	0.01
Oarfish	8	0.01
Northern Anchovy	7	0.01
White Seabass	7	0.01
plus 21 species <0.01 including black marlin, soupfin shark, white shark, megamouth shark, dolphinfish, basking shark, king of the salmon, dolphinfish and sailfish		
TOTAL	118,886	

NOTE: Data were collected at sea by NMFS observers and represents a total of 6,346 sets. See: http://swr.nmfs.noaa.gov/psd/codgftac.htm.

information on energy flow and dynamics of the pelagic realm. These studies could utilize hydroacoustic and/or LIDAR technologies in conjunction with ground-truth sampling with large midwater trawls and purse seines to enhance resolution at the species-level.

2. Population abundance assessments may still be made via large-scale tag-and-recapture studies. Satellite and other types of radio-tagging studies should continue to examine horizontal and vertical movements of large pelagic fishes (see chapter 20—Fish Movement & Activity Patterns).
3. Many ecomorphological and ecophysiological studies of the adaptations to pelagic realm by oceanic and coastal pelagic fishes remain to be undertaken. The learned works of Alexander (1990), Bone (1972), Bone and Roberts (1969), Magnuson (1973, 1978), and Marshall (1960, 1972), as described in Pelster (1977) have only scratched the surface.
4. Time series analyses of data from fisheries-dependent assessments of all pelagic fishes, large and small, must be continued and extended in order to track the effects of both exploitation and large-scale oceanographic variation.

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