p. 342-383. In: The Ecology of Marine Fishes: California and Adjacent Waters. 2006.
L.G. Allen, D.J. Pondella, and M. H. Horn (eds.). University of California Press, Berkeley, 670 pp.

CHAPTER 13

Deep Sea

MARGARET A. NEIGHBORS AND RAYMOND R. WILSON, JR.

Introduction

Below the euphotic epipelagic zone is the realm of deep-sea fishes. The depth zones of this major portion of the earth's oceans have been characterized by the physical features and types of organisms present (Hedgpeth, 1957; Angel, 1997). The upper limit of the mesopelagic zone (the interface with the epipelagic) occurs at approximately 100 m or even as deep as 200 to 250 m. The mesopelagic may be further subdivided into shallow and deep portions, often at about 600 to 700 m, based on the inhabitants (Angel, 1997). In the shallower portion, fish are silvery, and decapod crustaceans are a combination of red and transparent. Both groups may migrate upward through the thermocline at night. Nonreflective fishes and totally red decapod crustaceans inhabit the deeper zone. The vertically migrating micronekton from these greater depths usually do not cross the seasonal thermocline, and the majority of the macroplankton do not migrate vertically.

The bathypelagic zone, where daylight ceases to affect the distributions and behavior of the inhabitants, is found below approximately 1,000 m. At temperate latitudes, the mesopelagic-bathypelagic interface may be in the region of the permanent thermocline and the oxygen minimum layer (Angel, 1997). Accounting for 75% of the ocean, this dark, cold, sparsely populated region of increasing ambient pressure is the largest habitat type on earth (Helfman et al., 1997). Midwater assemblages may again change below 2,500 to 2,700 m in the abyssopelagic zone (Angel, 1997). This, then extends to near the ocean floor, where the benthopelagic inhabitants swim just above the bottom, in the so-called nepheloid layer.

The physical features of ocean waters change with increasing water depth. Pressure increases by one atmosphere (14.7 psi) per 10 m of depth. Temperature, which decreases in the upper 1,000 m, but then remains at fairly constant lows down to the bottom of the ocean (Marshall, 1971a), must influence the vertical ranges of organisms as it does the horizontal ranges of inhabitants of the epipelagic (Bruun, 1955). Light, however, is the feature most readily related to the vertical distributions of oceanic organisms. Phytoplankton are restricted to the epipelagial, where the solar energy is sufficient for their photosynthetic requirements. As a result of absorption and scattering, daylight intensity decreases to 1/10 for approximately every 75 m increase in depth, and the wavelengths that penetrate the deepest (about 430—530 nm, centered around 475 nm) are those of blue light (Denton, 1990).

The sun is not the only source of light in the ocean. Even in the epipelagic zone, organisms capable of producing light (bioluminescence) abound. At greater depths, any light present increasingly becomes due to bioluminescence, which generally is blue or blue-green. Daylight dominates the upper 200 m of the water column and diminishes to virtually absent at around 900 m; between 200 and 900 m, light from both sources is found (Denton, 1990), and in deeper regions, the only light present is produced by the inhabitants. Most deep-sea fishes, as well as many deep-sea invertebrates, produce their light with chemical reactions within specialized organs such as photophores; however, some species employ luminous symbiotic bacteria for this function.

The appearances of open water fishes living at different depths are related to the amount, directionality, and wavelengths of the light in their environment. These species lack structural features in their habitat where they can hide and, as a result have developed ways to blend into their open water backgrounds. Fishes of well-lit waters may be very brightly colored. Coral reef fishes are obvious in aquaria; in their natural habitats their frequently blue and yellow coloration may function in camouflage when viewed from afar against a reef or open blue water (Marshall, 2000). Larval fishes inhabiting the epipelagic are often transparent. Many juvenile and adult fishes of the upper waters, particularly schooling species, are silvery with a dark dorsal surface (McFall-Ngai, 1990). This countershading is cryptic when viewed either from above against darker deeper waters or from below against downwardly directed sunlight. Additionally, the orientations of their silvery reflecting scales on laterally flattened bodies that may taper ventrally (e.g., herring) further aid in hiding in the light filled environment of the epipelagic (Denton, 1970).

In the upper mesopelagial, numerous fishes are also largely transparent or silvery with dark dorsal surfaces. Many have broad vertical ranges, as they make regular upward movements (diel vertical migrations) to the epipelagic zone at night to feed. Light in their environment will change from that of their daytime depth regime as they swim upward in the late afternoon, perhaps encounter night-time downwelling light from a full moon, and then return to their daytime depths. Predators of the epipelagial, which largely rely on vision for prey detection and are not as active at night when migrators reach the upper portions of their ranges, may be the driving force behind these vertical movements (Robison, 2003). Some transparent mesopelagic fishes can darken their coloration at night by varying the distribution of the dark melanin pigment within their melanophores (Badcock, 1969).

The fish inhabitants found at increasing depths are less likely to migrate into well-lit waters. Lower mesopelagic and bathypelagic fishes often lack silvery scales and have black, brown, or reddish colorations. Pigments that do not reflect the blue light of bioluminescence will appear black and thus provide camouflage in this dark environment (Clarke and Denton, 1962).

Many deep-sea fishes are bioluminescent (Herring and Morin, 1978), even though light production would seem to make them stand out in their dark world. Indeed, this might be so for those species that utilize bioluminescence either to attract prey or conspecifics or to escape predation. The photophores of many mesopelagic and bathypelagic fishes are, however, arranged in rows along the ventral surface of the animal. These are thought to provide counterillumination by producing light that is similar to the ambient light in color, intensity, and angular dispersion (e.g., Denton et al., 1972; Case et al., 1977; Young and Roper, 1977; Denton et al., 1985), which, like countershading, renders the fish less visible when viewed from below against a background of downwelling light. Photophores near the eyes may enable some species to fine tune the match of their bioluminescence with the ambient light (Lawry, 1974; Herring, 1977). Photosensitive cells in the pineal complex of deep-living fishes (McNulty, 1976; McNulty and Nafpaktitis, 1976; McNulty and Nafpaktitis, 1977) occur under a window in the skull between the eyes and may also monitor the intensity of the downwelling light (Young et al., 1979). The ability to counterilluminate effectively may influence the upper daytime depth limits of mesopelagic organisms (Young et al., 1980).

The visual systems of the inhabitants must also be considered when discussing roles of bioluminescence in a region. The eyes of deep-sea fishes are quite varied and have been the subject of many studies (see Douglas et al., 1998; Wagner et al., 1998; and Herring, 2002 for recent reviews). The relatively large eyes of epipelagic fishes afford them high visual acuity. The retinas of these laterally-directed eyes contain two types of receptors: cones and rods, the latter assuming importance during periods of reduced light. The presence of different types of receptor cells containing visual pigments reactive to different wavelengths of light gives these fishes sensitivity to the many colors present in their well-lit environment (Herring, 2002). The eyes of many deep-sea fishes are also large but exhibit much variation related to differences in their visual environment. The retinas of the vast majority of these species contain only rods with one photopigment maximally sensitive to wavelengths in the range of bioluminescence rather than the blue of downwelling sunlight (Herring, 2002). The requirement of sensitivity outweighs that of acuity, and many deep-sea fish eyes collect as much light as possible from their dim environment. Often an aphakic space is present between the lens and the iris in the front of the eye (Nicol, 1978; Herring, 2002). Such cases of the pupil being larger than the lens allows light to strike the retina without passing through the lens and thus increases the chances of detection of light from obliquely placed sources (Denton, 1990). Additionally, the visual fields of a pair of aphakic eyes may overlap, resulting in binocular vision (Herring, 2002). Binocular vision is also possible with tubular eyes (Herring, 2002), which may be directed either upward or forward. This type of eye permits enlargement of the lens, which gathers the minimal light available and focuses it on a small area of retina. An upwardly directed eye might see prey silhouetted against the downwelling sunlight. Those fishes with forwardly directed tubular eyes may hang vertically in the water column (Herring, 2002).

Eye size tends to decrease in the fishes of the lower mesopelagic and bathypelagic zones. Warrant (2000), however, argues against the commonly held notions that the eyes of bathypelagic fishes are degenerate or regressed compared to those of the shallower deep-sea fishes. Instead, he notes that their eyes, although small, have relatively large pupils and other adaptations that are "quite adequate for seeing bioluminescent flashes up to several tens of metres away." Because these fishes are not well-muscled swimmers, such visual limits allow detection and localization of bioluminescence flashes within ranges they could cross for capture of prey or encountering a mate.

The acoustico-lateralis system of fish functions in electroreception (in sharks and their relatives), mechanoreception, and proprioception. Sound production is scarce in the midwaters, but is thought to be relatively common among benthopelagic fishes (Marshall, 1979). Midwater fishes show variation in their lateral line systems, the neuromasts of which may be free-standing and, thus, fully exposed or housed in mucus-filled canals (Marshall, 1980; Herring, 2002). Free neuromasts, which may be mounted on stalks or even at the end of filaments, occur on the heads, bodies, or tails of some species and are more a feature of slow moving bathypelagic fishes. Mesopelagic fishes are more likely to have neuromasts on their heads or along their lengths in a series of canals, which dampen the sensations caused by their own body movements. The main function of the lateral line as a whole is likely detection of near by movements (e.g., other fish in a school or potential predators or prey (Herring, 2002)). Greater differences in signal along the length of the lateral line may be related to the elongate shapes of many deep-sea fishes (Herring, 2002). The semicircular canals of the system are quite large in some bathypelagic fishes, which lack light cues for orientation (Montgomery and Pankhurst, 1997).

Although some midwater fishes are either synchronous or sequential hermaphrodites, in many species the sexes are separate (Herring, 2002). Olfaction is believed important in mate location in the dioecious species. A difference in the degree of development of the olfactory lamellae, as well as the olfactory nerves, bulbs, and forebrain, between males and females occurs in many bathypelagic fishes (Marshall, 1967; Herring, 2002). Olfactory receptors of these males increase in size and complexity (become macrosmatic), whereas in the females the receptors may regress (become microsmatic). Thus, in sexually dimorphic species pheromones might be important for mate location (Marshall, 1980). If pheromones are present, the search time for a male to find a female may be reduced to hours rather than days in the well-dispersed fishes of the midwaters (Jumper and Baird, 1991). In some species, both the males and females become microsmatic, leaving vision as the most likely means of locating a mate (Baird and Jumper, 1993). Herring (2000) suggested that for many deep-sea fishes bioluminescence and vision become important after detection of a long-range chemical cue and before close-range mechanosensory identification.

Food density decreases with depth; abundances of fishes and invertebrates diminish with increasing depth. The ability to consume any potential food item encountered is more important as encounters become scarcer. Many deeper living species have larger mouths relative to their body size with large entrapping teeth in addition to well-developed pharyngeal baskets for capture of small items (Ebeling and Cailliet, 1974; Herring, 2002). At an extreme, the black swallower, *Chiasmodon niger*, is capable of consuming fishes larger than itself (Marshall, 1980).

The body compositions of deeper living midwater fishes change. Species of the upper mesopelagic tend to have better developed bones and musculature and reduced body densities due to the presence of either gas-filled swimbladders or high lipid contents (Denton and Marshall, 1958; Marshall, 1960; Butler and Pearcy, 1972; Bone, 1973; Childress and Nygaard, 1973). Their neutral lipids consist largely of either triacylglycerols, the usual form of stored lipids in vertebrates, or lower density wax esters (Nevenzel et al., 1969; Kayama and Ikeda, 1975; Sargent et al., 1976; Sargent, 1978; Nevenzel and Menon, 1980; Neighbors and Nafpaktitis, 1982; Reinhardt and Van Vleet, 1986; Neighbors, 1988). Many of these fishes make diel vertical migrations of over hundreds of meters distance. Deeper-living species without functional swimbladders generally have less well developed skeletal, muscular, and circulatory systems in their flabby, watery bodies (Blaxter et al., 1971; Childress and Nygaard, 1973; Yancey et al., 1989; Yancey et al., 1992). Inconsistencies in the decrease of lipid and protein contents in species living at greater depths have been attributed to regional differences in constancy of food availability or visual predation (Bailey and Robison, 1986; Stickney and Torres, 1989; Childress et al., 1990; Donnelly et al., 1990).

Near the seafloor of even the world's deepest oceans, one finds that the fishes are typically much larger, more substantial, and usually more active than those of the overlying midwaters. Because the fish need not hang in midwaters, their tissues are generally not as watery or as flaccid, and their skeletal bones are more strongly developed. Although some species apparently do maintain their neutral buoyancy via some tissue reduction or have oily livers, most have functional physoclistous swimbladders. These bottom (benthic) and near-bottom (demersal or benthopelagic) fishes also generally lack photophores and are rarely bioluminescent, and, yet have well-developed eyes. They collectively feed on a diversity of prey, and the various Atlantic Ocean species have been classified into ten guilds (Gartner et al. 1997). By the definitions of those guilds, the abundant benthic and demersal species off California would be classified mostly as piscivores, macronekton foragers, micronekton/epibenthic predators, or specialist necrophages.

Many deep-sea benthopelagic fishes share the peculiar, apparently convergent, body form of a relatively long tail with a continuous anal fin of many rays that tapers to a fine tip. Marshall (1971a) dubbed them "rat-tailed" fishes and suggested that one function of the tail might be accentuation of the acoustico-lateralis system for prey and predator detection. If present, the caudal fin is indistinct or confluent with the anal and dorsal fins at the end of the tail, producing a rounded tip. The tapered tail of some benthic species is likely useful for burrowing into the sediment to lay eggs or to hide from predators.

General differences in the characteristics of fishes from the epipelagic through the benthopelagic regions of the open ocean are summarized in table 13-1.

Physical Features of the Deep Sea Off the Californias

Geologic Features

Geologic features determine water depth and thus influence the distribution of deep-sea fishes near the edges of continents as well as along the seafloor. The continental shelf, the edge of the continent under 200 m or less of water (Duxbury, 1971), north of Point Arguello, California (34° 35′ N), and south of Cedros Island, Mexico (28° 20′ N), is relatively broad and flat like other continental shelves (Uchupi and Emery, 1963). In the Southern California Bight, the continental borderland, a region with islands and deep basins, lies seaward of the shelf (fig. 13-1, Uchupi and Emery, 1963). The shelves of the mainland and around the islands of the borderland are narrow (Uchupi and Emery, 1963). Over 20 basins pit the borderland (Emery, 1960; Krause, 1965). Sills, the submerged elevations that separate basins (Sverdrup et al., 1942), and floors of the 13 northern basins (fig. 13-2) range from about 475 to 1,900 m and 625 to 2,570 m in depth, respectively (Emery, 1960). Areas of these basins at sill depth range from approximately 135 to 1,175 km^2 (Emery, 1960). The basin floors are typically silty-clay sediments, containing organic material and many infaunal species, chiefly polychaetes. In the Santa Catalina Basin, sediment organic carbon is near 55 mg C g^{-1} sediment with total macrofaunal abundance near 10,000 individuals m^{-2} (Smith et al., 1983). Tidally caused near-bottom currents generally travel at less than 5 cm sec^{-1} (Wilson, unpub.), and a zone of suspended particulates, the nepheloid layer, rises to about 50 m above the bottom.

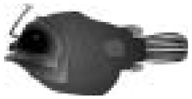
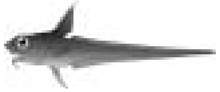
Seaward of the continental shelf or borderland, the continental slope descends to the deep-sea rise, which joins the ocean basin floor. North of Point Conception, the continental slope at first descends gently from the continental shelf to a depth of about 600 m, forming a plateau. Three deep-sea fans constituting the deep-sea rise at the base of this slope join the abyssal floor at about 4,000 m. Seaward of the borderland, the slope, as the Patton Escarpment, descends steeply to a depth of about 3,400 m. Off Cedros Island, the slope descends from the shelf to the Cedros Trench, which is up to 1,000 m deeper than the adjoining 3,600 m deep abyssal floor (Uchupi and Emery, 1963).

Rolling abyssal hills appear at the base of the Patton Escarpment, approximately 325 km west of San Diego. The seafloor there remains layered with sediments of silty clay, but organic content falls to about 10 mg C g^{-1} sediment (Smith et al., 1983); macrofaunal abundance drops 20% from that of the Santa Catalina Basin. Near-bottom currents are once again tidal at <5 cm sec^{-1} (Wilson and Smith, 1984). Proceeding west into the Pacific Basin, manganese nodules become prevalent features of the seafloor, but the sediments remain silty clay. Sediment organic carbon continues to drop slightly, but by 4,400 m depth, *ca*. 720 km west of San Diego, total macrofaunal abundance is only 1,000 individuals m^{-2}, one-tenth of that in the Santa Catalina Basin (Smith et al., 1983).

Submarine canyons, deep cuts in the continental slope that may extend into or cross the adjoining shelves (Emery, 1960), of various sizes occur along the length of California and Baja

TABLE 13-1

General Characteristics of Pelagic Oceanic Fishes by Vertical Zone

		Characteristics					
Appearance	*Pelagic Zone*	*Size*	*Shape*	*Musculature*	*Eye*	*Coloration*	*Bioluminescence*
	Epipelagic	Wide size range, from small to large	Varied, mainly fusiform, some elongate and laterally compressed	Strong dense muscles, fast swimming	Large eyes	Countershading, dark back and white or silver belly	Bioluminescence uncommon
	Mesopelagic (vertical migrators)	Small	Relatively elongate and/or laterally compressed	Moderately strong muscles	Very large, sensitive eyes	Black or black with silver sides and belly	Bioluminescence common, often used for counter-illumination
	Mesopelagic (non-migrators)	Small	Relatively elongate and/ or laterally compressed	Weak, flabby muscles	Very large, sensitive eyes, sometimes tubular eyes	Black or black with silver sides and belly	Bioluminescence common, often used for counter-illumination
	Bathypelagic	Small	Elongate, often globular in shape	Weak, flabby muscles	Eyes small or absent	Black, occasionally red	Bioluminescence common, often used to attract prey
	Benthopelagic	Relatively large	Very elongated	Strong muscles	Eyes varied, small to relatively large	Dark brown or black	Only a few groups bioluminescent

NOTE: After Castro and Huber, 1997.

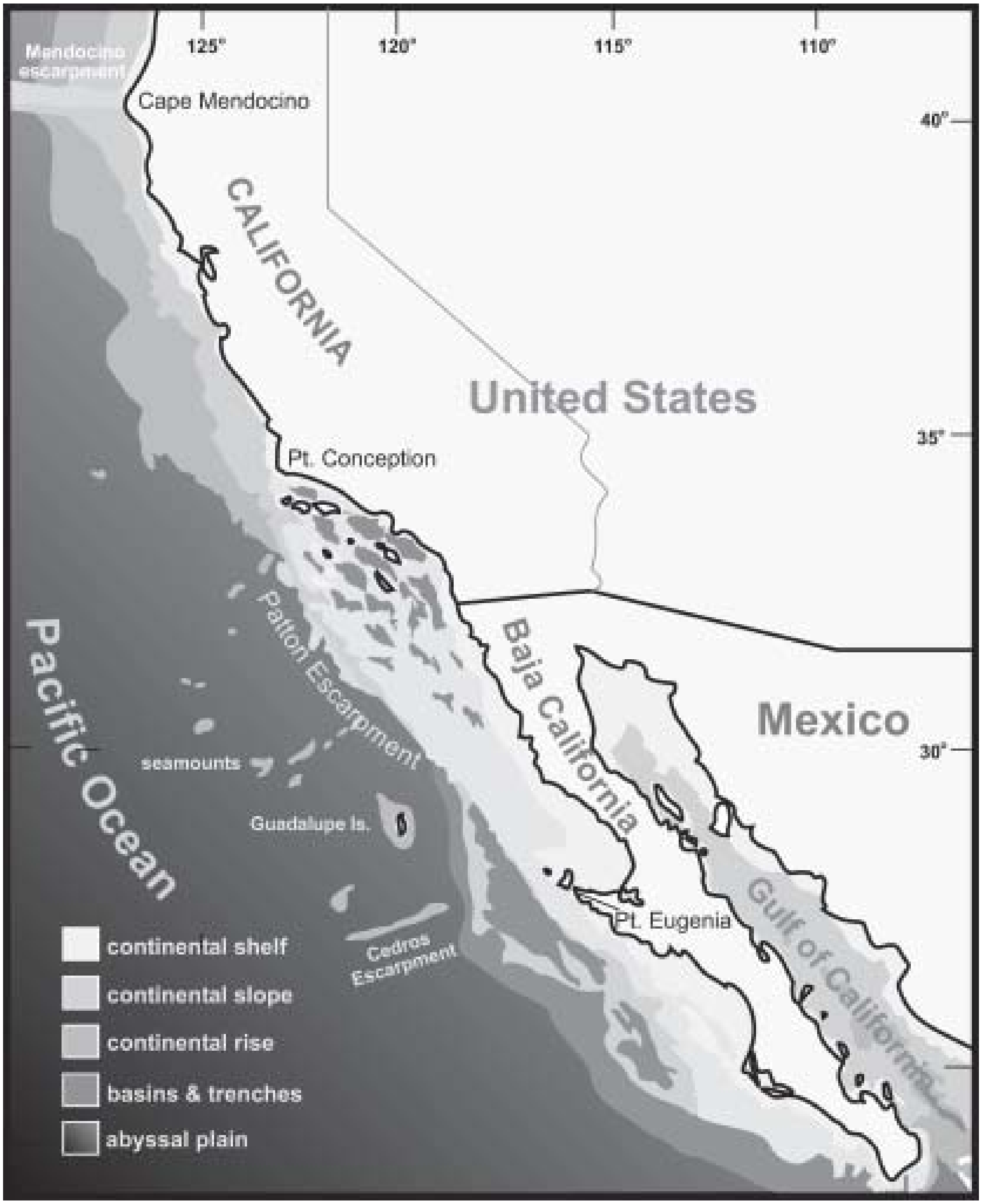


FIGURE 13-1 The seafloor off California (after Uchupi and Emery, 1963).

California (Uchupi and Emery, 1963). Four of these (Monterey, Arguello, Scripps, and Coronados canyons) are considered to be among the major submarine canyons of the world (Duxbury, 1971). Monterey and Scripps canyons in particular bring midwater species closer to shore.

Water depth limits the inshore occurrence of pelagic deep-sea fishes. Mesopelagic fishes may require water deeper than 200 or 300 m (Pearcy, 1964; Hulley, 1992). Depths over 183 m (100 fm contour on charts) occur within 20 km of the coast between Cape Mendocino, California (40° 30′ N), and Pt. Colnett, Baja California (30° 50′ N). Areas deeper than 914 m (500 fm contour) may be within 40 km of shore. In the Southern California Bight, the shallower inshore Santa Barbara, Santa Monica, and San Pedro basins have bottom depths of 627, 938, and 912 m, respectively (Emery, 1960), and thus provide habitats for lanternfishes and other deep-sea families relatively near shore.

Water Types and Currents

The complex of water types found off the coasts of California and Baja California influences the diversity of deep-sea fishes in midwaters. From the north Pacific Ocean, the Subarctic water mass adds water of relatively low temperature, low salinity, high dissolved oxygen, and high phosphate content (Reid

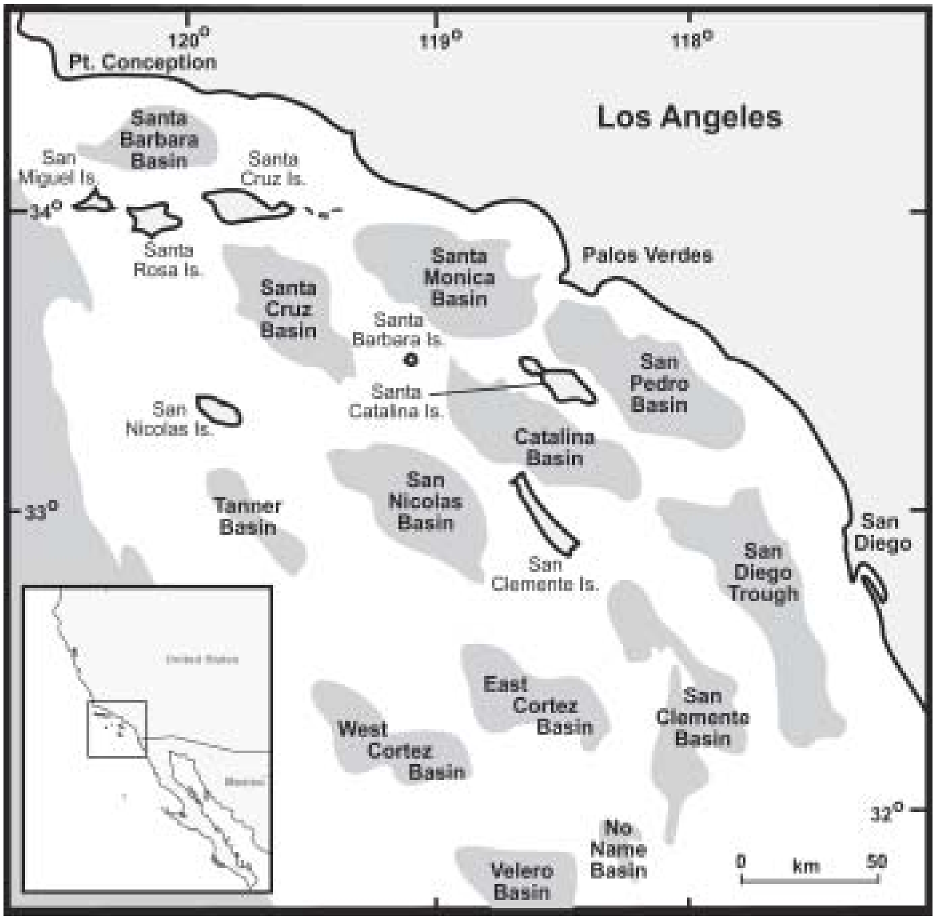


FIGURE 13-2 Thirteen northern basins of the Southern California Bight (after Hickey, 1993).

et al., 1958). To the south is found the Pacific Equatorial water mass ("southern" water, Hickey, 1993), whose water is characterized by relatively high temperature and salinity and, as it moves up the coast of Baja California, low dissolved oxygen and high phosphate content (Sverdrup et al., 1942; Reid et al., 1958). A region of transition exists below 300 m between 22° N and 45° N where waters from these two masses mix (Sverdrup et al., 1942). To the west lies the eastern north Pacific central water mass, whose water is characterized by relatively warm temperatures, high salinity, low dissolved oxygen, and low surface-layer nutrients (Reid et al., 1958).

Currents off the west coast of North America change seasonally in their transport of water to both the south and the north. The California Current is a wide, slow-moving southeastward flow between 48° N and a southern limit of 23° N (Sverdrup et al., 1942). The western limit of the California Current is the boundary region between subarctic water and eastern north Pacific central water, which at 32° N is about 700 km from the coast (Sverdrup et al., 1942). Where a dividing front is less well-defined, the western edge is often set at 1,000 km offshore (Longhurst, 1998). Horizontal surface mixing with central water occurs on this westward edge as the California Current flows southward. The majority of the water movement to the south occurs between 200 and 500 km offshore, and maximum water speeds are shallower than 200 m (Hickey, 1993). Therefore, the upper waters of the transition area are more influenced by subarctic water than are waters below 100 m (Reid et al., 1958). The California Current consists of multiple regions of flow at most latitudes. South of Cape Blanco, Oregon (42° 50′ N), nearshore flow is most fully developed during spring and early summer, and the offshore region is strongest in the late summer or fall (Hickey, 1979). Near the coast, various counterflows replace or displace the nearshore southward current. North of Point Conception, counterflow occurs during fall and winter. The Southern California Countercurrent exists in the upper half of the Southern California Bight all year except during April and in the lower half of the bight from April to December (Hickey, 1979). This countercurrent may be continuous with the Davidson Current (see below), particularly during winter (Hickey, 1979).

The California Undercurrent carries equatorial water northward along Baja California and California over the slope and borderland (Hickey, 1979, 1993). North of Point Conception in late fall and winter, its core rises from 200–300 m to the surface and becomes known as the Davidson Current (Hickey, 1979). Further south, maximum flow occurs in summer and early fall (Hickey, 1979).

The waters trapped in the borderland basins below the sill depths are nearly isothermal, isohaline, and typically low in dissolved oxygen (i.e., <1 ml O_2 l^{-1}, Emery, 1954; Smith et al., 1983). The northwest gradient of increasingly higher temperatures of the bottom water in the basins indicates movement of this deep water from the southeast (Emery, 1954). In the outermost basins, bottom water comes from the open sea to the west. Thus, northward flowing Equatorial water predominates in the deeper water of the borderland basins. Shallower Subarctic water is carried into the region from the north by the California Current, and central water is more likely to be found in the outer basins. Within the basins, the lower boundary of the mesopelagic zone is marked by the presence of 50% Southern water, resulting in the interface between this zone and the bathypelagic being a band of mixed northern and southern waters. The bathypelagial is predominantly Southern water. Shallow Santa Barbara Basin contains no Southern water and, therefore, no true bathypelagic zone (Lavenberg and Ebeling, 1967).

Where offshore of the Californias are the boundaries of the deep sea that in turn define which species are the deep-sea fishes? The shallow boundary of the demersal deep sea is typically regarded as 1,000 m; below this depth no sunlight penetrates, resulting in permanent darkness. Weitzman (1997), however, included many fishes occurring as shallow as 500 to 600 m in his systematic review of deep-sea fishes, chiefly to include highly specialized mesopelagic species not typically caught below 1,000 m. Yet the mesopelagic zone is shallower than even 500 m. The bathypelagic zone is also considered to begin in the darkness near 1,000 m (Hedgpeth, 1957; Angel, 1997). In the borderland basins of southern California the thermocline marks the lower limit of the epipelagic zone (Lavenberg and Ebeling, 1967). The mesopelagic zone ranges from the thermocline at 50 m or deeper to the 6° C isotherm near 500 to 600 m, and the bathypelagic zone extends from there to near the sea bottom (Lavenberg and Ebeling, 1967).

Fitch and Lavenberg (1968) included 259 species from 71 families in their list of deep-sea teleosts, both pelagic and benthic, from off California. The 70 species collected in more than one pelagic trawl survey off the Californias listed in table 13-2 represent 18 common midwater families. Not all fishes occurring in the deep waters of the Californias were collected in these studies. Some are too large or too quick to be captured by relatively small pelagic trawls; others (e.g., the umbrellamouth gulper, *Eurypharynx pelacanoides*) must be so rare or widely distributed that they are not collected with limited sampling.

Assigning the shallow boundary of the deep sea to between 500 and 600 m for benthic fishes results in about 41 species typically encountered as deep or deeper in surveys of the California slope, continental rise, and abyss (table 13-3). However, some fishes that occur below those depths, such as the Pacific electric ray *Torpedo californica*, also range much shallower off California. In addition, a few species display high-latitude emergence (i.e., ranging into cold, relatively shallow, waters at high latitudes). A fish occurring below 500 to 600 m off California might be found in less than 100 m in the Bering Sea. Thus, the more precise definition of a deep-sea benthic fish would be a species that is virtually never taken shallower than about 500 to 600 m over its full geographic range. Applying that definition here, however, would omit discussion of some important species of the California slope that display high-latitude emergence. Nevertheless, we adopt Weitzman's (1997) view of benthic deep-sea fishes as those mostly inhabiting depths of 500 to 600 m and deeper, but generally not shallower, with the caveat that the shallow boundary applies to benthic fishes off California (i.e., between about 32° and 42° North latitude).

Midwater Fishes

Knowledge about the midwater fishes from off the Californias has largely been gained by collecting with midwater trawls, often of 3 m or less width. Initially trawling was done with a net that was always open. Improved ecological information was obtained when trawls were fitted with opening-closing devices. Since fishes become scarcer and trawling takes longer with increasing depth, most hauls have been made within the upper 1,000 m of the water column. Many types of investigations (e.g., systematics, distributions, feeding, reproduction, morphology, chemical composition, enzymic activities) have utilized fishes collected by trawls. Another approach to learning about the biology of these fishes is the collecting of living animals with trawls. Thermally protected cod ends (Childress et al., 1978) facilitate the capture of living specimens, and systems for maintaining caught animals in the laboratory (Robison, 1973a; McCosker and Anderson, 1976) have been considered. Laboratory investigations (Childress and Meek, 1973; Belman and Anderson, 1979; Belman and Gordon, 1979) have been successfully completed with two particularly hardy deep-sea fishes that often live after capture, the midwater eelpout, *Melanostigma pammelas*, and fangtooth, *Anoplogaster cornuta*.

Observations from manned submersibles (e.g., Barham, 1971) or via video cameras in ROVs (remotely operated vehicles, e.g., Robison, 1992; Newman and Robison, 1992; Robison, 1999, 2004) have allowed viewing of the midwater inhabitants and their behaviors at the depths where they live. Direct observations enhance rather than replace collections by nets, as Smith-Beasley (1992) concluded that trawls are suitable for systematic, medium-scale studies and submersibles are more effective for microscale studies, especially of gelatinous organisms. *In situ* experiments have been conducted from submersibles (e.g., Smith and Laver, 1981). Another approach to the study of these fishes within their habitat has utilized the reflection of sound waves of certain frequencies by these organisms, particularly if they possess gas filled organs such as swimbladders in fishes and floats in siphonophores. Usual features of the world's oceans are aggregations of organisms, deep scattering layers (DSLs), in the midwaters that produce layers of sound scattering on echosounders, and much study has centered upon the organisms causing and the vertical migrations of DSLs (e.g., Farquhar, 1971; Andersen and Zahuranec, 1977). Acoustic measurements have been used in conjunction with trawl collections to study midwater assemblages and their behaviors (e.g., Kalish et al. 1986; Pieper and Bargo, 1980). Acoustics are now able to be used for study of both community (Benoit-Bird and Au, 2001) and individual fish (Torgersen and Kaartvedt, 2001) movements.

Representative Families and Species

The epipelagic zone, as well as the continental shelf region, is populated by numerous species of fishes, many of which belong to families in the order Perciformes and other more derived orders. Weitzman (1997) lists 22 orders of fishes that include some members of the deep-sea fauna and notes that the bony fishes that exhibit evolutionary adaptations to deep regions are generally derived from the relatively primitive groups of teleosts rather than the more derived orders. Some of the many teleost orders commonly occurring in deep ocean midwaters include the Anguilliformes, Argentiniformes, Stomiiformes, Myctophiformes, Lophiiformes, and Beryciformes.

The order Anguilliformes contains families of midwater eels whose larvae are transparent leaf-shaped leptocephali. Within the Serrivomeridae, the sawtooth eel, *Serrivomer sector* (fig. 13-3),

TABLE 13-2

Family Representatives Collected by More Than One Midwater Trawl Survey Off California and Baja California

				Latitude (°North)								
				38–23	*37–36*		*35–33*					*30–19*
				CALIF. & BAJA CALIF.	MONTEREY BAY	MONTEREY BAY	SANTA BARBARA AREA	SANTA BARBARA AREA	SANTA BARBARA AREA	SAN PEDRO BASIN	SANTA CATALINA BASIN	BAJA CALIFORNIA
Order	*Family*	*Species [synonym]*	*Common Name*	a	b	c	d	e	f	g	h	i
Anguilliformes												
	Nemichthyidae		Snipe eels									
		Avocettina bowersii (Garman, 1899)		X								X
		Nemichthys scolopaceus Richardson, 1848 [*N. avocetta*]	Slender snipe eel	X					X	X	X	X
	Serrivomeridae		Sawtooth eels									
		Serrivomer sector Garman, 1899	Sawtooth eel	X					X	X	X	
Argentiniformes												
	Bathylagidae		Deep-sea smelts									
		Bathylagoides nigrigenys (Parr, 1931) [*Bathylagus nigrigenys*]	Blackchin blacksmelt									X
		Bathylagoides wesethi (Bolin, 1938) [*Bathylagus wesethi*]	Snubnose blacksmelt	X	X	X			X	X	X	X
		Bathylagus pacificus Gilbert, 1890	Pacific blacksmelt, slender blacksmelt	X	X							
		Leuroglossus stilbius Gilbert, 1890 [*Bathylagus stilbius, L. stilbius stilbius*]	California smoothtongue	X	X	X	X	X	X	X	X	
		Lipolagus ochotensis (Schmidt, 1938) [*Bathylagus ochotensis*]	Popeye blacksmelt, eared blacksmelt	X		X		X	X	X		
		Pseudobathylagus milleri (Jordan & Gilbert, 1898) [*Bathylagus milleri*]	Robust blacksmelt, stout blacksmelt	X	X			X	X	X	X	
	Opisthoproctidae		Barreleyes or spookfishes									
		Bathylychnops exilis Cohen, 1958	Javelin spookfish		X					X		
		Dolichopteryx longipes (Vaillant, 1888)	Brownsnout spookfish	X					X	X		
		Macropinna microstoma Chapman, 1939	Barreleye	X					X	X	X	
	Alepocephalidae		Slickheads									
		Bajacalifornia burragei Townsend and Nichols, 1925	Sharpchin slickhead						X		X	
		Talismania bifurcata (Parr, 1951)	Threadfin slickhead	X	X					X	X	

TABLE 13-2 (continued)

				Latitude (°North)								
				38–23	*37–36*		*35–33*					*30–19*
				CALIF. & BAJA CALIF.	MONTEREY BAY	MONTEREY BAY	SANTA BARBARA AREA	SANTA BARBARA AREA	SANTA BARBARA AREA	SAN PEDRO BASIN	SANTA CATALINA BASIN	BAJA CALIFORNIA
Order	*Family*	*Species [synonym]*	*Common Name*	a	b	c	d	e	f	g	h	i
	Platytroctidae		Tubeshoulders									
		Holtbyrnia macrops Maul, 1957	Bigeye searsid	?					X	X		
		Holtbyrnia melanocephala (Vaillant, 1888)							X	X		
		Mentodus facilis (Parr, 1951) [*Pellisolus facilis*]		X	X				X	X		
		Sagamichthys abei Parr, 1953	Shining tubeshoulder	X	X				X	X	X	
Stomiiformes												
	Gonostomatidae		Bristlemouths									
		Cyclothone acclinidens Garman, 1899	Benttooth bristlemouth	X	X	X		X	X	X	X	X
		Cyclothone pallida Brauer, 1902 [*C. canina*]	Tan bristlemouth	X	X				X		X	
		Cyclothone signata Garman, 1899	Showy bristlemouth	X	X	X	X	X	X	X	X	X
	Sternoptychidae		Hatchetfishes									
		Argyropelecus affinis Garman, 1899 [*A. pacificus*]	Slender hatchetfish, Pacific hatchetfish	X	X	X		X	X	X	X	X
		Argyropelecus hemigymnus Cocco, 1829 [*A. heathi, A. intermedius*]	Spurred hatchetfish, half-naked hatchetfish	X				X	X	X	X	X
		Argyropelecus lychnus Garman, 1899 [*A. lychnus lychnus*]	Tropical hatchetfish	X	X		X	X	X	X	X	X
		Argyropelecus sladeni Regan, 1908 [*A. hawaiensis*]	Lowcrest hatchetfish, Sladen's hatchetfish	X	X	X			X		X	
		Danaphos oculatus (Garman, 1899)	Bottlelight	X	X	X		X	X	X	X	X
		Sternoptyx diaphana Hermann, 1781	Diaphanous hatchetfish	X	X				X	X		
		Sternoptyx obscura Garman, 1899			X						X	X
	Phosichthyidae		Lightfishes									
		Ichthyococcus irregularis Rechnitzer and Böhlke, 1958	Bulldog lightfish	X			X		X			
		Vinciguerria lucetia (Garman, 1899)	Panama lightfish	X	X				X	X	X	X
	Stomiidae		Barbeled dragonfishes									
		Aristostomias scintillans (Gilbert, 1915)	Shining loosejaw	X	X		X		X	X	X	

		Bathophilus flemingi Aron and McCrery, 1958	Highfin dragonfish	X	X			X	X	X	X	
		Borostomias panamensis Regan and Trewavas, 1929	Panama snaggletooth	X							X	
		Chauliodus macouni Bean, 1890	Pacific viperfish	X	X	X	X	X	X	X	X	
		Idiacanthus antrostomus Gilbert, 1890	Pacific blackdragon	X	X	X	X		X	X	X	X
		Photonectes margarita (Goode and Beane, 1896)		X				X				
		Stomias atriventer Garman, 1899	Blackbelly dragonfish	X					X	X	X	X
		Tactostoma macropus Bolin, 1939	Longfin dragonfish	X	X	X	X		X	X		
Aulopiformes												
	Scopelarchidae		Pearleyes									
		Benthalbella dentata (Chapman, 1939)	Northern pearleye	X					X	X		
		Benthalbella linguidens (Meade and Böhlke, 1953)	Longfin pearleye						X	X		
	Paralepididae		Barracudinas									
		Lestidiops ringens (Jordan and Gilbert, 1880) [*Lestidium ringens*]	Slender barracudina	X	X				X	X		
Myctophiformes												
	Neoscopelidae		Blackchins									
		Scopelengys tristis Alcock, 1890	Pacific blackchin	X		X			X	X	X	X
	Myctophidae		Lanternfishes									
		Ceratoscopelus townsendi (Eigenmann and Eigenmann, 1889)	Dogtooth lampfish	X				X		X	X	X
		Diaphus anderseni Tåning, 1932	Andersen's lantern fish	?				X				X
		Diaphus theta Eigenmann and Eigenmann, 1890 [*D. protoculus*]	California headlightfish	X	X	X	X	X	X	X	X	
		Diogenichthys atlanticus (Tåning, 1928)	Longfin lanternfish	X		X		X	X	X	X	X
		Diogenichthys laternatus (Garman, 1899)	Diogenes lanternfish	X				X		X		X
		Lampadena urophaos Paxton, 1963	Sunbeam lampfish	X						X		
		Lobianchia gemellarii (Cocco, 1838) [*Diaphus nipponensis*]	Cocco's lanternfish	X				X				
		Nannobrachium regale (Gilbert, 1892) [*Lampanyctus regalis*]	Pinpoint lampfish	X	X	X			X	X	X	
		Nannobrachium ritteri (Gilbert, 1915) [*Lampanyctus ritteri*]	Broadfin lampfish	X	X	X	X	X	X	X	X	
		Notolychnus valdiviae (Brauer, 1904)	Topside lampfish	X				X				
		Parvilux ingens Hubbs and Wisner, 1964	Giant lampfish	X					X	X	X	
		Protomyctophum crockeri (Bolin, 1939) [*Hierops crockeri*]	California flashlightfish	X	X	X	X	X	X	X	X	X
		Stenobrachius leucopsarus (Eigenmann and Eigenmann, 1890) [*Lampanyctus leucopsarus*]	Northern lampfish	X	X	X	X	X	X	X	X	
		Symbolophorus californiensis (Eigenmann and Eigenmann, 1889)	California lanternfish, bigfin lanternfish	X	X			X	X	X	X	
		Taaningichthys bathyphilus (Tåning, 1928)		X						X		X
		Tarletonbeania crenularis (Jordan and Gilbert, 1880)	Blue lanternfish	X	X	X	X	X	X	X	X	
		Triphoturus mexicanus (Gilbert, 1890) [*Lampanyctus mexicanus*]	Mexican lampfish	X			X	X	X	X	X	

TABLE 13-2 (continued)

				Latitude (°North)								
				38–23	37–36		35–33					30–19
				CALIF. & BAJA CALIF.	MONTEREY BAY	MONTEREY BAY	SANTA BARBARA AREA	SANTA BARBARA AREA	SANTA BARBARA AREA	SAN PEDRO BASIN	SANTA CATALINA BASIN	BAJA CALIFORNIA
Order	*Family*	*Species [synonym]*	*Common Name*	a	b	c	d	e	f	g	h	i
Lophiiformes												
	Oneirodidae		Dreamers									
		Oneirodes acanthias (Gilbert, 1915)	Spiny dreamer	?					X	X	X	
		Oneirodes eschrichtii Lütken, 1871	Bulbous dreamer	X						X		
Beryciformes												
	Melamphaidae		Bigscales					X				
		Melamphaes acanthomus Ebeling, 1962	Slender bigscale	X					X	X	X	
		Melamphaes lugubris Gilbert, 1891	Highsnout bigscale or melamphid	X					X	X	X	
		Melamphaes parvus Ebeling, 1962	Little bigscale	X								X
		Poromitra crassiceps (Günther, 1878)	Crested bigscale	X	X				X	X	X	
		Scopeloberyx robustus (Günther, 1887)	Longjaw bigscale	X							X	
		Scopelogadus mizolepis bispinosus (Gilbert, 1915) [*Melamphaes bispinosus*]	Twospine bigscale	X	X				X	X	X	X
	Anoplogastridae		Fangtooths									
		Anoplogaster cornuta (Valenciennes, 1833)	Fangtooth	X					X	X	X	X
Perciformes												
	Zoarcidae		Eelpouts									
		Lycodapus mandibularis Gilbert, 1915	Pallid eelpout		X	X						
		Melanostigma pammelas Gilbert, 1896	Midwater eelpout	X	X	X			X	X	X	

Sources and collecting gear:

[a] Berry and Perkins (1966): 3 m IKMT, 3 m × 4.3 m collapsible midwater beam trawl, 1.5 m × 1.5 m nekton net, 21m × 24m, *Cobb* Mark II pelagic trawl
[b] Anderson et al. (1979): 1.8 m modified opening-closing Tucker Trawl
[c] Smith-Beasley (1992): modified 1.8 m.opening-closing RMT
[d] Best and Smith (1965): intermediate-sized midwater trawl with 3.3 m^2 mouth
[e] Pieper (1967): instrumented 1.8 m IKMT with 4 chamber cod end. Trawls 36–45 in modified Subarctic region.
[f] Brown (1974): instrumented 1.8 m IKMT with 4 chamber cod end
[g] Lavenberg and Ebeling (1967) and Paxton (1967a): 3 m IKMT
[h] Rainwater (1975): 1.8 m opening-closing modified Tucker trawl
[i] Wisner (1962): 3 m IKMT

NOTE: Species synonyms used in cited literature are in brackets (Eschmeyer 1998, on-line version May 10, 2004, www.calacademy.org/research/ichthyology). Common names from Moser (1996a) and Froese and Pauly (2003).

TABLE 13-3

Common Benthic and Benthopelagic Fishes Below 500 to 600 m on the California Slope and in the Eastern North Pacific Ocean Basin

Order	*Family*	*Species*	*Common Name*	*Principal Depth Range off California (m)*
Myxiniformes				
	Myxinidae			
		Eptatretus deani	Black hagfish	107–2,743
Carcarhiniformes				
	Scyliorhinidae			
		Apristurus kampae	Longnose cat shark	367–1,888
		Parmaturus xaniurus	Filetail cat shark	327–936
Squaliformes				
	Dalatiidae			
		Centroscyllium nigrum	Combtooth dogfish	400–1,143
		*Somniosus pacificus**	Pacific sleeper shark	1,044–2,000
Rajiformes				
	Rajidae			
		Bathyraja abyssicola	Deep-sea skate	644–2,910
		Bathyraja trachura	Black skate	565–1,993
Argentiformes				
	Alepocephalidae			
		*Alepocephalus tenebrosus**	California slickhead	327–1,253
		Talismania birfurcata	Threadfin slickhead	584–2,000
Aulopiformes				
	Synodontidae			
		Bathysaurus mollis	Highfin lizard fish	1,680–4,900
Ophidiiformes				
	Aphyonidae			
		Barathronus pacificus		3,334–3,860
	Ophidiidae			
		Lamprogrammus niger	Paperbone cuskeel	797–2,000
		Spectrunculus grandis	Pudgy cuskeel	800–4,255
Gadiformes				
	Merlucciidae			
		*Merluccius productus**	Pacific whiting	181–1,205
	Moridae			
		Antimora microlepis	Pacific flatnose	335–3,048
	Macrouridae			
		Coryphaenoides acrolepis	Pacific grenadier	600–2,500
		Coryphaenoides armatus	Abyssal grenadier	2,000–4,300
		Coryphaenoides filifer	Threadfin grenadier	2,065–2,904
		Coryphaenoides leptolepis	Ghostly grenadier	2,000–3,860
		Coryphaenoides pectoralis	Giant grenadier	565–2,170
		Coryphaenoides yaquinae	Rough abyssal grenadier	3,600–6,400
		Echinomacrurus occidentalis		???–4,000
		Nezumia kensmithi	Bluntnose grenadier	500–???
		Nezumia liolepis	Smooth grenadier	681–2,825
		Nezumia stelgidolepis	California grenadier	285–800
Scorpaeniformes				
	Psychrolutidae			
		Psychrolutes phrictus	Blob sculpin	800–2,800
	Anoplopomatidae			
		*Anoplopoma fimbria**	Sablefish	181–2,740
	Liparidae			
		Careproctus cypselurus	Blackfinned snailfish	378–1,608
		*Careproctus gilberti**	Smalldisk snailfish	187–1,181
		*Careproctus melanurus**	Blacktail snailfish	200–2,286
		Paraliparis cephalus	Swellhead snailfish	604–1,384
		Rhinoliparis barbulifer		775–1,128
	Scorpaenidae (=Sebastidae)			
		*Sebastolobus alascanus**	Shortspine thornyhead	181–1,524
		*Sebastolobus altivelis**	Longspine thornyhead	409–1,757

TABLE 13-3 (continued)

Order	*Family*	*Species*	*Common Name*	*Principal Depth Range off California (m)*
Perciformes				
	Zoarcidae			
		Bothrocara brunneum	Two-line eelpout	432–1,253
		Lycenchelys crotalinus	Snakehead eelpout	392–1,236
		Lycodapus endemoscotus	Deepwater eelpout	555–2,122
		Lycodes diapterus	Black eelpout	242–1,007
		Lycodapus fierasfer	Black mouth eelpout	416–1,046
	Pleuronectidae			
		*Microstomus pacificus**	Dover sole	367–1,253
		Embassichthys bathybius	Deep-sea sole	416–1,433

*Shows high-latitude emergence

NOTE: Principal depth ranges determined from data in Lauth (1999), museum collection records, and various published accounts.

a silvery fish with elongate jaws and a saw-edged vomerine plate in the midline of the roof of its mouth, feeds primarily on crustaceans and occasionally small cephalopods and fishes (Fitch and Lavenberg, 1968). The blackline snipe eel, *Avocettina infans* (fig. 13-3), and its relatives in the Nemichthyidae have elongate bodies and long recurved jaws lined with many minute, posteriorly directed teeth, which Mead and Earle (1970) suggested ensnare the long antennae of the shrimp-like crustaceans, sergestids and their relatives, upon which they feed while hanging vertically in the water column. However, Gartner et al. (1997) reported snipe eels to be active predators. Males of the slender snipe eel, *Nemichthys scolopaceous*, were originally assigned to a different genus until Smith and Nielsen (1976) determined that nemichthyid males undergo a second metamorphosis at maturity, after which they have short jaws, no teeth, and tubular anterior nostrils, which presumably detect pheromones produced by the females.

Three deep-sea families within the Argentiniformes are the Bathylagidae, Alepocephalidae, and Platytroctidae. Bathylagids, or deep-sea smelts, are common mesopelagic fishes throughout the world's oceans. Three species regularly occurring in the waters off California are illustrated in fig. 13-4. The shallower, smaller members of this family (e.g., California smoothtongue, *Leuroglossus stilbius*, and snubnose blacksmelt, *Bathylagoides wesethi*) have a silvery countershaded pigmentation and large eyes, whereas deeper living species (e.g., Pacific blacksmelt, *Bathylagus pacificus*) still have large eyes but are darker, with larger and flabbier bodies. Slickheads (Alepocephalidae), which lack scales on their heads, are deep living, darkly pigmented species that may be mesopelagic to benthopelagic or abyssal. Their close relatives the midwater tubeshoulders (Platytroctidae), represented by the shining tubeshoulder, *Sagamichthys abei*, in fig. 13-4, are similar in appearance but able to bioluminesce with two types of light organs. In addition to their ventrally placed photophores, near their pectoral girdle and lateral line they have a shoulder organ or sac with an external tube through which luminous cells or particles can be expelled. This cloud of flickering light left behind a fish moving forward could aid in escape from a potential predator (Herring, 1972).

The order Stomiiformes includes four common oceanic families of mesopelagic or occasionally bathypelagic fishes; representatives of many of the genera are found worldwide. The arrangements of the photophores on the bodies of the various stomiiforms characterize the many subgroups (Weitzman, 1997), and typically consist of two rows on the ventral portion of the head and trunk regions and one row at the same level along the tail per side (Marshall, 1980). Some of the strangest looking fishes in this order belong to the family Sternoptychidae, the hatchetfishes, of which five representatives are illustrated in fig. 13-5. The bottlelight, *Danaphos oculatus*, is a small largely transparent mesopelagic species. The slender hatchetfish, *Argyropelecus affinis*, and the lowcrest hatchetfish, *A. sladeni*, are small silvery fishes that are laterally compressed and deep bodied anterior to the caudal peduncle, giving them the hatchet shape from which they derive their common names. Their narrow ventral surfaces are lined with photophores and their backs are darkly pigmented. These hatchetfishes have upwardly directed mouths and tubular eyes with yellow lenses (McFall-Ngai et al., 1986), which have been hypothesized to allow distinction of the bioluminescence of their counterilluminated invertebrate prey from background ambient light (Muntz, 1976; Somiya, 1976; Douglas et al., 1998). *Argyropelecus* spp. have been observed to swim downward diagonally, thus maintaining their horizontal body posture and the vertical orientation of their ventral photophores and tubular eyes (Janssen et al., 1986). The diaphanous hatchetfish, *Sternoptyx diaphana*, like its congeners, has an abdominal flap of transparent tissue, laterally directed eyes, and ventrally directed photophores. Photophores in the mouths of *Sternoptyx* species may improve counterillumination by enabling comparison of the ambient light and an animal's luminescence (Herring, 1977).

The family Gonostomatidae (bristlemouths) contains some of the most abundant marine fishes in the genus *Cyclothone*. These small, bioluminescent fishes may be mesopelagic (e.g., the transparent showy bristlemouth, *C. signata*, fig. 13-5) or bathypelagic (e.g., the darker benttooth bristlemouth, *C. acclinidens*, fig. 13-5). Their elongate mouths are lined with needlelike teeth. Females grow larger than the males, and the males become macrosmatic, which presumably allows them to locate pheromones produced by the females in the wide open, dark waters of their habitat (Marshall, 1967, 1980).

The fishes thus far discussed prey on invertebrates, largely crustaceans although some specialize on gelatinous species. In contrast, the family Stomiidae consists of many larger species

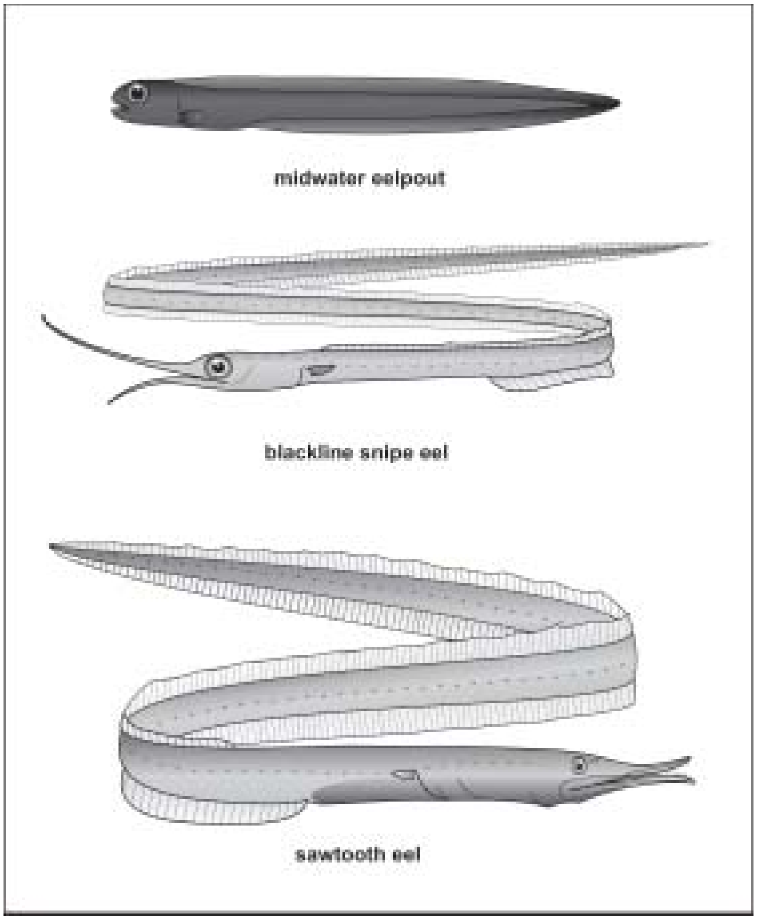


FIGURE 13-3. Representative midwater fishes: eel-like fishes.

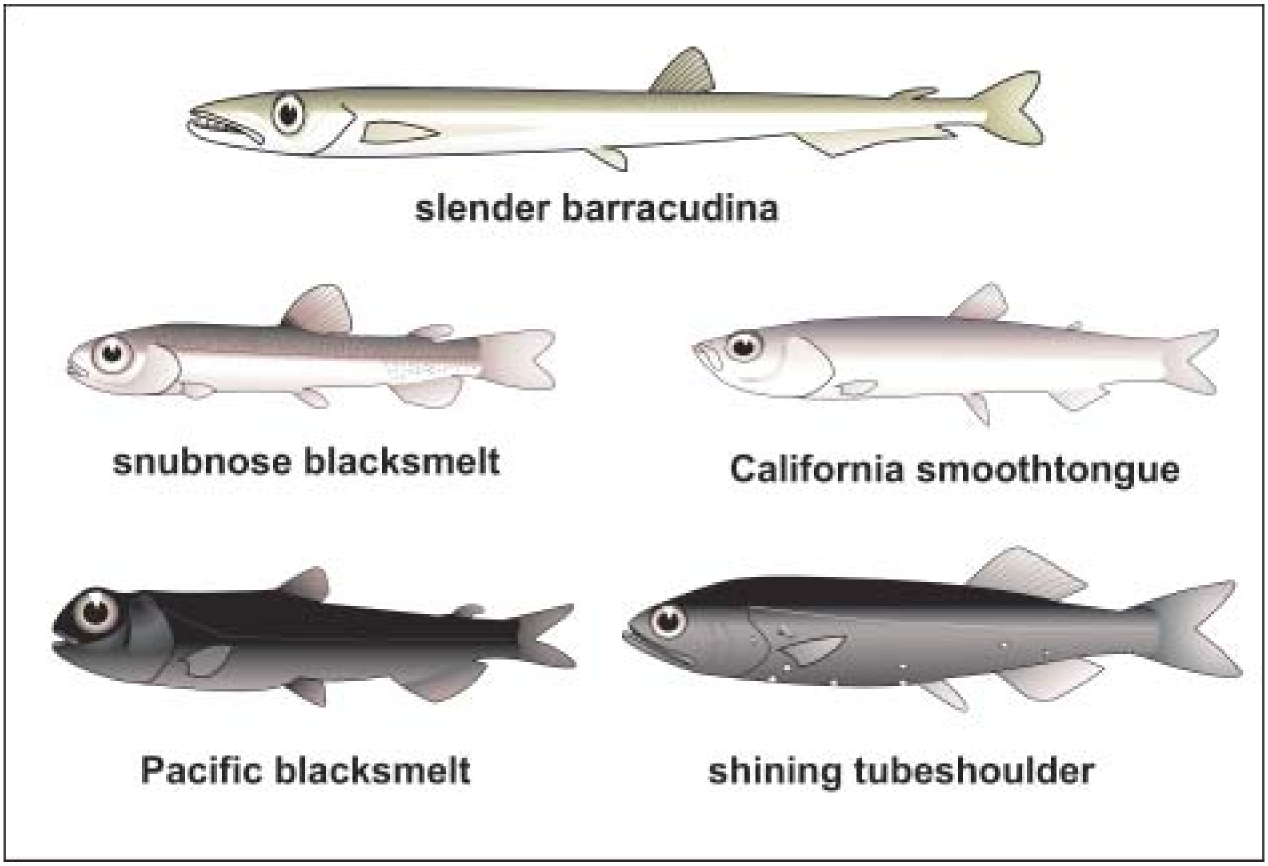


FIGURE 13-4. Representative midwater fishes: barracudina, deep-sea smelts, and tubeshoulder.

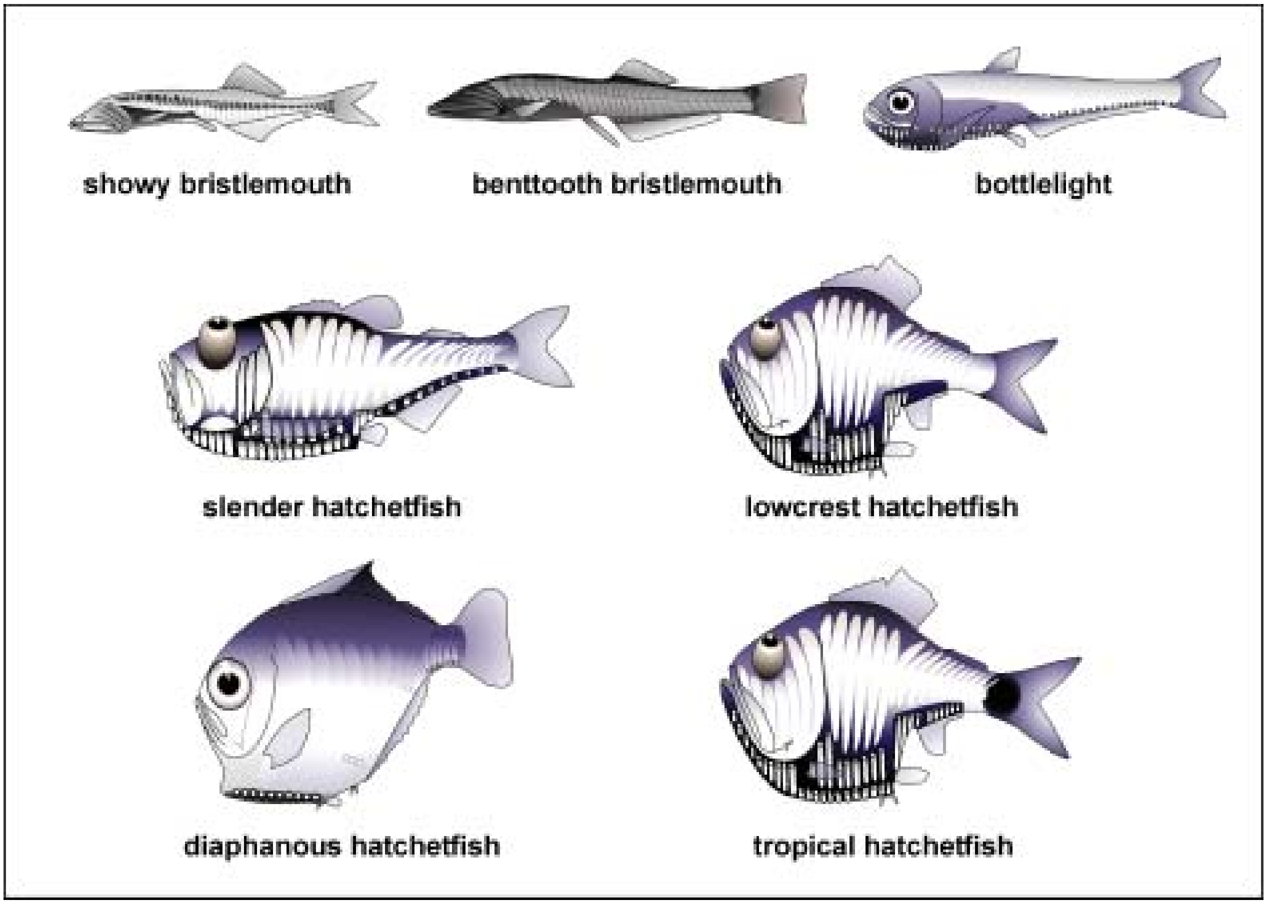


FIGURE 13-5. Representative midwater fishes: bristlemouths and hatchetfishes.

living in the mesopelagic zone (Marshall, 1980) that prey on other midwater fishes. Stomiids have ventral rows of photophores, large photophores below and behind the eyes, large elongate mouths with needle-like teeth, and often chin barbels that are tipped with a light organ lure. Viperfishes (e.g., Pacific viperfish, *Chauliodus macouni*, fig. 13-6), lack a chin barbel, but have an elongated dorsal fin ray with a luminous tip that could lure in prey for capture by teeth that are so long they do not fit within their mouths. In addition to their ventral and venterolateral rows of photophores, the elongate bodies of viperfishes and dragonfishes (e.g., the blackbelly dragonfish, *Stomias atriventer*, fig. 13-6) are enveloped in a gelatinous sheath that contains many small round red luminescent organs along the dorsal and ventral margins and on the fins of the fish. When lit, these cause the whole body outline to glow (O'Day, 1973). The Pacific blackdragon (*Idiacanthus antrostomus*, fig. 13-6) has a row of luminous tissue in chevron shaped patches along its back and rows of small patches of luminous tissue along its ventral surface and fin rays with which it can also outline its body with light (O'Day, 1973). Large blackdragons with chin barbels and teeth are females, as these features are absent in the much smaller pale-colored males, who lack a functional digestive tract (Marshall, 1954; Fitch and Lavenberg, 1968). The proportionately larger cheek photophore of the males may attract the females for mating (Marshall, 1954). In contrast to the dominant colors of bioluminescence in deep waters, the suborbital light organs of three stomiid genera produce far-red bioluminescence (Widder et al., 1984). Thus far the eyes of these species alone have been found to be sensitive to bioluminescence of this color (e.g., O'Day and Fernandez, 1974; Crescitelli, 1989; Douglas et al., 1998). These fishes, one of which is the shining loosejaw, *Aristostomias scintillans* (fig. 13-6), may be able to avoid detection while illuminating within a range of about 2 m (Partridge and Douglas, 1995) red crustaceans and other midwater fishes that have retinal pigments sensitive only to the predominantly blue and blue green wavelengths of ambient and most bioluminescent light.

The Myctophiformes contains the Myctophidae (lanternfishes), the most speciose family of midwater fishes. These fishes are common in the deep waters of all oceans. Fitch and Lavenberg (1968) list 33 species as occurring in the waters off California. Seven of these lanternfishes are shown in fig. 13-7. Like all but one lanternfish species, these have photophores arranged in species-specific patterns. The majority of the photophores are found along the fish's ventral surface, as are those of many other midwater fishes. Additionally, lanternfishes have photophores elevated on their sides to the level of or even above the lateral line. Well-developed photophores on the snout of *Diaphus theta* give it the common name of California headlightfish. Often species have luminescent organs on the caudal peduncle whose development probably coincides with sexual maturity (Paxton, 1972). In some species, (e.g., the northern lampfish, *Stenobrachius leucopsarus,* and the broadfin lampfish, *Nannobrachium ritteri*), these occur on both the dorsal and ventral surface with no differences between the sexes. In others, the caudal organs are sexually dimorphic; those of males are on the dorsal surface and those of females

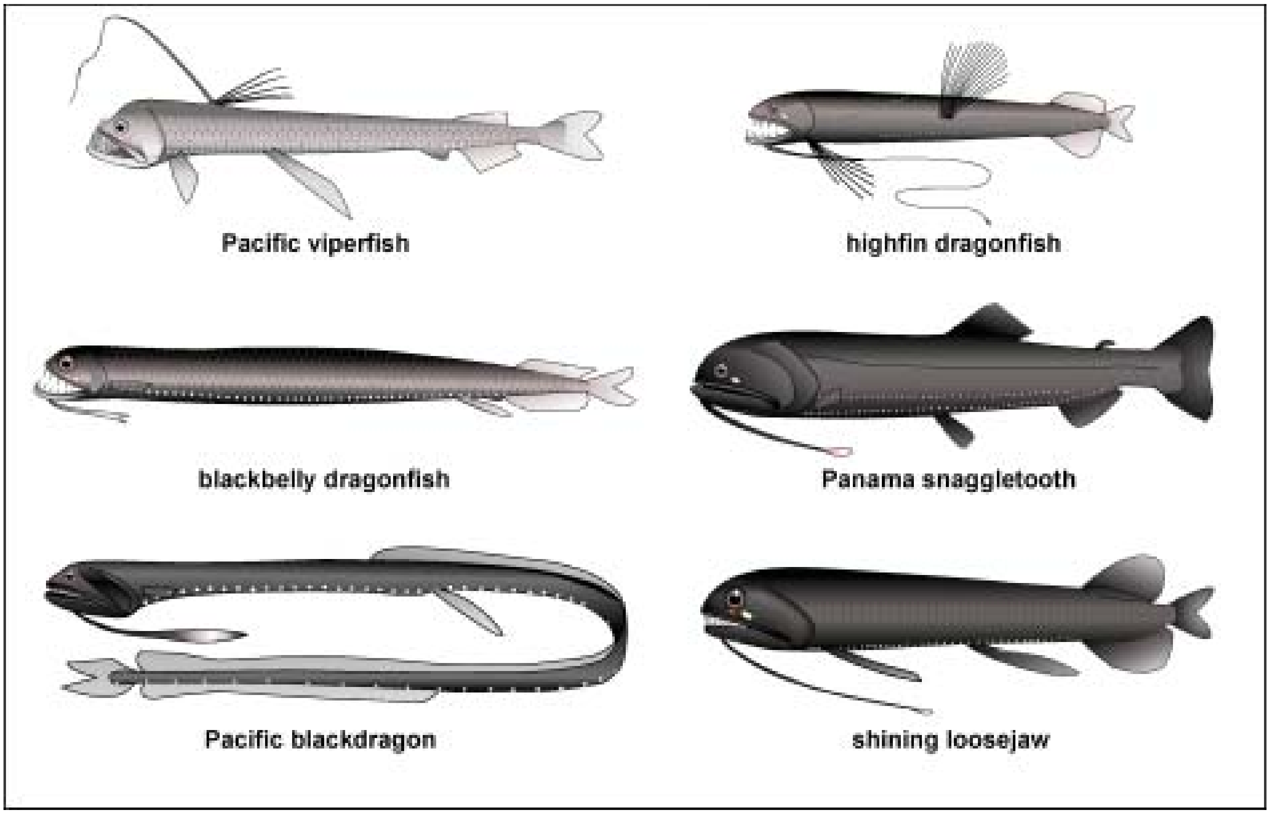


FIGURE 13-6. Representative midwater fishes: barbeled dragonfishes.

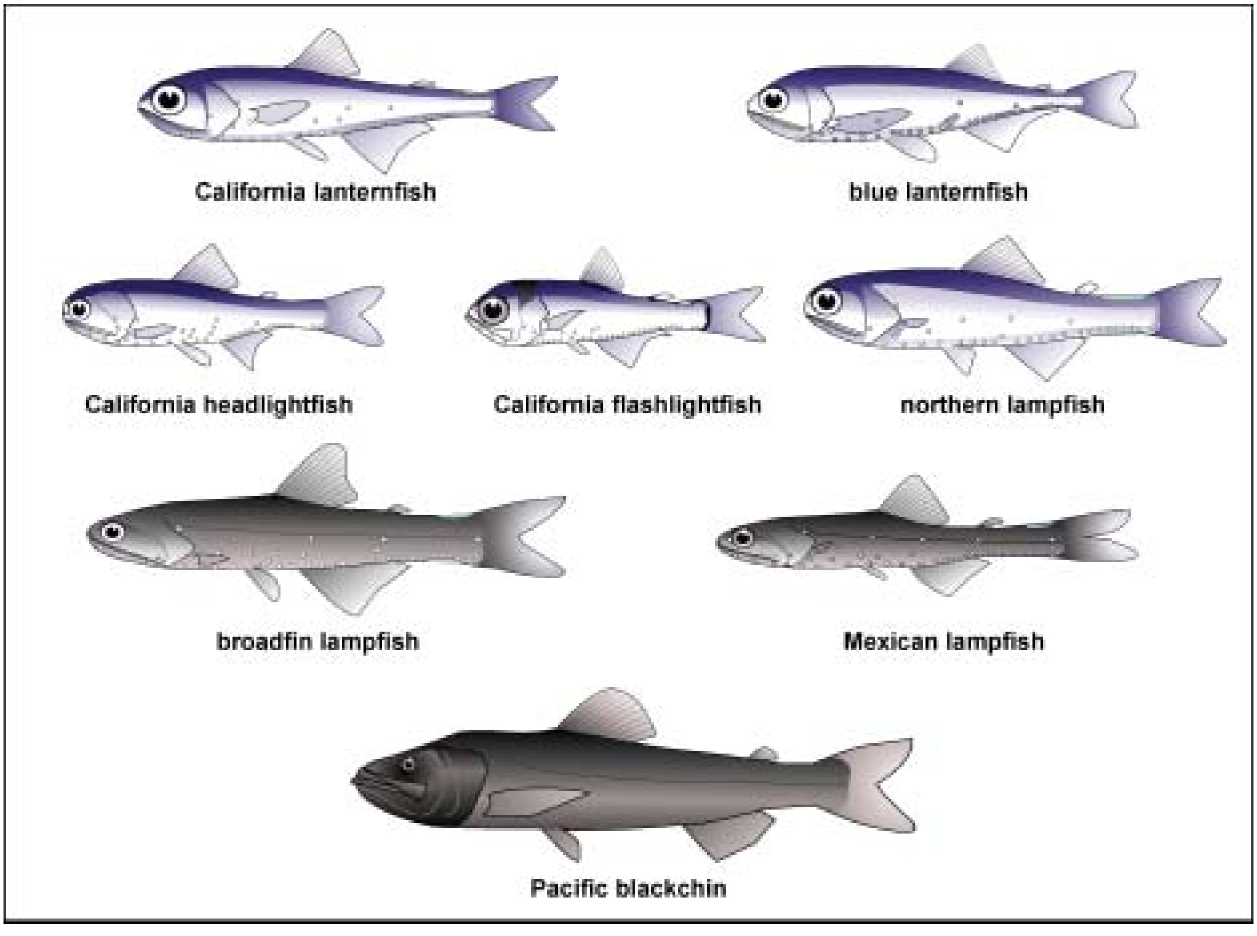


FIGURE 13-7. Representative midwater fishes: lanternfishes and blackchin.

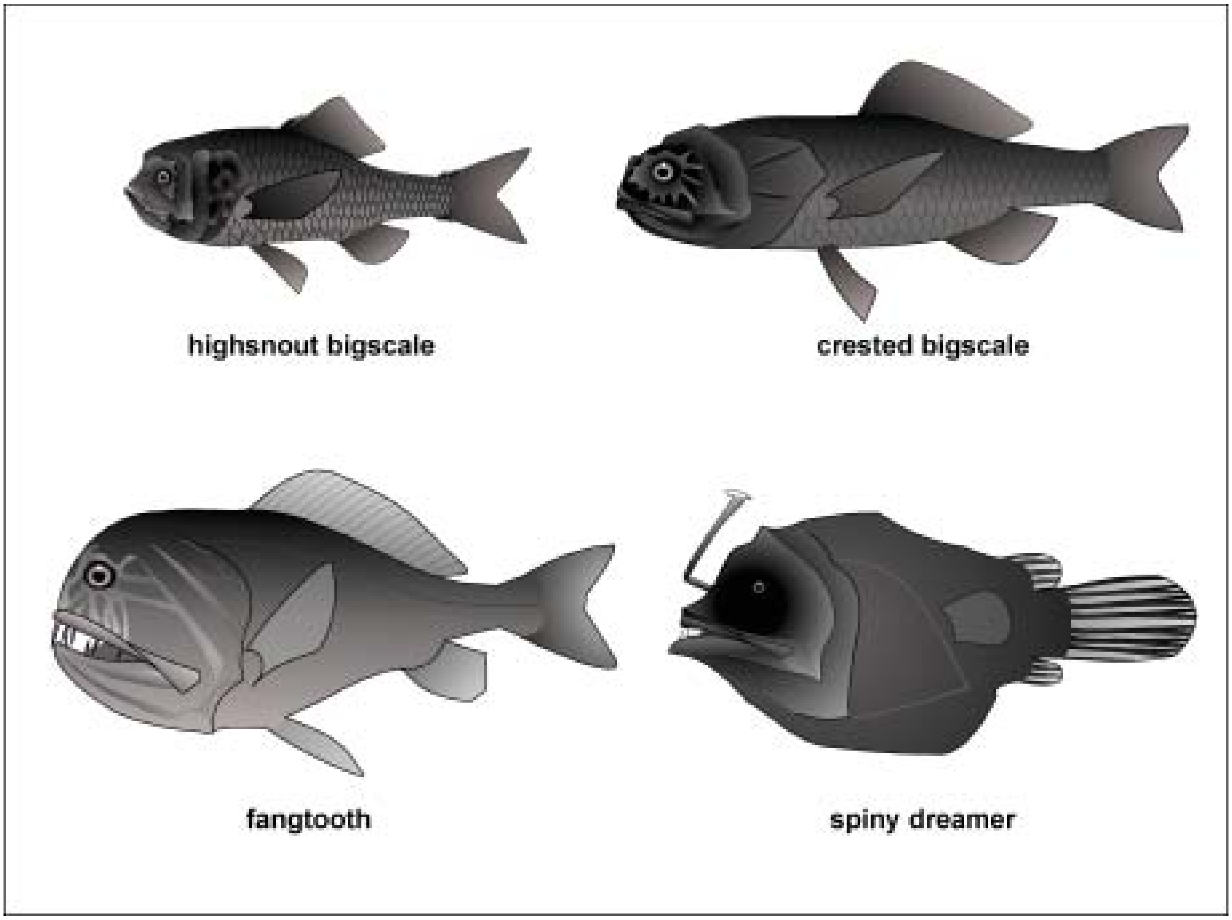


FIGURE 13-8. Representative midwater fishes: bigscales, fangtooth, and dreamer.

either on the ventral surface (e.g., the California lanternfish, *Symbolophorus californiensis*) or absent (e.g., the blue lanternfish, *Tarletonbeania crenularis*). Other patches of luminescent tissue may be found in species-specific regions such as over the eyes, near the origin of the pectoral fin, and on the dorsal and ventral margins of the body of the dogtooth lampfish, *Ceratoscopelus townsendi*. Even though lanternfishes typically have large eyes, their ability to distinguish the species-specific photophore and other luminescent tissue patterns that allow us to tell the species apart has been questioned. Mensinger and Case (1997) suggested that species specific flash patterns of the caudal organs may better serve this purpose in addition to possibly aiding in the avoidance of predators. Deeper living members of the family (e.g., the pinpoint lampfish, *Nannobrachium regale*) are often darker, grow larger but have flabbier bodies, and may have smaller photophores and eyes. Species of a second myctophiform family, the blackchins (family Neoscopelidae), are far less numerous then myctophids and are represented off California by only one species, the Pacific blackchin (*Scopelengys tristis*, fig. 13-7), which lacks photophores.

In members of the order Lophiiformes, the anterior dorsal fin spine is modified to form the flexible illicium tipped with a fleshy esca that together are used as a fishing pole with a lure. In most genera of the midwater dwelling anglerfishes (suborder Ceratioidei), the females have esca containing luminescent bacteria (O'Day, 1974; Herring and Morin, 1978) that presumably allow these animals to fish for prey even in their dark midwater environment. Unexpectedly, whip nose anglerfish (*Gigantactis* sp.) observed drifting and swimming upside-down with their escas close to the ocean bottom might be seeking benthic prey (Moore, 2002). The much-smaller males of most species become macrosmatic; free-living males with small olfactory organs have well developed eyes (Marshall, 1980). Pheromones may direct the males to the females, and eyesight allow species identification by species-specific differences in the esca (Marshall, 1971a; 1980). The normal jaw teeth of the males are lost during metamorphosis and replaced by pincher-like denticles at the anterior tips of the jaws that allow attachment to a female (Pietsch, 1976). Some species form only a temporary attachment during spawning and fertilization, whereas in others attachment by the male is followed by fusion of epidermal tissues and joining of the circulatory systems, resulting in the male becoming a parasite of the female. The males of some species appear to be obligate parasites, whereas those of others may be facultative sexual parasites (Pietsch, 1976). The spiny dreamer, *Oneirodes acanthias* (fig. 13-8), is a California representative of the Oneirodidae, the most speciose family of the anglerfishes.

Two beryciform families of midwater fishes that occur worldwide have representatives that are caught off California. The fangtooth, *Anoplogaster cornuta*, of the family Anoplogastridae, is a stout bodied, flabby black fish that has a large sculptured head and mouth bearing the impressive teeth (fig. 13-8) from which it gets its common name. Unlike most of the midwater fishes, this species is often still alive after being collected from hundreds of meters depth with a midwater trawl. Bigscales (family Melamphaidae) are short bodied, brown fishes with round snouts, large midset dorsal fins, and bands of minute teeth in their jaws (Marshall, 1980). These mesopelagic and bathypelagic fishes lack photophores. As in some other mesopelagic species (e.g., lanternfishes and tubeshoulders), bigscales have well developed portions of the lateral line on their heads consisting of both free neuromasts and large neuromasts set in wide canals covered with membranes pierced with pores (Herring, 2002). The neuromasts in the body canal are relatively small (Marshall, 1980). Species found off California include the crested bigscale, *Poromitra crassiceps*, and the highsnout melamphaid, *Melamphaes lugubris* (fig. 13-8).

Geographic Variations in Diversity and Abundance

Variation in sampling protocols and equipment, as well as differences in regional abundances and diversities, complicates comparison of areas that have been surveyed and permits only general conclusions. Clearly, however, the diversity and abundance of midwater fishes changes with latitude and longitude off the west coast of North America, mostly in relation to differing proportions of water types present. Off Oregon, with subarctic water to the north and transitional water to the south, the number of mesopelagic species increases to the south (Pearcy, 1964). Mesopelagic fishes dominated the list of about 50 species captured in trawls to depths of 1,000 m, both in number and variety. Three lanternfishes, northern lampfish (45% of the catch), California headlightfish (21%), and blue lanternfish (10%), were taken in over 80% of the tows and absent only from shallow daytime tows and tows in shallow water. The longfin dragonfish, *Tactostoma macropus* (8%), was next in abundance.

Offshore of California in the central Pacific, midwater fish diversity increases and abundance decreases. Between Hawaii and Santa Barbara, organisms were 100 times less abundant in hauls to depths of 550 m in the Central Pacific than in the cooler modified Subarctic water near California (Pieper, 1967); this decrease in numbers held for lanternfishes, bristlemouths, and invertebrates. Whereas lanternfish and bristlemouth biomass increased shoreward, their diversity was greatest in the warmer central water. Of the fish and invertebrate species collected, 85% were associated with either central or subarctic water, and species characteristic of either region were found in the area of mixing. Thus, rich coastal subarctic water supports fewer but more abundant species than central water, which supports a higher diversity of species that are less abundant (Pieper, 1967). Bailey (1984) compared the midwater fish faunas of three different regions of increasing depth and distance from San Diego: a California Current station above the Patton Escarpment 300 km west of San Diego, a transition station 672 km west, and a gyre station 1,536 km west (tables 13-2 and 13-4). Temperature-salinity profiles showed characteristics of subarctic water at the transition station and Pacific central water at the gyre station. The catch at the gyre station had the greatest diversity and lowest overall numbers and biomass. Diversity again decreased shoreward, with highest faunal abundance at the transition station. Average fish size was greatest at the California Current station. Bristlemouths, *Cyclothone* spp., were the most abundant fishes at all three stations (table 13-4). Lanternfishes were approximately 66% less abundant at the outermost station, and the mean weight per fish increased shoreward. The rate of decrease in biomass with increasing depth was significantly higher at the gyre station than at the other two. Bailey (1984) concluded that the total micronekton biomass appears to be directly related to the level of primary production of an area.

In a study conducted within a region influenced by the California Current, Brown (1974) compared the abundance (relates to productivity), diversity (indicates complexity), composition (reflects adaptations of its species), and distribution (indicates heterogeneity in space and time) of midwater faunas at increasingly seaward locations with differing water depths (Santa Barbara Basin, 600 m deep; Santa Cruz Basin, 2,000 m deep; the continental slope east of Rodriquez Dome seamount, 1,000–2,500 m deep). Santa Barbara Basin had a relatively large standing crop of fishes composed of relatively few species and lacked a bathypelagic fauna due to its shallow depth. A smaller standing crop of characteristically oceanic species, as well as an obvious bathypelagic fauna, exists at the locales farther offshore. The two offshore locations exhibited much greater faunal overlap than either did with the fauna of the Santa Barbara Basin; 61% of the total 81 species occurred only offshore. The number of species making up 90% of the fish fauna increased from three to seven to 15 at increasingly seaward locales (table 13-4). Santa Cruz Basin, at the northern portion of the chain of basins in the borderland, receives deep southern water flowing northward. Its deep-water species are derived more from the south than from central water to the west. Central and northern species have more direct access to the continental slope (Brown, 1974).

Lavenberg and Ebeling (1967) concluded that the complexity of the water types present influences the diversity of the midwater fishes of an area. In the borderland, the northern faunal component of 32 species associated with the Pacific subarctic water mass generally occupies the mesopelagic region where northern water predominates. The southern faunal component of 76 species occurs mostly deeper in the lower-mesopelagic and bathypelagic regions of Southern water. The central faunal component of 16 species is most abundant offshore where central water occurs in the mesopelagic zone. Within the basins, deeper-living, seasonally abundant, northern fishes generally co-occur with southern species. Many of the mesopelagic species make diurnal vertical migrations, but few of the southern species are strong migrators.

Great differences in species abundances became clear from the survey of pelagic fishes from off central California to central Baja California conducted by Berry and Perkins (1966). Over 189 fish species were collected up to 970 km seaward of the coast from between the surface and 2,234 m over bottom depths of 5,124 m or less. Forty-four species were each represented by a single specimen. Among the deep-sea fishes, lanternfishes were taken at more stations than any other fish family. Mexican lampfish were collected at more stations (76) than any other species and were the most abundant fish in a single tow, with a haul of around 3,000 individuals. Other commonly collected myctophids were California flashlightfish (66 stations), dogtooth lampfish (66 stations), broadfin lampfish (63 stations), California headlightfish (61 stations), California lanternfish (55 stations), and northern lampfish (54 stations). Commonly collected species from four other deep-sea families were the gonostomatids showy bristlemouth (64 stations) and benttooth bristlemouth (49 stations); the sternoptychids tropical hatchetfish (54 stations), slender hatchetfish (49 stations), bottlelight (47 stations), and spurred

TABLE 13-4

Composition of Midwater Fish Collections from Off Southern California

	Bailey (1984)			*Brown (1974)*			*Atsatt and Seapy (1974)*			
	Gyre 33° 08′ N 133° 03.4′ W	Transition 32° 38′ N 124° 09.3′ W	Current 32° 34′ N 120° 22.5′ W	Rodriguez Dome area	Santa Cruz Basin	Santa Barbara Basin	Santa Catalina Basin		San Pedro Basin	
							Day	Night	Day	Night
Trawl (mouth or sampling area)	opening-closing RMT-8 (8m^{2})			1.8 m IKMT, 4 chambered cod end (2.9 m^{2})			open 3 m IKMT (7.8 m^{2})			
Sampling protocol	horizontal tows at depth			horizontal and oblique tows			oblique tows			
Number of trawls	15	13	11	91	267	210	9	5	8	6
Deepest trawl (m)	>2500	2000	1250	1000[a]	1000[a]	500?	650 m	650 m	650 m	650 m
Bottom depth (m)	?	?	?	1000-2500	2000	600	1357[b]		912[b]	
Bristlemouths	87.1	79.2	63.2							
Cyclothone spp.	83.7	77.5	62.4							
Benttooth bristlemouth				19	27		41.5	32.9	41.0	43.1
Showy bristlemouth				28	15	4	12.9	10.4	9.5	7.0
Deep-sea smelts	0.1	2.1	3.0							
California smoothtongue				2	16	58	2.0	1.8	10.1	7.4
Snubnose blacksmelt				2						
Lanternfishes	8.1	10.6	18.4							
Blue lanternfish				1						
Broadfin lampfish				6	2		4.4	10.7	4.0	2.0
California headlightfish				6	4					
California flashlightfish				2						
Mexican lampfish				2	17		0.6	21.1	9.8	7.6
Northern lampfish				15	11	33	24.1	7.6	15.3	24.2
Larvae				2						
Hatchetfishes	1.1	4.0	6.9							
Bottlelight				1						
Slender hatchetfish				1						
Tropical hatchetfish				1						
Dragonfish predators	2.0	1.1	3.9							
Anguilliformes	0.0	0.6	0.2							
Big scales	1.0	1.6	3.5							
Other fishes	0.3	0.7	0.9	3						
Not reported				9	8	5	14.5	15.5	10.3	8.7

NOTE: Percentage of catch.

[a] DeWitt (1972).

[b] Emery (1960).

hatchetfish (*Argyropelecus hemigymnus*, 45 stations); the melamphaid the twospine bigscale (*Scopelogadus mizolepis bispinosus*, 50 stations); and the stomiid Pacific blackdragon (50 stations).

Four Abundant Species

The surveys of Berry and Perkins (1966) and others provided information regarding the distributions of the many midwater fishes off California and Baja California, but the biology of only a few abundant species of the California Current region has been studied in any detail. Among these are the myctophids northern lampfish and Mexican lampfish and the gonostomatids showy bristlemouth and benttooth bristlemouth. Although not representative of the life histories and ecologies of many other important midwater fishes (particularly their own predators) these species constitute a huge proportion of the assemblages of midwater fishes off the Californias and thus in an indirect way represent a "typical" midwater fish.

STENOBRACHIUS LEUCOPSARUS

The northern lampfish is likely the most ecologically important myctophid in the subarctic Pacific, where its biomass may approach 21×10^6 tons (Beamish et al., 1999). This lanternfish ranges from Japan and the Bering Sea to northern Baja California (Miller and Lea, 1972). It has numerically dominated catches of mesopelagic fishes from the subarctic region of the north Pacific to the coastal waters off San Luis Obispo Bay and in Santa Barbara Channel (Aron, 1962; Pearcy, 1964; Best and Smith, 1965; Pieper, 1967; Frost and McCrone, 1979; Willis, 1984; Balanov and Il'inskii, 1992; Lapko, 1995; Sinclair et al., 1999). Northern lampfish are also common in catches from borderland basins (Paxton, 1967a; Brown, 1974; Rainwater, 1975). Fast (1960) suggested that because the range of northern lampfish covers a large portion of the north Pacific, its total standing population comprises billions of individuals; the young must therefore number in the hundreds of billions to support the adult population. The larva of this species was the seventh most common fish larva collected during California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey cruises between 1951 and 1984, and its abundance was calculated to be over 326,000 individuals $10\ m^{-2}$ of sea surface (Moser et al., 1994).

Local populations of northern lampfish vary seasonally in abundance. Adults were almost twice as common in collections off Oregon during summer as during winter (Pearcy et al., 1977). In Monterey Bay, northern lampfish abundance was maximal at the time of the Davidson Current in winter and minimal during the upwelling period from March to June (Fast, 1960). Comparison of the Monterey Bay catch data with that from collections offshore (Ahlstrom, 1959) showed that the Monterey Bay population peaked in December, whereas the offshore population peaked in June and October (Fast, 1960). In San Pedro Basin, population size was greatest from November through March (Paxton, 1967a).

Northern lampfish occur in horizontal patches (Pearcy and Mesecar, 1971; Willis and Pearcy, 1980) and display diel vertical migration (Pearcy and Laurs, 1966). Individual fish may not migrate every night into the surface waters (Pearcy et al., 1977). Depth distribution of northern lampfish off southern California varies slightly with location. Maximum abundances are near 250 m in Santa Barbara Basin, above 400 m offshore near Rodriquez Dome, and somewhat deeper in Santa Cruz Basin (Brown, 1974). In Santa Catalina Basin, northern lampfish occurred with other relatively shallow-living midwater species that had their maximum abundance at about 350 m during the day (Rainwater, 1975). The San Pedro Basin population is centered above 650 m and makes nightly migrations to below 50 m. (Paxton, 1967a).

Vertical distributions and migratory patterns of northern lampfish change with age (Fast, 1960; Willis and Pearcy, 1980). Larvae up to 10 mm SL are found in the surface waters, and metamorphosing larvae move deeper to 400–500 m. Juveniles return to the upper levels of the adult range at 200–300 m and begin making diel vertical migrations to within 30 m of the surface. With age, fish move deeper in the water column to depths of between 300 and 600 m and continue to migrate vertically, although not to as shallow waters (75–95 m). The largest fish (70–80 mm SL) off Oregon were not usually caught above 200 m at night (Willis and Pearcy, 1980). Watanabe et al. (1999) also found northern lampfish off Japan to have a bimodal vertical distribution at night. Fast (1960) concluded that the primary factors influencing the vertical distribution of northern lampfish are levels of light penetration and fish age.

Time and place of northern lampfish feeding may vary with location. Off Oregon, Pearcy et al. (1979) collected the highest percentage of fish with very full stomachs in the morning and the lowest in the afternoon, whereas the percentage of fish with empty stomachs was highest in the afternoon and lowest at night. The rank order of the common prey of fish from the upper 100 m at night differed from that of fish that had remained between 300 and 500 m. Comparison of stomach fullness and content digestion further indicated that fish captured in deep water at night probably had fed at deeper depths as well as in shallow water on the previous night. Gorbatenko and Il'inskii (1992) suggested that on the average only 11% of the Bering Sea population migrates to the epipelagic zone (0–200 m) during a night, and that more prey is consumed in the mesopelagic zone (200–500 m) during either day or night than in the epipelagic at night. In contrast, Moku et al. (2000) found that nonmigratory northern lampfish in the western north Pacific had significantly higher proportions of empty stomachs than did migrators and probably did not actively feed at night.

Crustaceans make up the bulk of the diet of northern lampfish. Stomachs of Oregon fish contained primarily euphausiids and secondarily copepods, but typically only one type of food was present in a single stomach (Tyler and Pearcy, 1975). Of 95 specimens with distended abdomens taken from San Pedro Basin, 73% had eaten euphausiids, 11% copepods, 8% sergestids, and 8% fishes (Paxton, 1967b). Fish collected in Santa Barbara, Santa Cruz, and Santa Catalina basins had also foraged predominately on euphausiids and copepods (Collard, 1970). Variability in the frequency of occurrence of these and other crustaceans was related to both season and location. The greatest seasonal difference was seen between spring, when copepods were eaten twice as often as euphausiids, and summer, when euphausiids were eaten 10 times as often as copepods. Other prey made up a larger portion of the diet during fall and winter (Collard, 1970). Gorbatenko and Il'inskii (1992) estimated that 1.8×10^6 tons of this small fish consume 1.9×10^4 tons of food per day in the Bering Sea alone. In turn, northern lampfish are the prey of squid, fishes, birds, and mammals (Beamish et al., 1999).

Growth rates are similar between populations of northern lampfish off California and Oregon, and fish attain an average 59–68 mm SL in three years (Bolin, 1956; Fast, 1960; Smoker and Pearcy, 1970). Maximum life expectancy has been estimated as four (Bolin, 1956) or five (Fast, 1960) years. Smoker and Pearcy (1970) suggested some individuals may live eight years but were confident of assigned ages based on otolith analysis only to five years or less.

In Oregon waters, northern lampfish mature at about 65 mm SL (approximately four years old) and spawning occurs from December to March; 20 to 25 mm SL individuals appear in largest proportions in trawl samples in winter, presumably about eight months after spawning (Smoker and Pearcy, 1970). In Monterey Bay, only northern lampfish over 50 mm SL had large eggs (Fast, 1960). Fast suggested that spawning occurred once in a season and possibly only once in a lifetime. Larvae of 3 mm total length (TL) were first found in the Monterey Bay plankton during early November, and larvae of less than 6 mm were present until August, indicating an approximately nine month spawning season. Gravid females occurred in San Pedro Basin samples from October through April, and individuals termed "postlarvae" were captured during five months of the year (Paxton, 1967b). The larvae were most common in CalCOFI collections along the California coastline between January and March (Moser et al., 1993).

TRIPHOTURUS MEXICANUS

The Mexican lampfish is a more important myctophid species in the southern portion of the region influenced by the California Current. This smaller fish ranges between northern Chile and San Francisco but is seldom caught north of Point Conception (Miller and Lea, 1972). Populations can be quite concentrated in areas with transitional or Equatorial water. In the CalCOFI region, Mexican lampfish were collected at more stations than any other species and were also among the most abundant species in a single tow (Berry and Perkins, 1966). This fish was also a commonly collected species in surveys of the Gulf of California (Lavenberg and Fitch, 1966; Robison, 1972; Brewer, 1973). Brewer noted that as over 23,000 specimens were caught at a single Gulf of California station, the Gulf population must be enormous. Imsand (1982) calculated the total population sizes of Mexican lampfish in the California Current and the Gulf of California to be approximately 2×10^{12} individuals each. However, densities of the two populations are quite different, as their areas of distribution have the ratio 5 (California Current): 1 (Gulf), where each unit of area equals approximately 10^6 km^2.

The abundance of Mexican lampfish in the California borderland varies by location and depth. It is more common in Santa Cruz Basin than offshore over the slope or in shallow Santa Barbara Basin and localized near the surface at night and at 500 m by day (Brown, 1974). It is the third most abundant fish in Santa Catalina Basin and occurred with fishes characterized by maximum daytime concentrations at around 450 m (Rainwater, 1975). In San Pedro Basin, Mexican lampfish have a diurnal center of distribution above 650 m and are seldom found shallower than 50 m at night (Paxton, 1967a). Captures there were greatest in November and December.

Mexican lampfish forage on crustaceans, particularly euphausiids and copepods. Imsand (1981) compared the food of Mexican lampfish from the California Current region and Gulf of California with that of its congener the highseas lampfish, *Triphoturus nigrescens,* and found no significant difference in their feeding habits. The diet biomass of each was at least 88% euphausiids, less than 5% copepods, and less than 8% "other." During a single diel-feeding period, both species prey on a variety of copepods but generally only a single species of the available euphausiids, apparently gorging on these when they are found (Imsand, 1981). The stomach contents of Mexican lampfish collected in the southern portion of the Gulf of California included ostracods, copepods, small shrimp, and, rarely, fish larvae (Holton, 1969).

Information about Mexican lampfish growth and reproduction is limited. It attains a maximum size of about 70 mm SL (Wisner, 1976) at around four years of age (Childress et al., 1980). Their larvae were the sixth most common fish larva collected by CalCOFI survey cruises between 1951 and 1984, with an estimated abundance of over 404,000 individuals 10 m^{-2} of sea surface (Moser et al., 1994), and were most commonly collected July to September off Baja California (Moser et al., 1993).

CYCLOTHONE SIGNATA AND *C. ACCLINIDENS*

Species of the gonostomatid genus *Cyclothone* are among the most common oceanic pelagic fishes (Kashkin, 1995). *Cyclothone* "spp." was the fifteenth most abundant larval taxon collected in CalCOFI survey cruises between 1951 and 1984 with over 68,000 individuals 10 m^{-2} sea surface (Moser et al., 1994). The larvae were plentiful throughout the year off the coasts of both California and Baja California (Moser et al., 1993).

Several *Cyclothone* species have been collected off California and Baja California, but only the showy and benttooth bristlemouths are abundant (Berry and Perkins, 1966). The showy bristlemouth is largely an eastern Pacific species, although it has been collected at low latitudes of the central Pacific east of about 160° E (Kobayashi, 1973). The benttooth bristlemouth, probably the most abundant species of the genus, occurs in the Atlantic, Indian, and Pacific oceans (Kobayashi, 1973). In the eastern Pacific, it ranges from Oregon to the Peru-Chile Trench (Miller and Lea, 1972) and extends westward in equatorial waters to the Indo-Malayan archipelago and off Japan (Kashkin, 1995). Showy bristlemouth adults reach a maximum size of about 40 mm SL and usually live at depths between 200 and 800 m with maximum abundance at about 400 to 500 m (Kobayashi, 1973). Benttooth bristlemouth adults attain a length of approximately 65 mm SL and are collected mainly between 300 and 1,700 m deep with peak abundance at 600–700 m (Kobayashi, 1973). The vertical size distribution pattern of benttooth bristlemouths is similar to that of other *Cyclothone* species. Relatively small specimens occur within the upper portion of the range (300–500 m). Size then increases with depth to or deeper than the region of maximum abundance. No clear size trend is seen among individuals collected deeper than 1,100 m, and occasionally a larger specimen is found shallower than the usual range (Kobayashi, 1973).

Distributions of these two species of bristlemouths vary in the borderland. Off Santa Barbara, the less pigmented showy bristlemouth is mesopelagic, with adult distribution maxima at both the surface to 100 m and 400 to 500 m, whereas seaward of the Channel Islands the darker benttooth bristlemouth lives between 300 and 1,200 m with a maximum abundance at 700 to 800 m (DeWitt, 1972). Young fish occupy shallow waters (DeWitt, 1972; Talbot, 1973). In Santa Catalina Basin, adult benttooth bristlemouth abundance was significantly correlated with depth down to 1,000 m (Talbot, 1973). Neither species appears to migrate vertically (DeWitt, 1972; Talbot, 1973).

Benttooth bristlemouths live in zones of the eastern Pacific with low oxygen concentration (Kashkin, 1995); long gill filaments may allow them to thrive in these regions (DeWitt, 1972). Gill lamellae on the first branchial arch of benttooth bristlemouths vary depending on where the fish are collected. Those from areas with low dissolved oxygen concentrations have gill lamellae that are greatly expanded, heavily branched, and unfused, whereas gill lamellae of specimens from waters with high oxygen concentrations are either fused or otherwise greatly reduced in surface area (Kobayashi, 1973).

Both *Cyclothone* species prey mainly on crustaceans. Stomachs of 277 showy bristlemouths from Santa Cruz Basin and the slope contained copepods (35%), and less often unrecognizable material and ostracods (DeWitt and Cailliet, 1972). Most of the observed prey organisms live in the upper 200 m, and, therefore, stomach contents suggest some vertical migration. More than 50% of the stomachs were empty, and deeper caught fish had empty stomachs more often than those caught shallower. "Unrecognizable material" was the most common food category in the stomachs of 225 benttooth bristlemouths from the same area, followed by copepods, chaetognaths, ostracods, and amphipods. The copepods eaten are found predominantly below 200 m (DeWitt and Cailliet, 1972).

Bristlemouth males are smaller than the females and become macrosmatic when mature (Marshall 1967; 1980). Showy bristlemouths may be single spawners, with most females reaching sexual maturity at age 3 (Aughtry, 1953 cited in Miya and Nemoto, 1991). The larger benttooth bristlemouths may spawn multiple times and have a higher fecundity (Miya and Nemoto, 1991). More information about the life histories of these two species would allow comparisons with those of other bristlemouths such as the study by Miya and Nemoto (1991) of three species from off Japan.

Vertical Distributions

The vertical distributions of the myctophids and neoscopelid in San Pedro Basin do not necessarily follow groupings of the species based on their horizontal distributions, which largely coincide with the presence of the waters from three water masses or mixtures thereof (Paxton, 1967a). Paxton divided these species into five geographic groups: 1) Subarctic-Transitional (blue lanternfish, California headlightfish, northern lampfish, broadfin lampfish); 2) Transitional (California lanternfish, sunbeam lampfish *Lampadena urophaos*, giant lampfish *Parvilux ingens*); 3) Subarctic-Central Pacific (California flashlightfish, pinpoint lampfish); 4) Eastern Equatorial (Diogenes lanternfish *Diogenichthys laternatus*, Mexican lampfish, Pacific blackchin); and 5) Cosmopolitan (longfin lanternfish *Diogenichthys atlanticus*, *Taaningichthys bathyphilus*, dogtooth lampfish). Included in his five observed vertical distribution patterns were: two deep species that do not migrate and have an apparent upper nocturnal limit of 650 m (*T. bathyphilus*, Pacific blackchin); three deep species with diurnal centers below 650 m that migrate to 50 m (sunbeam lampfish, pinpoint lampfish, giant lampfish); nine shallow species with a diurnal distribution above 650 m, four of which migrate into the upper 10 m (longfin lanternfish, California lanternfish, California headlightfish, dogtooth lampfish) and five of which migrate to between 10 and 50 m (Diogenes lanternfish, blue lanternfish, northern lampfish, Mexican lampfish, broadfin lampfish); and one shallow species (California flashlightfish) found below 350 m during daytime and 150 m at night. Paxton (1967a) hypothesized that the broad ranges of dogtooth lampfish and longfin lanternfish are probably the result of a wide tolerance of conditions. Yet, other species lacking horizontal ranges that extend over all three water masses may encounter all three water types over their vertical ranges. Depths of occurrence are possibly related to the thermocline at 50 m and the year round halocline at 150 m, but apparently not to dissolved oxygen. Paxton (1967a) concluded that temperature and light strongly influence both vertical and horizontal limits of lanternfishes.

Vertical distributions of midwater species may change in locales differing in water depth and distance from shore. Offshore of Santa Barbara, Brown (1974) found California smoothtongue to be most abundant between 150–450 m in Santa Barbara Basin, but seaward in Santa Cruz Basin the population of mostly young fish lived deeper. Northern lampfish concentrations varied from around 250 m in Santa Barbara Basin to above 400 m over the slope and deeper in Santa Cruz Basin. California headlightfish had a relatively shallow distribution maximum at above 200 m in Santa Cruz Basin, but over the slope were most commonly caught at about 400 m. Showy bristlemouths were caught at each of the three areas; they occurred at 300–500 m in open water and had less defined concentrations in the basins. Benttooth bristlemouth were most abundant in Santa Cruz Basin between 700 to 900 m and scarce in shallow Santa Barbara Basin.

Ecological Groupings and Community Compositions

Several studies have searched for ecological groupings of the midwater fauna of the southern California borderland. Ebeling et al. (1970) tested for groupings of fishes and some invertebrates collected in open 3 m Isaacs-Kidd midwater trawl (IKMT) collections from the San Pedro (36 samples) and Santa Catalina (55 samples) basins and the continental slope between Guadalupe Island and San Juan Seamount (11 samples). Species distributions were clumped, especially those of vertically migrating mesopelagic species living at intermediate depths during daytime; bathypelagic species were less clumped. Common species segregated into three general groups (upper mesopelagic, mesopelagic, and bathypelagic), with some rare species as outliers. As in an earlier study by Lavenberg and Ebeling (1967), species of subarctic, transitional and central waters dominated mesopelagic groups, whereas bathypelagic groups contained largely equatorial water, pantropic, and cosmopolitan species. Even though the fauna of deeper Santa Catalina Basin is more diverse and oceanic than that of the shallower inshore San Pedro Basin, 60% of the San Pedro groupings clustered in a manner similar to those produced by analysis of the total data set.

Ebeling et al. (1970) did not find evidence of taxonomically similar species competitively excluding one another from similar ecological niches. Taxonomic diversity varied in the ecological groups formed, some of which contained closely related species. Many rare species may be transients that contribute little to the structure of the communities specifically adapted to the borderland and surrounding regions. However, rare species in this region are not necessarily rare species elsewhere and might be ecologically more important in other areas. Groups differed in the depth, locality, season, and vertical migration patterns of their members. Bathypelagic groups were better defined than mesopelagic groups, and more of their variance could be related to physical parameters. Thus, Ebeling et al. (1970) determined that deep-sea animals do assemble into ecological groups, but these groupings are less obvious in the mesopelagic region because of interactions and overlapping vertical ranges. The middle mesopelagic transition groups contain the most abundant species, followed by the bathypelagic and upper mesopelagic groups. The mesopelagic zone constitutes approximately 33% of the environment sampled in this study, yet supports 75% of the groups containing 60% of the species; its faunal complexity is greater than that of the vast bathypelagic zone, which is comparatively uniform and sparsely populated.

Ebeling et al. (1971) used factor analysis to produce 10–14 groups of intercorrelated species and environmental measures based on data from monthly collections in Santa Barbara and Santa Cruz basins with a 1.8 m IKMT equipped with a four-chambered cod end. Four groupings of fishes and invertebrates were termed "resident communities", which overlap in space and time and interact with the remaining transitory groups of offshore species, larvae, and environmental factors. Resident communities remained intact no matter how many factors were analyzed and were predicted to be more stable in composition, abundance, and function than were transitory groups, members of which may have seasonal abundances that do not always vary synchronously. Members of transitory groups may be almost equally abundant or replace each other in abundance seasonally or year-to-year.

The Ebeling et al. (1971) model indicates that midwater animals live in associations with varying degrees of structure. The parameters depth, location, and time have direct effects on species associations and behavior. Within the basins, abundances of animals are related to features such as time of day, location, bottom depth, trawl depth, and temperature. However, as species abundances were not correlated with the group of bathythermograph temperatures and seasonal parameters, water mass characteristics such as temperature-depth profiles influence the animals either indirectly or not at all. Ebeling et al. (1971) hypothesized that the resident communities of this region are not greatly affected by localized variations in the water resulting from upwelling or currents bringing in different water mass types. The resident communities overlap in space and time but are distinguishable by the relatively stable concordant abundances of their members. Transitory species, in contrast, move in and out of the area and often segregate into relatively unstable groups by their different daily and seasonal movements.

Based on a year's data from monthly water samples and discrete-depth collections taken with a 1.8 m modified Tucker trawl, Rainwater (1975) examined the species associations of fishes living between 200 and 800 m in Santa Catalina Basin to determine if the midwaters could be partitioned as habitat regimes that relate to environmental factors and these associations. A subset of 27 frequently-caught species with significantly distinct bathymetric distributions clustered into seven species groups of two to five species with differing depth distributions and vertical migration patterns. Daytime and nighttime associations each contributed to the formation of two species groups; species of three groups co-occur both day and night. Based on the same species, 151 sites (trawls) clustered into five shallow-depth (upper mesopelagic, 55 sites) regime groups, four middle-depth (lower mesopelagic, 48 sites) regime groups, and two deep-water (bathypelagic, 48 sites) regime groups. Only four relatively rare species were randomly distributed among the site groups. The upper mesopelagic regime contained significant portions of the abundances of members of four species groups. The lower mesopelagic was inhabited largely by members of two species groups. The two bathypelagic regime site groups had the lowest total abundances of fishes. One of the species groups was well represented in the bathypelagic collections from 550–800 m, as was the benttooth bristlemouth from another. Of temperature, salinity, oxygen, depth, and month of year, only month of year was found not to be significant in explaining the separation of the site groups with the exception of one pair. Thus season appears to have little or no effect on the groupings of trawls because of changing species abundances and composition.

Members of each of Rainwater's (1975) seven species associations frequently co-occurred in trawls and displayed similar abundance trends in those trawls. The members of each association appear to be adapted to a set of environmental conditions and co-occur wherever those conditions are found. Two of her species groups contain a mixture of the six fish species in two resident communities of Ebeling et al. (1971). Unfortunately, Rainwater (1975) collected only in the mesopelagic zone between 200 and 800 m, so many vertically migrating species were not sampled in the upper portions of their ranges above these depths at night. Information about shallower nighttime abundance peaks could change the composition of the species associations as well as the trawl groupings.

Detailed reports of the abundances and distributions of at least the important members of the midwater community for major portions of their vertical ranges, such as have been completed in the eastern Gulf of Mexico (e.g., Hopkins and Lancraft, 1984; Gartner et al., 1987; Sutton and Hopkins, 1996a), are lacking for the waters off the Californias. Thus, comparisons of community composition within a basin over time, between basins, or with other geographic areas are difficult. Bailey (1984) included some information on the proportions of fishes in his catches at three stations increasingly seaward of San Diego (table 13-4). Bristlemouths were the most common fishes at all three locations. Two species of bristlemouths also dominated the Rodriguez Dome and Santa Cruz Basin catches of Brown (1974) and the San Pedro and Santa Catalina Basin catches of Atsatt and Seapy (1974, table 13-4). Because the objective of this latter study was analysis of sampling variability in replicated midwater trawls, only the upper 650 m were sampled.

Feeding

Many midwater fishes are hard-bodied (crustacean) zooplanktivores (Gartner et al., 1997). Not surprisingly, the great majority of the midwater fishes in the California Current region feed on small crustaceans (Paxton, 1967b; Collard, 1970; DeWitt and Cailliet, 1972; Tyler and Pearcy, 1975; Pearcy et al., 1979; Imsand, 1981). Two northern species that are common in inshore basins of the borderland exhibit very different feeding habits (Cailliet and Ebeling, 1990). The northern lampfish is abundant in both near and offshore basins of the borderland, but the California smoothtongue occurs in large numbers only inshore. The lanternfish eats larger, faster, more elusive prey and feeds mainly on crustaceans, whereas the deep-sea smelt eats smaller, less active prey and feeds mostly on larvaceans and salps, which are less dense and only seasonally available offshore. Cailliet and Ebeling (1990) concluded that feeding differences might account for the offshore density differences of these two species.

Basic information on the food web of the midwater fishes off California exists (See fig. 14-11, chapter 14). The midwater fish assemblage consists of vertically migrating zooplanktivores (e.g., lanternfishes), nonmigrating zooplanktivores (e.g., hatchetfishes), ambush predators (e.g., anglerfishes, most barbeled dragonfishes), and active foragers (e.g., barracudinas, Robison and Bailey, 1982; Gartner et al., 1997). More thorough food web investigations, such as those completed in the eastern Gulf of Mexico (e.g., Hopkins and Baird, 1985; Hopkins and Gartner, 1992; Sutton et al., 1995; Sutton and Hopkins, 1996b; Hopkins et al., 1996; Hopkins and Sutton, 1998), are still needed for these midwater fishes and invertebrates. Little is known about the impact of feeding on prey populations, resource partitioning, or the role of this community in the energy budget of the area.

Clarke (1972) concluded that myctophids and other vertically migrating micronekton probably account for most of the zooplankton consumption in the tropical open ocean. The very large populations of some midwater fishes off the Californias must be supported by large quantities of localized prey, and their feces must represent a great source of energy to deeper waters, particularly the benthos (Robison and Bailey, 1981). Also transported either to the benthos (Robison and Bailey, 1981) or to predators (e. g., Thompson et al., 1998) will be metals, pesticides, or any other contaminants (e.g., Cox, 1970; Robison, 1973b; MacGregor, 1974; Baird et al., 1975; Zdanowicz et al., 1996; Takahashi et al., 2000) present in the population of midwater fishes.

Chemical Compositions, Swimbladders, and Buoyancy

Prey availability is reflected in fish tissue densities and thus may affect whether or not a species is neutrally buoyant. Pelagic fishes utilize several means of maintaining their position in the water column (Gee, 1983). If their bodies are denser than seawater, they must swim to avoid sinking. Hydrodynamic lift provided by outstretched pectoral fins while moving forward aids in the maintenance of vertical position. Pelagic teleosts commonly have a swimbladder filled with gases. Usually a swimbladder volume of about 5% of the fish's body volume is necessary for neutral buoyancy (Taylor, 1922). The density of the body tissues may be decreased either by increased water contents often accompanied by decreased skeletal density (Denton and Marshall, 1958) or increased lipid stores, usually as triacylglycerols but sometimes as lower density wax esters (Hølmer, 1989; Lee and Patton, 1989; Morris and Culkin, 1989). In some cases, the juveniles of a species have inflated swimbladders, and then the buoyancy mechanism changes with growth. Examples of each of these means of achieving buoyancy are found in the midwater fishes from off California (table 13-5).

Species that have decreased densities due to higher water contents (≥83% wet weight, WW) tend to live at deeper depths, lack inflated swimbladders, not make extensive diurnal vertical migrations, and have low protein (≤8% WW), skeletal ash (≤1.3% WW), and lipid (≤7% WW) contents (Childress and Nygaard, 1973). Examples of California fishes with higher water contents are the Pacific blacksmelt, shining tubeshoulder, fangtooth, Pacific blackchin, and pinpoint lampfish, as well as the stomiids the shining loosejaw, Pacific viperfish, and blackbelly dragonfish (Childress and Nygaard, 1973; Neighbors and Nafpaktitis, 1982; Neighbors, 1988). Pinpoint lampfish from the northern subarctic Pacific off Japan had lipid contents averaging over 14% WW. These, like those from off California, accumulated wax esters (Seo et al., 1996; Saito and Murata, 1998). Pacific blacksmelt and Pacific viperfish were two of the four species in which Yancey et al. (1989) found gelatinous material containing glycosaminoglycans. These polysaccharides, which are major components of animal gelatinous tissue in general, are highly hydroscopic and thus hold some of the water that aids in the buoyancy of these species. This gelatinous material is particularly evident as a subcutaneous layer in Pacific blacksmelt.

The deep-sea smelts off California fall into two ecological groupings (Childress and Nygaard, 1973). Like the already mentioned Pacific blacksmelt, the robust blacksmelt, *Pseudobathylagus milleri*, a fish with a high water and low lipid content (Childress and Nygaard, 1973; Neighbors, 1988), lives deep in the water column and does not make extensive vertical migrations. Other species, such as the snubnose blacksmelt, popeye blacksmelt (*Lipolagus ochotensis*), and California smoothtongue, make at least diffuse migrations to shallower waters. None of these bathylagids have inflated swimbladders as adults. Increased lipid contents, in the form of triacylglycerols, may be important in the buoyancy of at least the larger individuals of these migrators, particularly in the latter two species (Neighbors, 1988).

Inflated swimbladders are found in the adults of many mesopelagic fishes, including representatives of the hatchetfishes, lightfishes, bigscales and lanternfishes (Marshall, 1960, 1971b, 1972). Fishes collected by trawls brought rapidly to the surface are subjected to rapid pressure decreases of one atmosphere per 10 m depth decrease. The state of inflation of the swimbladders at the time of capture in fishes hauled up over many meters is difficult to determine. Despite this pressure change, burst swimbladders or ruptured body walls are rarely seen (Marshall, 1960) or seen only in some species (Kleckner and Gibbs, 1972). Hatchetfishes often float at the surface of a catch with greatly expanded swimbladders forcing the viscera out of their mouths. Hatchetfishes do not migrate into shallow waters at night, but rather remain at similar depths both day and night. These fishes appear to maintain inflated swimbladders (Marshall, 1960; Capen, 1967; Neighbors, 1988). Hatchetfishes from off California are high in protein and skeletal ash contents and low in lipid and water contents, although deeper living *Sternoptyx* species may have higher water contents (Childress and Nygaard, 1973). Buoyancy strategies in the big scales from off California vary. The highsnout melamphaid has a low water content and inflated swimbladder (Childress and Nygaard, 1973); information about its lipid content is lacking. A longjaw bigscale, *Scopeloberyx robustus*, with an inflated swimbladder had a high lipid content (22% WW) consisting largely of triacylglycerols (Neighbors, 1988). Crested and twospine, *Scopelogadus mizolepis bispinosus*, bigscales have high water contents and lack inflated swimbladders (Childress and Nygaard, 1973; Neighbors, 1988).

Bristlemouths also differ in their buoyancy mechanisms. Some, such as *Diplophos taenia* from off Baja California, have inflated swimbladders and low lipid contents with triacylglycerols used for energy storage (Neighbors, 1988). The shallower living showy bristlemouth has an inflated swimbladder (DeWitt, 1972) and a lipid content of around 4% or less, consisting largely of both wax esters and triacylglycerols (Nevenzel and Menon, 1980; Bailey and Robison, 1986; Neighbors, 1988). Many species of *Cyclothone*, including the deeper living benttooth bristlemouth (Marshall, 1960; DeWitt, 1972), develop fat-invested swimbladders (Marshall, 1960). In these

TABLE 13-5

Chemical Compositions and Swimbladder States of Selected Midwater Fishes

	Nonfunctional Swimbladders			*Functional Swimbladders*		
Type of Neutral Lipid Present	*Wax Esters*	*WE & Tag*	*Triacylglycerols*	*WE & Tag*	*Triacylglycerols*	*Sometimes Inflated? Triacylglycerols*
Chemical composition (% wwt)						
Higher water content (≥ 81%) Lower lipid content (≤ 8%)	Pinpoint lampfish	Pacific viperfish** Benttooth bristlemouth	Snubnose blacksmelt California smoothtongue Blackbelly dragonfish Pacific blackdragon Crested bigscale Two spine bigscale Panama snaggletooth Shining loosejaw Fangtooth Pacific blackchin Giant lampfish Pacific blacksmelt**	Showy bristlemouth	Slender hatchetfish *Sternoptyx* spp.	
Lower water content (≤80%) Higher lipid content (≥ 11%)	Mexican lampfish Northern lampfish Broadfin lampfish Pinpoint lampfish (Japan)		Popeye blacksmelt		Longjaw bigscale	California lanternfish* California headlightfish Dogtooth lampfish
Lower water content (≤ 80%) Lower lipid content (≤ 6%)					Lowcrest hatchetfish Tropical hatchetfish Bottlelight California flashlightfish *Taaningichthys bathyphilus*	Blue lanternfish*

* Species with large pectorals and therefore possibly utilizing hydrodynamic lift (Gee, 1983).

** Species with buoyant glycosaminoglycan layers present (Yancey et al., 1989).

NOTE: Compositions of specimens from the California Current region off southern California unless otherwise noted. As chemical composition may change with age, composition classification based on highest values reported in the literature. Nonfunctional swimbladders may be absent, regressed, or fat invested. Functional swimbladders may or may not be inflated. Neutral lipids stored classified as mixture if both wax esters and triacylglycerols account for over 10% of the lipid content. From Nevenzel et al., 1969; Butler and Pearcy, 1972; Childress and Nygaard, 1973; Torres et al, 1979; Nevenzel and Menon, 1980; Bailey and Robison, 1986; Neighbors and Nafpaktitis, 1982; Neighbors, 1988; Seo et al., 1996; Saito and Murata, 1998.

fishes, lipids are deposited between the peritoneum and the outer wall of the swimbladder. Lipid deposition, which begins in the larva, continues as the fish grows and ultimately surrounds the regressing swimbladder. Marshall (1960) noted that in a number of midwater fishes "the swimbladder regresses after metamorphosis and becomes a convenient site for the deposition of fat, but this plays a relatively small part on the 'credit side' of the 'buoyancy balance sheet.' The benttooth bristlemouth has a lipid content of 4–6% WW consisting largely of wax esters and triacylglycerols (Childress and Nygaard, 1973; Nevenzel and Menon, 1980; Bailey and Robison, 1986). DeWitt (1972) observed oily globules both around the swimbladder and along the vertical septum between the muscle masses along the back in this species.

Lanternfishes, a speciose family found in all oceans at various depths, exhibit the range of buoyancy mechanisms (Bone, 1973). Much of the variation is related to the state of the swimbladder present. Some species do not have a swimbladder. If their bodies are denser than seawater, these species must constantly swim to maintain their position in the water column. Many juvenile lanternfishes have functional swimbladders. A swimbladder that ceases to grow as the fish grows has been termed "regressed." Such a swimbladder is seen in the deep-living pinpoint lampfish (Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1982), a species already noted to have a higher water content. Some regressed swimbladders become fat invested (Capen, 1967; Zahuranec and Pugh, 1971). Species that deposit large stores of lipids do so throughout their bodies, e.g., around the viscera and in the musculature, subcutaneous sacs, and bones (Nevenzel et al., 1969; Falk-Petersen et al., 1986; Reinhardt and Van Vleet, 1986; Phleger et al., 1997, 1999). Some lanternfishes have inflated swimbladders both as juveniles and adults. Species that remain within a relatively narrow depth range both day and night may have constantly inflated swimbladders. Lanternfishes commonly undergo extensive diel vertical migrations and may even reach the upper 50 m or the surface at night. Whether lanternfishes with functional swimbladders maintain either constant volumes (gas volume maintained at approximately 5% of the fish's body volume as required for neutral buoyancy throughout the vertical range) or constant masses (amount of gas remains the same and thus swimbladder volume is sufficient for neutral buoyancy only in the decreased pressure of the upper portion of the vertical range) of gas throughout their vertical ranges has been discussed by many (e.g., Kanwisher and Ebeling, 1957; Marshall, 1960; Alexander, 1971, 1972; D'Aoust, 1971; Ross, 1976; Vent and Pickwell, 1977; Blaxter and Tytler, 1978; Kalish et al., 1986). Additionally, the swimbladders of some species may not always be inflated with gas. Specimens have been collected with well developed but uninflated swimbladders (Marshall, 1960; Butler and Pearcy, 1972; Kleckner and Gibbs, 1972; Neighbors, 1992). Such swimbladders are different from regressed or fat invested swimbladders and have the appearance of still being functional and able to be inflated at some time.

Lanternfishes from off California exhibit inflated, noninflated, and fat invested swimbladders. The California flashlightfish, which lives at depths similar to those of some hatchetfish (*Argyropelecus*) species, does not make extensive vertical migrations into surface waters and maintains an inflated swimbladder (Butler and Pearcy, 1972; Neighbors and Nafpaktitis; 1982). Although adults of both blue and California lanternfishes may be collected with inflated swimbladders, those of some specimens contain no obvious gas (Butler and Pearcy, 1972; Neighbors, 1992). These two species migrate to shallow depths and can be collected at the surface with a neuston net at night. Neighbors (1992) found that fish collected at the surface at night more often had inflated swimbladders than fish collected at daytime depths and hypothesized that these species maintain neither a constant mass nor constant volume of gas but rather inflate their swimbladders on the way to the surface and remove gas as they descend. The northern and Mexican lampfish have fat invested swimbladders as adults (Capen, 1967; Butler and Pearcy, 1972). That of the broadfin lampfish is regressed and not observed to contain gas in adults (Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1982).

Variations in lipid contents as well as swimbladder states complicate a discussion of buoyancy mechanisms in the common lanternfishes. The blue lanternfish, with high protein and skeletal ash and low lipid and water contents (Childress and Nygaard, 1973), must swim to maintain its position if its swimbladder is not inflated to a size sufficient to result in neutral buoyancy. Its large pectoral fins add hydrodynamic lift (Gee, 1983). Lipids, largely in the form of triacylglycerols, remain below 4% WW even in larger individuals (Neighbors and Nafpaktitis, 1982). The density of California lanternfish must be more variable. Not only are these fish found with and without inflated swimbladders, but some larger fish have lipid contents of over 10% WW, or even over 20% WW off Japan (Seo et al., 1996; Saito and Murata, 1998), consisting largely of triacylglycerols, whereas others do not. Differences in lipid content may be seasonal (Neighbors and Nafpaktitis, 1982) and represent usage of stored lipids for metabolism. The northern, Mexican, and broadfin lampfishes all accumulate large stores of lipids (>11% WW), predominantly as wax esters (Nevenzel et al., 1969; Neighbors and Nafpaktitis, 1982). Lipid levels as percentages of body weight increase as the swimbladder becomes less important in buoyancy and then appear to remain relatively constant (Capen, 1967; Butler and Pearcy, 1972; Neighbors and Nafpaktitis, 1982). In addition to providing buoyancy, these lipids consisting largely of wax esters and only small amounts of triacylglycerols must also function as energy stores.

The question of why some fishes store wax esters while others deposit the more usual triacylglycerols remains intriguing. The waxes are not simply transferred to the fishes from wax-ester rich crustaceans (Lee at al., 1971; Lee and Hirota, 1973; Saito and Murata, 1998) in their diet, but rather are synthesized by the fishes (Kayama and Nevenzel, 1974, Seo et al., 2001). The lower specific gravities of wax esters as compared to triacylglycerols (Lewis, 1970) makes them better buoyancy agents, but Phleger (1991, 1998) notes that fish lipid densities at the pressures and temperatures encountered by deep-sea fishes need to be examined. When present in substantial quantities, both types of lipids will increase buoyancy. As species with high lipid contents tend to accumulate either wax esters or triacylglycerols, both types of lipid must serve as energy reserves (Sargent, 1976; Falk-Petersen et al., 1986). Hypotheses concerning wax ester deposition, some based on studies of deep living herbivorous crustaceans that also deposit wax esters, are generally ecologically based. One leading hypothesis states that the ability of deep-sea fishes to deposit lipids rapidly (Sargent et al., 1976) when seasonal or scarce resources are available would offer a great advantage. Rapid deposititon of lipids would be particularly advantageous in the case of temperate, polar or deeper living species (Lee et al., 1971; Lee and Hirota, 1973). Seo et al. (1996) found 17 tropical western Pacific lanternfishes generally to lack large stores of lipids and contain only trace amounts or no wax esters, whereas subarctic species had larger stores of either triacylglycerols or wax esters. Wax ester containing species exhibited limited or no diel vertical migration (Seo et al., 1996; Saito and Murata, 1998.)

Midwater species living in the same region, both geographic and vertical, often vary in the type of lipid deposited, as noted for California fishes. Even midwater fishes in highly seasonal polar regions differ in their storage lipids, as shown by studies near Antarctica (Reinhardt and Van Vleet, 1986; Phleger et al., 1997; Phleger et al., 1999). For whatever reason, some very abundant midwater fish species, including members of the genus *Cyclothone* and the lanternfishes *Electrona antarctica* off Antarctica, glacier lanternfish, *Benthosema glaciale*, off Norway (Falk-Petersen et al., 1986), northern lampfish in the Subarctic Pacific, and the Mexican lampfish in the eastern Pacific, deposit large stores of wax esters.

Information about whether or not California midwater fishes are neutrally buoyant comes from observations made at middepths by Barham (1971) from deep submersible vehicles off San Diego, California. Hatchetfishes were sometimes motionless and always oriented horizontally. Active snipe eels were vertically oriented with their heads uppermost and their elongate bodies in sinusoidal curves. Benttooth bristlemouths, California smoothtongues, and northern and Mexican lampfishes were seen hanging vertically in the water column. The two lanternfishes appeared to drift in loose aggregations during daytime. Most myctophids were hanging in the water column with their heads upward in the late afternoon and downward in the morning. Respiratory water currents may push them up or down, depending on their orientation. Barham (1971) proposed that lanternfishes fall into two groups: Those that are active, which may have functional swimbladders, large eyes, and firm silvery bodies with thin caudal peduncles, and those that are lethargic, which lack functional swimbladders, have small or medium-sized eyes, and soft dark bodies with thick caudal peduncles. Active myctophids migrate to the surface at night, whereas lethargic species only rarely reach the surface during their vertical migrations. Bone (1973) suggested that emphasis for characteristics of active and inactive species should be placed on the lipids present and fish densities. The active blue and California lanternfishes may or may not have inflated swimbladders and, in some members of the latter species, large stores of triacylglycerols. Thus many, if not all, of these fishes may need to swim to maintain their position in the water column. The lethargic northern and Mexican lampfishes, with their fat-invested swimbladders and large, relatively constant stores of wax esters, are apparently at least close to neutrally buoyant.

Growth and Reproduction

Childress et al. (1980) compared growth rates of four mesopelagic (California smoothtongue, northern lampfish, Mexican lampfish, and broadfin lampfish) and five bathypelagic (crested bigscale, Panama snaggletooth *Borostomias panamensis,* pinpoint lampfish, robust blacksmelt, and sharpchin slickhead *Bajacalifornia burragei*) species with values from the literature for two epipelagic fishes (Pacific sardine and northern anchovy). The epipelagic species appeared to have the highest and mesopelagic species the lowest growth rates, but standard methods for comparing growth rates (e.g., von Bertalanffy's *K* parameter) were not used. Supposed faster growth rates of bathypelagic fishes compared to mesopelagic ones were attributed to higher relative growth efficiencies achieved by having low metabolic rates. Longevities, determined by counting otolith rings that were assumed to be annual, ranged from 4 to 8 years for epipelagic and bathypelagic species, and 5 to 8 years for mesopelagic species. Egg diameter data suggested that California smoothtongue, northern lampfish and broadfin lampfish first reproduce in their third year, whereas the five bathypelagic species do so only in their last year. Childress et al. (1980) characterized the epipelagic species as generally being large and having rapid growth, long life, and early and repeated reproduction. Small size, slow growth, long life, and early and repeated reproduction were thought to typify mesopelagic species. Bathypelagic species were characterized as generally having large size, rapid growth, somewhat shorter lives, and late, possibly singular, reproduction.

The longevities that Childress et al. (1980) determined for the lanternfishes are greater than those of myctophid growth studies based on *validated* growth increments (e.g., Gartner, 1991a). Gartner (1991b) found that three mesopelagic myctophids from the eastern Gulf of Mexico grew rapidly, reaching their largest observed sizes in about one year. Moreover, these fast myctophid growth rates matched those of epipelagic fishes from the western North Atlantic. Gartner (1991b) suggested that because lanternfishes generally feed, reproduce, and develop in the epipelagial, their life history patterns are strongly influenced by that habitat. Greely et al. (1999) reached conclusions similar to those of Gartner (1991b) in their study of the age and growth of a mesopelagic myctophid of the Southern Ocean. Further study of mesopelagic and bathypelagic fishes from off California, particularly multiple species in common families, would improve our knowledge of growth rates, longevities, and reproduction of these fishes and help support or refute the above hypotheses.

Information about the spawning of mesopelagic fishes in the California Current is limited to very general knowledge, even for abundant families such as the myctophids. Lanternfishes are oviparous; their larvae commonly occur in collections of larval fishes. Presumably, these fishes all have planktonic eggs, but myctophid eggs are infrequently collected (Robertson, 1977; Moser and Ahlstrom, 1996). Unlike other types of fish eggs that are collected by nets, myctophid eggs may be so fragile that they disintegrate during capture (Moser and Ahlstrom, 1996). In the eastern Gulf of Mexico, myctophid spawning occurs in the epipelagic zone and peaks after midnight (Gartner, 1993). In contrast, the lanternfish *Benthosema pterotum* spawns early in the night at depths of 100 to 300 m in the Gulf of Oman, and Gjøsæter and Tilseth (1988) proposed that these eggs hatch before they reach surface waters. Myctophid larvae may occur deep in the water column but generally are found in the upper mixed layer (Moser and Ahlstrom, 1996). These and other deep-sea fish larvae might be transported by surface currents during their time in shallower waters.

Moser et al. (1994) listed the ranked abundances of the larval fish taxa from CalCOFI collections between 1951 and 1984. Deep-sea fishes that ranked above 20 in the list of the 245 most commonly collected larvae were Panama lightfish *Vinciguerria lucetia* (3), California smoothtongue (5), Mexican lampfish (6), northern lampfish (7), Diogenes lanternfish (11), snubnose blacksmelt (12), popeye blacksmelt (13), *Cyclothone* spp. (15), California flashlightfish (16), blue lanternfish (17), dogtooth lampfish (18), and *Lampanyctus* spp. (includes *Nannobrachium* spp.) (19). Moser and Watson (see chapter 11) summarize the distributions, abundances, and seasonalities of common midwater fish larvae present in the ichthyoplankton off California and Baja California.

Distributions in the waters off the coasts of the Californias for adults and larvae of midwater fishes with known larval ranges (Moser et al., 1993, 1994) are shown in fig. 13-9. This limited portion of the ranges of these species and their larvae largely overlap. Larvae of many other fishes living in the CalCOFI region are collected there but less commonly (see chapter 11; Moser, 1996a). Larvae of the stomiid the Panama snaggletooth (Moser, 1996b), the platytrochtids shining tubeshoulder and streaklight tubeshoulder *Holtbyrnia latifrons* (Ambrose, 1996), and fangtooth (Watson, 1996) have not been taken in CalCOFI collections. Thus, a few species might be transported by currents from other areas to the region of the Californias during some portion of their life cycle.

Benthic and Benthopelagic Fishes

Clearly, as with midwater fishes, the extent of our knowledge of deep-sea benthic fishes is ultimately a function of our ability to sample the deep-sea habitat efficiently. The fishes of the California deep slope and adjacent eastern Pacific Ocean basin have been thoroughly studied with benthic otter trawls (e.g., Stein, 1985; Wakefield and Smith, 1990; Lauth, 1999), free-vehicle baited traps (Wilson, 1984; Wilson and Smith, 1985; Drazen et al., 2001), free-vehicle hook lines (Phleger and Soutar, 1971; Smith et al., 1979; Wilson, 1982, 1984), *in situ* observations from submersibles (Smith and Hamilton, 1983), towed camera sleds (Wakefield and Genin, 1987; Wakefield and Smith, 1990), and baited camera/video arrays (Isaacs and Schwartzlose, 1975; Wilson and Smith, 1984; Priede et al., 1990). Repeated deployments of such sampling devices by dozens of investigators over at least the past 50 years have led to our present knowledge of deep benthic and benthopelagic fishes of California.

The California slope and rise between about 550 and 2,000 m is dominated by benthic and benthopelagic fishes of the following families (table 13-3): cuskeels (Ophidiidae), cat sharks (Scyliorhinidae), codlings (Moridae), dogfishes (Squalidae), eelpouts (Zoarcidae), flatfishes (Pleuronectidae), grenadiers (Macrouridae), hake (Merlucciidae), hagfishes (Myxinidae), lumpfishes (Cyclopteridae), rockfishes (Scorpaenidae), sablefish (Anoplopomatidae), skates (Rajiidae), sleeper sharks (Dalatiidae), slickheads (Alepocephalidae), and snailfishes (Liparidae) (Lauth, 1999; Wilson pers. obser. & various capture records). Between about 2,000 and 4,400 m off California, only about 20 species from the above families are likely present. Chiefly, these are grenadiers, followed by comparatively sparse occurrences of the highfin lizard fish, *Bathysaurus mollis* (Synodontidae), aphyonids, and cuskeels such as *Bassozetus* sp. (Stein, 1985) and *Spectrunculus grandis*. Deeper than about 4,400 m, and extending into the central Pacific basin to *ca.* 5,900 m depth and deeper, probably fewer than five or so abundant species exist, first among them the relatively abundant rough abyssal grenadier, *Coryphaenoides (Nematonurus) yaquinae*, likely followed by the cuskeel *S. grandis*.

The few important benthic and benthopelagic species inhabiting depths greater than about 2,000 m off California, chiefly grenadier species, are relatively well studied ecologically. The same is not as true for many of the species living between 550 and 2,000 m, save the most abundant and commercially important ones: the shortspine thornyhead (*Sebastolobus alascanus*), longspine thornyhead (*S. altivelis*), Dover sole (*Microstomus pacificus*), and sablefish (*Anoplopoma fimbria*), each of which has recognized fishery importance. Along the slope off Pt. Conception between about 550 and 732 m, the most abundant species by biomass from trawling (Lauth, 1999) is Dover sole (*ca.* 3.4 mt km^{-2}), followed by the longspine (*ca.* 2.7 mt km^{-2}) and shortspine (*ca.* 1.1 mt km^{-2}) thornyheads, and sablefish (*ca.* 0.9 mt km^{-2}). The 16 next most abundant species together make up less biomass than either Dover sole or longspine thornyhead alone. These four aforementioned species dominate the fish biomass to about 1,100 m depth. Below this depth, and to about 1,280 m, the Pacific grenadier, *Coryphaenoides acrolepis*, is significantly more abundant than any other slope species. This basic pattern of dominance persists between southern California (e.g., 34°N, 118°W) and the California slope off Eureka (e.g., 41.5°N, 125°W), except that shortspine thornyheads become less abundant, and Pacific hake (*Merluccius productus*) more abundant, between 550 and 1,100 m depth. Sablefish and the giant grenadier (*Coryphaenoides pectoralis*) become increasing more abundant between 1,100 and 1,280 m. As the longspine thornyhead is probably the most successful benthic species of the lower mid-portion of the California slope, maintaining significant abundance below 1,100 m where Dover sole and shortspine thornyhead do not, it could be regarded as a paradigm benthic species of the slope.

Among the truly deep-sea fishes, the grenadiers (Macrouridae) form the richest depth replacement series down the California slope in terms of both numbers of species as well as collective extent of bathymetric range. The shallowest reported species (200 to 300 m) are the shoulderspot (*Caelorinchus scaphopsis*) and softhead (*Malacocephalus laevis*) grenadiers. The latter is known from very few records and reports from the California slope, but is abundant (Wilson, 2001) on an offshore guyot of 500-m crest depth (Fieberling Guyot; 32°27.82′N 127°47.00′W). Wilson (1985) summarized the depth replacement order off California for the grenadiers he studied as follows: California (*Nezumia stelgidolepis*), smooth (*Nezumia liolepis*), Pacific (*Coryphaenoides acrolepis*), ghostly (*Coryphaenoides leptolepis*), abyssal (*Coryphaenoides armatus variabilis*), and rough abyssal (*Coryphaenoides yaquinae*) grenadiers. The two additional California species are the giant grenadier, close in depth distribution to the Pacific grenadier (Iwamoto and Stein, 1974), and the threadfin grenadier (*Coryphaenoides filifer*), overlapping the depth distributions of the Pacific and ghostly grenadiers (Iwamoto and Stein, 1974; Stein and Pearcy, 1982) but with a more extensive bathypelagic habitat (Stein, 1985). Thus, there exist an upper-slope group of grenadiers abundant between about 200 and 600 m consisting of the shoulderspot, softhead, and California, a mid- to lower slope group abundant between about 600 and 2,000 m consisting of the smooth, Pacific, and giant, an upper continental rise group abundant between about 2,000 and 4,300 m consisting of the filamented, ghostly, and abyssal, and one truly Pacific basin species abundant below about 4,300 m—the rough abyssal grenadier (Wilson and Waples, 1983).

Life in the Deep-Slope and Basin Habitats

Off southern California, the abundant deep-sea benthic and benthopelagic fishes inhabiting the borderland basins are

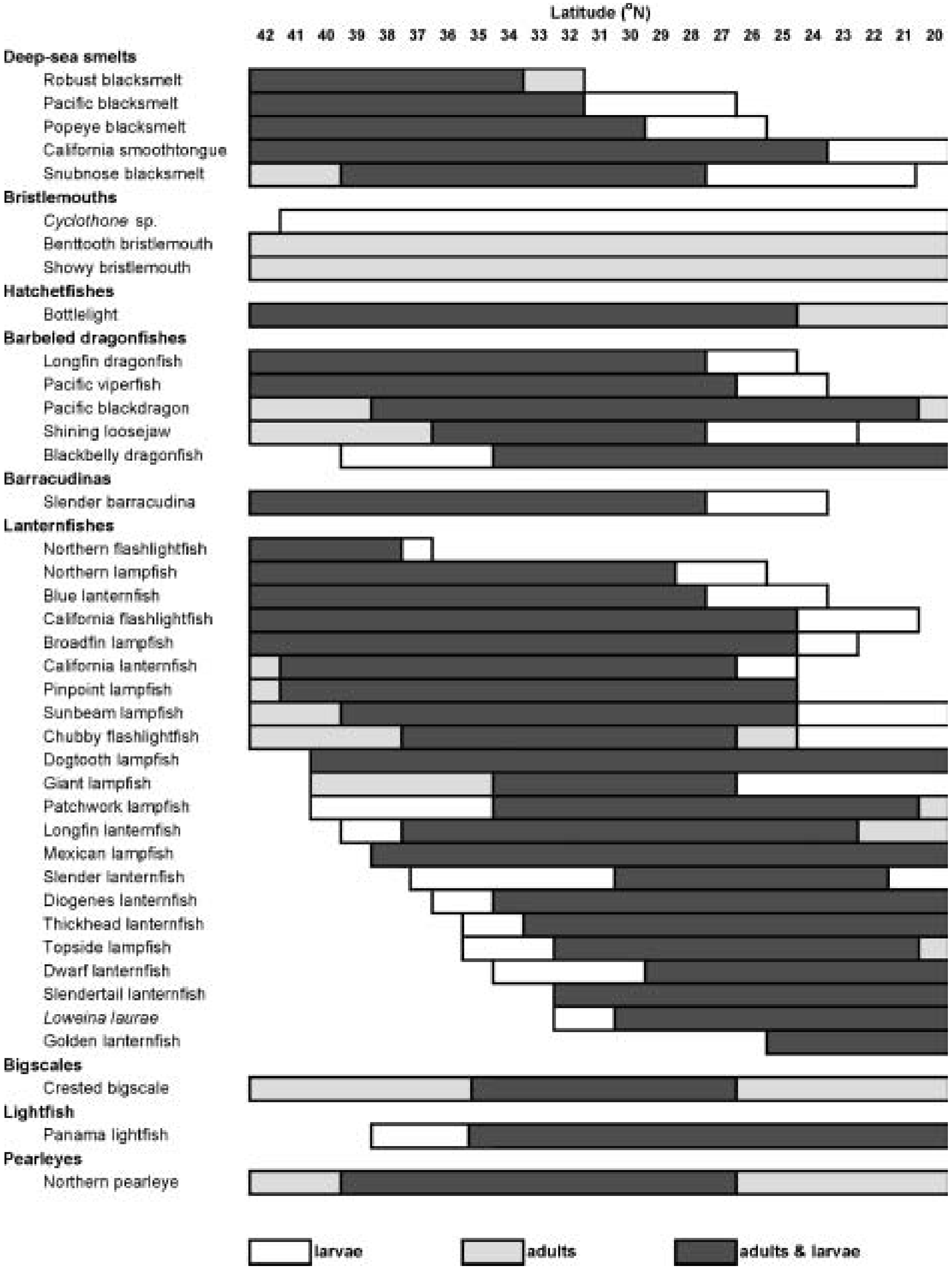


FIGURE 13-9. Distributions off the coasts of California and Baja California of the larvae and adults of selected midwater fishes. (Data sources: Miller and Lea, 1972; Hart, 1973; Wisner, 1976; Moser et al., 1993; Moser et al., 1994; *Fish Base* Froese and Pauly, 2003).

among the best studied ecologically. These include black hagfish, Pacific grenadier, smooth grenadier, longspine thornyhead, and sablefish. The most studied borderland basin where the above assemblage plus several other species (table 13-3) can be found is the Santa Catalina Basin (SCB) lying at about 1,340 m (fig. 13-2). The benthic community of this deep-sea basin has been thoroughly studied as a unit with all of the sampling devices listed above. In addition, the various fish species have been separately studied elsewhere in their respective ranges; our focus here is the best-known species.

The longspine thornyhead (fig. 13-10) is the most abundant benthic fish in the SCB at a density of *ca.* 2 individuals 100 m^{-2} and is uniformly distributed (Smith and Hamilton, 1983). Black hagfish and smooth grenadier are likely next in abundance there. Elsewhere along the central and northern California slope between Point Conception and Eureka, longspine thornyhead is in greatest abundance between about 700 and 900 m where it numerically dominates the mid- to deep-slope assemblage by a huge degree (Lauth, 1999). Wakefield and Smith (1990) estimated its average density on the California slope off Big Sur at as high as 8 individuals 100 m^{-2} near 1,000 m depth, decreasing to *ca.* 2 individuals 100 m^{-2} near 1,200 m (as in the SCB). In the deep waters of Monterey Bay, the estimate was *ca.* 4 individuals 100 m^{-2} at 800 m, and 1.3 individuals 100 m^{-2} near 1,200 m (Vetter and Lynn, 1997). Wakefield and Smith (1990) suggested that 83% of the population (biomass) was contained between 600 and 1,000 m depth on the slope. Along the entire extent of the slope between Pt. Conception and Vancouver Island, Canada, approximately 81% of the total biomass reported for this species was between 550 and 1,100 m (Lauth, 1999). The catch per unit effort (CPUE) in the above depth interval ranged between *ca.* 3.3 mt km^{-2} off Point Conception to *ca.* 3.6 mt km^{-2} off Eureka, California, where it is the most abundant fish in that depth interval.

Longspine thornyhead is a determinate spawner that spawns annually (but with multiple iterations per female over several years) during February and March off California (Wakefield and Smith, 1990, plus authors cited therein). Newly hatched larvae occur in the near-surface plankton into late spring, but the pelagic development phase can last for 18 to 20 months (Moser, 1974) before juveniles settle at *ca.* 55 mm SL (Wakefield and Smith, 1990). Within the first year after settlement, fish probably reach 80 mm SL, and adults evidently spawn by about 150 mm SL. Based on the growth rings of sagittae, a fish that size would be between 5 and 8 years old (Kline, 1996).

Daytime observations from the deep submersible *Alvin* of pelagic juveniles of longspine thornyhead in midwater over the SCB indicated greatest abundance near 600 m (Smith and Brown, 1983). That pelagic juveniles concentrate near that depth in midwater over a deep (1,300 m) basin is notable because it coincides with the shallowest depth of occurrence of newly-settled juveniles on the slope (Wakefield and Smith, 1990). Juveniles near settlement size and impinging the slope would settle frequently near this depth. *In-situ* respirometry performed on two pelagic juveniles of 41.3 and 37.7 mm SL indicated diel activity, with the fish becoming most active at night, possibly to forage on their principal prey, the krill *Euphausia pacifica* (Smith and Brown, 1983). Similar respirometry measurements on four benthic adults did not show the same diel fluctuations as the juveniles (Smith and Brown, 1983).

Comparison of direct metabolic rate measurements from *in situ* respirometry (Smith and Brown, 1983) and metabolic rates inferred from an analysis of enzymatic activities suggested that the population oxygen consumption rate of longspine thornyhead at maintenance metabolism in the depth zone of its greatest abundance could be as high as 285 $\mu l\ O_2\ m^{-2}\ d^{-1}$ (Vetter and Lynn, 1997). To service its resting metabolism by these estimates a 200 g individual would have to consume an average of a 10-g meal only 3 or 4 times a year! An individual of 200 g biomass would likely be in the upper third of the size distribution, reproductively mature, and probably near 15 y old. Its resting *in-situ* oxygen consumption rate would be *ca.* 2.3 $\mu l\ O_2\ g^{-1}$ wet wt hr^{-1} (Smith and Brown, 1983). Relative to this maintenance requirement, the evident principal prey of adult longspine thornyhead, the brittle star, *Ophiopthalmus normani*, would represent a tremendously abundant food resource in the SCB (Smith and Hamiltion, 1983), even if the fish required substantial multiples over the maintenance requirement for its ultimate growth and reproduction.

Such minimal food requirement might explain why longspine thornyhead are not as readily or as easily attracted to bait as other species of the SCB community mentioned above. Many deployments of vertical baited hook lines and experimental bait drops in the SCB and in the San Diego Trough (SDT) observed with time lapse and video cameras attracted very little interest from them (Wilson, pers. obser.) in comparison to sablefish, black hagfish, grenadiers (SDT), and the Pacific flatnose (SDT). Regarding longspine thornyhead on the slope of California or in the borderland basins as a paradigm of a food-limited, deep-sea fish population is difficult. One should perhaps consider predation, possibly from deep-diving pinnipeds or benthic/benthopelagic sharks, as a factor limiting its population size. One need barely handle freshly trawled specimens to appreciate the defensive nature of the thorny spines about the head that surely exist to deter predators.

Kline (1996) and Cailliet et al. (2001) studied growth rates and longevities of longspine thornyheads in the size range of 104 to 307 mm TL from specimens trawled on the California slope between 100 and 1,400 m depth. Ages estimated from growth-ring (increment) counts of the sagittal otoliths reached 40 y for fish near 300 mm TL. Validation of the growth increments as annual marks was accomplished by radiometric ageing of pooled cores of otoliths of similar mass (size), over a range of sizes. Cores were pooled from otoliths composing one of the native pair of an individual whose other pair member had increment counts similar to others in the pool. Longevities estimated from increment counts plus radiometric ageing of cores largely agreed, suggesting ages of near 40 y for 300 mm TL fish. Although the radiometric technique does not permit direct ageing of individuals, because of the requirement that cores be combined from few to several individuals, the technique appears at least to support growth-ring (increment) periodicities as annual. The von Bertalanffy parameter was estimated at 0.072, inside the range (0.05 to 0.15) biologists generally consider low.

The 18 to 20 months that longspine thornyhead spend in the pelagial evidently allow dispersal widely along the coast of western North America, and even colonization of seamounts in the depth range near 500–600 m 500 nautical miles offshore of California (Wilson, 2001) as well in the Gulf of Alaska (Kaufmann and Wilson, 1991). Population genetic studies (Siebenaller, 1978; Stepien et al., 2000) have found but scant evidence of genetic population structure, evidence that could disappear entirely with additional population sampling.

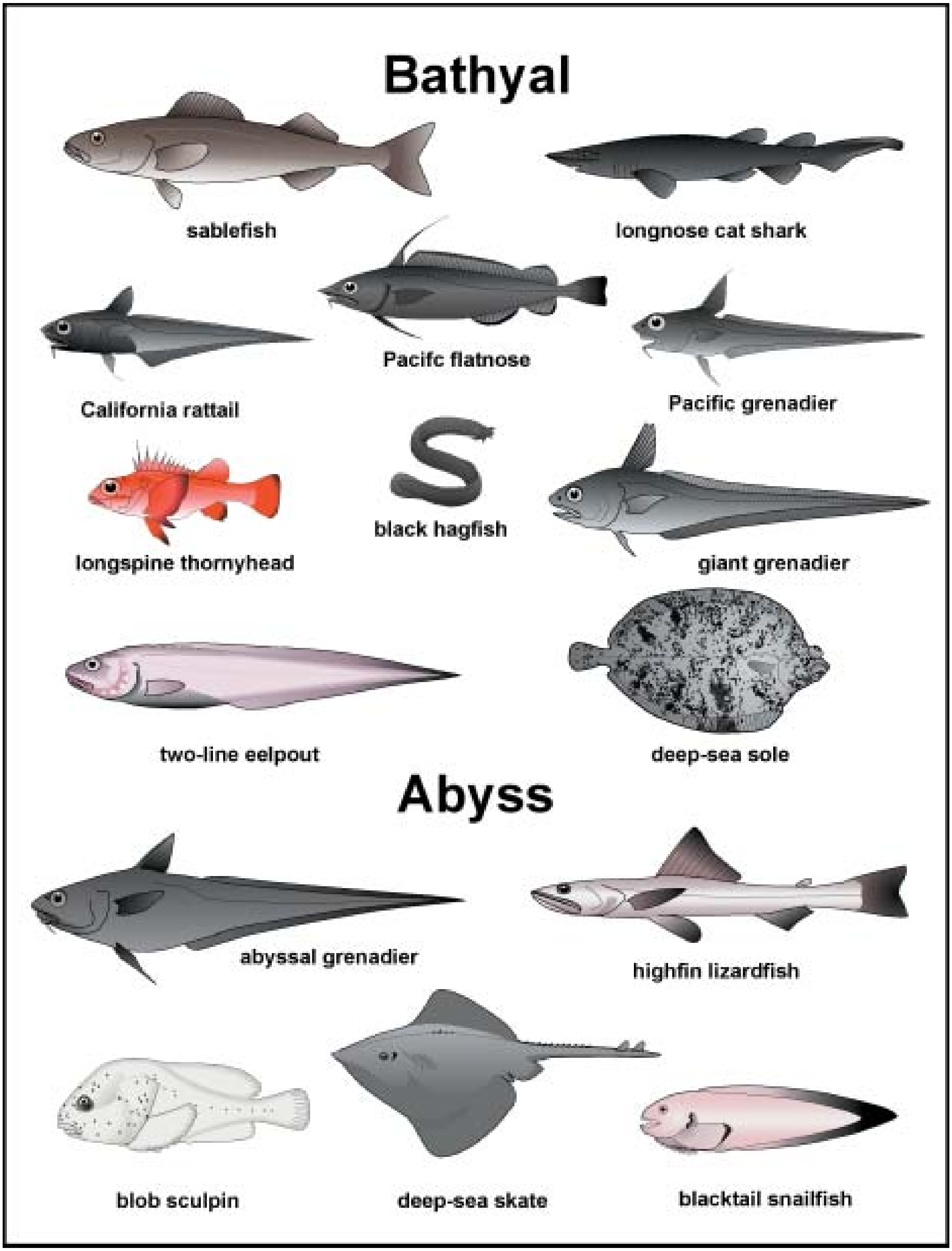


FIGURE 13-10. Representative benthic and benthopelagic fishes of the bathyal (deep slope) and abyss.

Average allozyme heterozygosity (0.047) and its mtDNA equivalent, haplotype diversity (0.96), were not low in this species, indicating a sufficient level of genetic diversity exists to detect population genetic structure if indeed present.

Partially sharing the deep-slope with the benthic longspine thornyhead are the grenadiers. These benthopelagic fishes, which have a gas-filled swimbladder conferring neutral buoyancy even under tremendous hydrostatic pressure, are able to "swim freely and habitually near the ocean floor" (Marshall, 1965). Thus, benthopelagic fishes typically have a diet that is a mixture of both benthic and pelagic prey items (Marshall and Merrett, 1977).

The Pacific grenadier (fig. 13-10) is likely the most abundant grenadier inhabiting the deep slope below about 900 m off California, particularly off southern California. Nearly 97% of its population biomass caught between 550 and 1,280 m on the California slope occurs below 915 m (Lauth, 1999), averaging about 1.8 mt km^{-2} of biomass between Pt. Conception and Oregon's Columbia River region (CPUE data of Lauth, 1999). Its full geographic range extends from off Baja California along the Pacific Rim to northern Japan, where it ranges to *ca.* 2,500 m (Iwamoto and Stein, 1974). Pacific grenadier is apparently surpassed in abundance deeper than about 1,000 m off Eureka and points north by the giant grenadier, its closest phylogenetic relative in the eastern Pacific Ocean (Morita, 1999; Wilson and Attia, 2003). The deepest capture known to us is from about 3,680 m off the Patton Escarpment (32°29.6′N, 120°26.8′W; SIO82-2), where two individuals were caught on a free-vehicle hook line where the hooks were at *ca.* 20 m above the bottom. Although other captures of Pacific grenadier over deep bottoms with trawls have been attributed to capture in midwaters (Iwamoto and Stein, 1974), such would not be the case here.

The Pacific grenadier also inhabits the borderland basins of southern California (fig. 13-2). Large adults are uncommon in the SCB where chiefly only benthic juveniles, in combination with adults of the smaller smooth grenadier, are seen with submersibles and camera sleds, or captured in trawls. Smooth grenadiers there are roughly three times more abundant than juveniles of Pacific grenadier and together they average about 1–2 individuals 1,000 m^{-2} (Wilson, pers. obser.), which is less than one-tenth the density of longspine thornyhead. Thus, the abundance of Pacific grenadier at sizes common in SCB (i.e., 200 to 300 mm) appears lower than the average density of similar-sized individuals on the California slope, which is near 2 individuals 1,000 m^{-2} (Drazen, 2002). In the adjacent SDT and San Clemente Basin large adult grenadiers are frequently caught on vertical hook lines along with sablefish and Pacific flatnose (Wilson, pers. obser.)

The earliest developmental stages of the Pacific grenadier are known from but a few specimens collected off Oregon (Stein, 1980). The larvae probably develop rapidly in the water column and then settle to as shallow as 600 m (Drazen et al., 2001) as alevins (Merrett, 1989) at about 80 mm TL (Stein and Pearcy, 1982); planktonic duration is not known. Benthic juveniles forage on the bottom, consuming polychaetes and epibenthic crustaceans (Drazen et al., 2001; Drazen, 2002). With increasing size fish migrate to greater slope depths below 1,000 m (Stein and Pearcy, 1982) and consume progressively larger and more pelagic prey, including fishes (hake), squids, and larger crustaceans, although forging on epibenthic organisms continues. Scavenging is evident among the large adults. Drazen (2002) determined that the slope population of Pacific grenadier likely consumes about 2.7 kg km^{-2} d^{-1} of prey, chiefly as squid, fish, and scavenged materials. Unlike the benthic thornyheads, Pacific grenadier becomes benthopelagic in habitat with increasing size.

Also, unlike the thornyheads, Pacific grenadier is readily attracted to bait—a fact exploited in studies of this species. Smith and Hessler (1974) baited it to an *in-situ* respirometer in the SDT and obtained the first metabolic rate measurement for any deep-sea benthopelagic fish. At 2.4 μl O_2 g^{-1} wet wt hr^{-1} the resting metabolism of the 1.8 kg fish was 1/25 that of a codfish measured at the same temperature. Wilson and Smith (1985) similarly baited Pacific grenadiers to a hyperbaric trap/aquarium system and brought a fish successfully to the surface under hydrostatic pressure near what it had experienced at depth. That fish was subsequently maintained for 41 h in a laboratory cold room on shore and was clearly able to maintain neutral hydrostatic buoyancy under high pressures.

Wilson (1982), Matsui et al. (1990), and Andrews et al. (1999) studied the age and growth of Pacific grenadier. Wilson (1982) published data from vertebrae stained with alizarin red, but also studied sagittal otoliths sectioned in the sagittal plane. Matsui et al. (1990) used the break and burn technique to count otolith grow rings, and Andrews et al. (1999) used radiometric ageing of the sagittae in conjunction with counting sagittal growth rings in transverse sections. Even small, seemingly young individuals of 251 mm TL have relatively large sagittae (e.g., 5.5 mm) with as many as 8–10 growth rings (Wilson, pers. obser.). The radiometric ages of Andrews et al. (1999) fall between about 48 and 67 years for the largest fish (*ca.* 800 mm TL); the von Bertalanffy parameter was 0.041. Radiometric ages essentially agreed with ages estimated from ring counts in the sagittae, although the rings indicated slightly younger ages overall (*ca.* 38 to 62 y). Unpublished counts (Wilson) from sectioned sagittae agreed with Andrews et al. (1999) for fish up to about 400 mm TL, the lumped average length of fish with 15, 16, or 17 sagittal growth zones, but were lower for the larger fish.

Pacific grenadier mature by *ca.* 580–600 mm TL and are spawning by this size, if not earlier. Based on Andrews et al. (1999), fish this size would be near 30–32 y of age. In the San Diego Trough, females dominate the sex ratio and are larger on average than the males, reaching over 800 mm TL versus approximately 700 mm for males. Ripe and spent ovaries have been seen among fish taken from the San Diego Trough in October, December, and February (Wilson, pers. obser.). Off Oregon, females with ripe ovaries occur in April and September, and those with ripe or spent ovaries in October (Stein and Pearcy, 1982).

The giant grenadier (fig. 13-10) is likely the most abundant deep-slope grenadier off California after the Pacific grenadier, especially off northern California. They share a coincident Pacific Rim distribution in approximately the same depth zone, and giant grenadier has been captured in the SCB on vertical hook lines (Wilson, pers. obser. SIO80-3, SIO80-4). However, the species generally ranges shallower on the California slope than the Pacific grenadier as only 77% (compared to 97%) of the population biomass sampled between 550 and 1,280 m occurs deeper than about 915 m. This species greatly dominates trawl catches of grenadiers in northern California and further north into the Bering Sea and along Kamchatka (Novikov, 1970; Lauth, 1999).

Albatrossia pectoralis is the binomen often used for the giant grenadier, but the species has variously been referred to the genera (or subgenera) *Coryphaenoides, Nematonurus,* and *Chalinura* (Iwamoto and Stein, 1974; Iwamoto and Sazonov, 1988). Adults reach the unusual size of over a meter in length and can weigh 7.5 kg (Novikov, 1970; Iwamoto and Stein, 1974); the muscle tissue is flaccid, and the small scales highly deciduous, rendering the fish ungainly in appearance upon capture by trawls. Despite its unusual appearance and probably derived morphological features (Iwamoto and Stein, 1974), phylogenetic studies (Wilson, 1994; Morita, 1999; Wilson and Attia, 2003) have repeatedly shown it to be a species of *Coryphaenoides*, probably closest to *Coryphaenoides acrolepis* among the eastern north Pacific species that have been studied. Its derived features, pointed out by Iwamoto and Stein (1974), include the flaccid tissue, poorly ossified skull bones, and a reduced swimbladder. The features are possibly a result of a protracted life history stage in midwater (Novikov, 1970; Iwamoto and Stein, 1974).

Drazen et al. (2001) found that giant grenadier over a range of sizes forage in midwater on squids and fishes. Chief among the food items were the bathypelagic squids *Octopoteuthis deletron* and *Vampyroteuthis infernalis,* plus assorted stomiids (e.g., Pacific viperfish), bathylagids, alepocephalids, and myctophids. The largest adults appear to adopt a more benthopelagic, scavenging habit. Other authors have reported similar findings (Novikov, 1970). Little is known about its early life history except that spawning/fertilization probably occurs deep, and the larvae are planktonic at relatively shallow depths (e.g., < 200 m). Yolk-sac larvae persist until about 7.1 mm TL. The anal fin is formed on specimens larger than 22.1 mm TL, and by 38.9 mm the alevin stage (Endo et al., 1993) is reached. Recruitment to the benthic habitat might be delayed until individuals reach about 500 mm TL (Novikov, 1970). Off California the smallest giant grenadier obtained with benthic trawls (Lauth, 1999) were 130 mm preanal length (Drazen et al., 2001). By comparison, the smallest Pacific grenadier caught in the same survey were near 20 mm preanal length (175 mm TL), much larger than the estimated settling size on the Oregon slope of about 80 mm TL (Stein and Pearcy, 1982). The age and growth of the giant grenadier were described in a radiometric age validation study, as was the case with the Pacific grenadier (Andrews et al., 1999), where longevity was described as approaching or exceeding 56 years (Burton, 1999). Estimates of age from otoith sections were difficult to determine because of irregular growth and shape of the sagittal otolith.

The eastern north Pacific populations of Pacific and giant grenadiers are also not lacking in genetic diversity (i.e., average heterozygosity). Siebenaller (1978) reported an average observed heterozygosity for Pacific grenadier of 0.033 over 25 presumptive loci. Wilson's (1994) data produced a value of 0.052 over 24 loci for Pacific and 0.034 over 24 loci for giant grenadier, values highly comparable to those determined for 90 species of deep-sea fishes (Creasey and Rogers, 1999).

Life in the Abyssal Habitat

The few abyssal fishes inhabiting the eastern north Pacific Ocean tend to bias perceptions of abyssal ecology to that reflected by the well-studied grenadiers. Considering the somewhat richer abyssal ichthyofauna of the north Atlantic Ocean might broaden perceptions, but in the deepest parts of both ocean basins grenadiers dominate the ichthyofauna and consequently are the best-studied fishes. Among the few abyssal (non-grenadier) fishes of the north Atlantic Ocean that are also known in the eastern north Pacific Ocean, two have received study, the flatnose, *Antimora rostrata* (*Antimora microlepis* is the north Pacific form, fig. 13-10) and the highfin lizard fish (*Bathysaurus mollis*) (fig. 13-10), the latter inhabiting much deeper regions.

In the eastern north Pacific, highfin lizard fish has been taken off Oregon, northern and southern California, and Baja California (Stein and Butler, 1972; Stein, 1985; Sulak et al., 1985; Wilson, pers. obser., SIO85-132) and is generally found between about 1,680 and 4,900 m (Sulak et al., 1985). Off northern California, at least, it occurs with grenadiers, cusk-eels, and snailfishes (e.g., Stein, 1985). It is possibly an ecological depth replacement in the Atlantic Ocean for its close congener, *Bathysaurus ferox* (*ca*. 860 to 3,460 m). Adults reach between 400 and 600 mm TL, but an individual of 835 mm is reported (Sulak et al., 1985).

Lizard fishes are ambush apex predators. The large size of highfin, coupled with its burst-swimming ability (Sulak et al., 1985), indicates its capacity to ambush even large fishes drifting or swimming near the ocean bottom, such as the abyssal grenadier (*Coryphaenoides armatus*), a known prey (Sulak et al., 1985). For example, in the Charlie-Gibbs Fracture Zone of the north Atlantic Ocean many relatively small (150 to 250 mm TL) abyssal grenadiers were recently observed "hanging" horizontally in the water near the bottom of 4,300 m depth, appearing simply to drift (Wilson, pers. obser.). Highfin lizard fish lie perfectly still, seemingly rigid, on the seafloor in total darkness with pectoral and pelvic fins extended. They can be approached in a submersible with lights on to within two meters without the fish flinching or moving noticeably. The dorso-ventrally flattened head is triangular with the mouth well positioned to open and snatch prey such as abyssal grenadier from the overlying water. A close view of the living fish in its native realm revealed its lateral line to be a very prominent feature, one that must alert the predator to the presence of prey such as abyssal grenadier or nektonic shrimp.

As an apparent synchronous hermaphrodite, the highfin lizard fish is monoecious, a possible reproductive adaptation for thinly distributed populations (Sulak et al., 1985). Gonadal maturation appears to be seasonal in Atlantic *Bathysaurus ferox,* but the pattern of gonadal maturation is not known for the highfin. Relatively large (38–83 mm TL) post-larvae occur in the mesopelagial, suggesting protracted planktonic development as in longspine thornyhead, although highfin might grow rapidly once becoming demersal (Sulak et al., 1985).

Sharing the Pacific abyssal habitat with the highfin lizard fish but in far greater abundances are the benthopelagic abyssal grenadier and the more benthic ghostly grenadier, *Coryphaenoides leptolepis*. Of the two, the abyssal grenadier is the more widespread and possibly the most abundant grenadier in the world's oceans. If not, it is likely second only to its congener, the rough abyssal grenadier *Coryphaenoides yaquinae*. Although the earliest capture records of abyssal grenadier are from the Pacific Ocean (H.M.S. *Challenger*), it has been most studied in the north Atlantic Ocean where it is the most abundant and widespread grenadier of the abyss, especially in the northeastern portion (Merrett, 1992). The abyssal grenadier has long been viewed as different from the other species of *Coryphaenoides* having first been assigned (Günther, 1887) to a new subgenus *Nematonurus* that was subsequently recognized as a full genus (Koefoed, 1927). Iwamoto and Stein (1974) returned *Nematonurus* to subgeneric status within *Coryphaenoides* although the subgenus is still used in the name as in *C. (Nematonurus) armatus*. Wilson's (1994) phylogenetic study suggested that *C. armatus* was derived from the slope-dwelling *Coryphaenoides* species as also seemed true for the co-occurring abyssal *C. leptolepis*—the apparent sister species to *C. armatus* among the species he studied. Morita's (1999) phylogenetic study of North Pacific species conversely suggested that *Coryphaenoides armatus* (+ *Coryphaenoides yaquinae*) was the sister group to the other *Coryphaenoides* species that inhabit the slope, sharing a common ancestor with them. Wilson and Attia (2003) in a further study that included *C. leptolepis* confirmed that a clade containing the abyssal-dwelling species (*C. leptolepis* + (*C. armatus* + *C. yaquinae*)) was sister to the slope-dwelling species of *Coryphaenoides*. Thus, the three abyssal-dwelling grenadier species represent a radiation into the deep sea that parallels that of the other *Coryphaenoides* species inhabiting the slope.

Wilson and Waples (1984) studied the population genetics of the abyssal grenadier between the western north Atlantic and eastern north Pacific oceans. The two populations differed significantly in allele frequencies at two variable loci, *LDH*-A and *PGDH*-A, in a suite of morphometric and meristic characters (Wilson and Waples, 1984; Iwamoto and Sazonov, 1988), and in otolith morphology (Wilson, 1985). (A similar difference in otolith morphology was noted between Atlantic and Pacific specimens of the ghostly grenadier.) The evidence suggested that the abyssal grenadier of the north Pacific Ocean comprised a geographic subspecies, *Coryphaenoides armatus variabilis* Günther (fig. 13-10), apparently confined to a rim distribution at deep-slope and rise depths along the western North American and eastern Asia continents. The rough abyssal grenadier dominates the basin of the north Pacific Ocean where there are no abyssal or ghostly grenadiers present deeper than about 4,300 m (Wilson and Waples, 1983; Endo and Okamura, 1992). In the other ocean basins, the abyssal grenadier occurs at the greatest basin depths, persisting much deeper than the ghostly.

Abyssal grenadiers of the Pacific Ocean reach at least 100 cm TL, but neither the average growth rate nor average longevity is known. Sagittal otoliths have what appear to be periodic growth zones similar to those observed in the otoliths of shallow-dwelling fishes (Wilson, 1988). The zones have also been reported for abyssal grenadiers of the Atlantic as well as for many other grenadier species (Swan and Gordon, 2001). Although the zones were countable, there was no assurance that they represented the full growth record. The number of growth zones was low even among large individuals, thus not suggesting great longevities. Marginal increment analysis of the sagittae (Swan and Gordon, 2001) suggested seasonal periodicity in the formation of tertiary (Wilson, 1988) growth zones, but their analysis pertained to relatively small (young) fish and might not hold for full-sized adults (Campana, 2001).

Even though there are apparent annual growth zones, counting them would probably remain a problem among large fish. Sagittae of large specimens are dome-shaped and appear to grow allometrically by accretion at the lateral surface with little along the antero-posterior axis (Wilson, 1985). Radiometric ageing might establish longevities for abyssal grenadier, but the small size and low mass of the sagittae, particularly in the Pacific form, would hinder the core method of recent use (Cailliet et al., 2001).

The abyssal grenadier appears to be an active fish at its largest sizes both in the Atlantic and in the Pacific oceans where the largest individuals in the eastern North Pacific are females (Stein and Pearcy, 1982; Wilson, 1984). The fish are well-known to scavenge bait and other organic materials that fall to the seafloor (Pearcy and Ambler, 1974; Wilson and Smith, 1984), arriving at experimental bait falls in as few as 8 min after baits hit bottom (Wilson and Smith, 1984). Analyses of arrival times of first individuals at experimental bait falls (Priede and Bagley, 2000) suggested that its average standing abundance in the eastern north Atlantic Ocean (exclusive of the Maderia Abyssal Plain) was about 342 fish km^{-2}. The average density in the eastern north Pacific Ocean is about 463 fish km^{-2} representing *ca.* 0.15 mt km^{-2} (Priede and Bagley, 2000), about one-tenth that of the Pacific grenadier on the slope.

Acoustic tagging and tracking studies have shown that after feeding at an experimental bait drop fish depart the area somewhat irrespective of current direction but with a slight bias toward a cross-current track (Priede and Bagley, 2000). Thus, abyssal grenadiers would appear to be active searchers given the reasonable assumption that a fish with an ingested acoustic tag, but not necessarily satiated, will more-or-less resume its before-feeding behavior after tagging. Departing fish eventually swim much farther from the bait than the distance from which they probably had come, as estimated from arrival times, in obvious response to current-borne bait odors. The large ones, at least, apparently do not return to waiting positions (Wilson and Smith, 1984) near where they had been prior to responding to bait odors (Priede et al., 1990). Recent submersible observations at 4,400 m in the Charlie-Gibbs Fracture Zone (north Atlantic Ocean) support the notion that unlike small individuals, large fish do actively swim about (Wilson, pers. obser.).

Stomach-content analyses (Pearcy and Ambler, 1974) agreed with reports for other species such as the Pacific grenadier (Pearcy and Ambler, 1974; Drazen et al., 2001) in that as a fish grows, pelagic prey items increase in importance. Fish larger than 500 mm TL fed almost entirely on scavenged pelagic prey, but this appeared to be less so for the ghostly grenadier where only about half the prey items were pelagic (Pearcy and Ambler, 1974).

Priede et al. (1990) suggested that the amount of time grenadiers remain near an experimental bait fall after the bait has been consumed (i.e., the staying time) is possibly an inverse indicator of the commonness of naturally-occurring food falls to that bottom habitat, essentially an inverse indicator of the relative amount of overlying oceanic productivity. Video recordings of behavior at experimental bait drops (Wilson and Smith, 1985; Wilson, unpubl. data) set near 3,800 m off the Patton Escarpment show large abyssal grenadiers arriving very quickly, consuming the bait, and then dispersing quickly—all in less than an hour. Thus, relatively few fish accumulate at the bait, producing the shortest staying times observed of *ca.* 30 min (Wilson, unpubl. data). Near 4,400 m in the eastern north Pacific Ocean, large individuals of both the abyssal and the rough abyssal grenadier are present. The average staying time there is about is 60 min (Priede et al., 1991). In the central north Pacific basin near 5,900 m where only the rough abyssal occurs (Wilson and Waples, 1983), the staying time of 261 min is the greatest seen among the three sites studied in the north Pacific (Priede et al., 1991). The much longer staying time allows for the accumulation of many fish at the bait drop. Thus, beneath the moderate-productivity waters of the eastern north Pacific Ocean where the most food potentially available for scavenging is produced the staying time is the least, so the least number of fish are seen at once. Beneath the low-productivity waters of the central gyre the staying time is the greatest, and many more fish are seen at once. This same pattern of staying time with respect to productive versus unproductive regions of the Atlantic Ocean has been seen for abyssal grenadier there (Priede et al., 1991; Priede and Merrett, 1998), as well for other species in the other oceans of the world (Isaacs and Schwartzlose, 1975).

Priede et al. (1990) suggested that the behavior of these grenadiers with respect to staying time is governed by optimal foraging pressure, influenced by the amount of food striking the seafloor. In low productivity regions where food striking the seafloor is a relatively rare and unpredictable event, fish remain longer at a site where food previously was found, rather than resume searching anew with the comparatively low chance of an encounter; fish therefore accumulate. Where food striking the seafloor is a relatively frequent, comparatively predictable event, the chance of finding additional food anew from a random search would be greater. Remaining at the present site would have less potential benefit, so the fish disperse quickly after the bait has been consumed and do not accumulate.

Bailey and Priede (2002) modeled expected fish arrival and accumulation rates at bait for three alternative foraging strategies—cross-current searching, sit and wait, and passive drifting. Modeled (i.e., predicted) rates were based on empirical estimates of fish densities and were assumed to be in response to odor plumes emanating and spreading out from bait sources (food falls) on the seafloor. None of the models completely described foraging behavior of abyssal grenadiers at bait falls. Observed arrival rates agreed best with those predicted from the cross-current foraging model, and that model accurately described accumulation around large carcasses. Although the sit-and-wait model more accurately predicted peak numbers of fish, numbers that were much lower than predicted from the cross-current model, its predictions did not agree with arrival rates. The passive-drifting model was the least predictive.

No *in situ* estimates of basal metabolism exist for the abyssal grenadier of the Pacific Ocean, but Smith (1978) measured the O_2 consumption rate for three specimens in the Atlantic Ocean. The rate for the largest fish (1.2 kg) was 2.7 μl O_2 g^{-1} wt wet hr^{-1}, close to that determined for the slope-dwelling Pacific grenadier (2.4 μl O_2 g^{-1} wt wet hr^{-1}) of similar size. Analysis of stores of neutral lipids and glycogen indicated that abyssal grenadier in the Atlantic might survive 186 d without feeding. If the average basal metabolism of the Atlantic and Pacific abyssal grenadiers proved nearly the same, there would be little metabolic difference between abyssal and Pacific grenadiers in the Pacific. Thus, invasion of the deeper habitat by the abyssal grenadier (i.e., 3,800 to 4,400 m versus 1,100 m for Pacific grenadier) has not caused a reduction in basal metabolism. Therefore, the decreased food resources in the deeper habitat of the abyssal grenadier must be met by a reduced population biomass (i.e., approximately 1/10 that of Pacific grenadier on the slope). Population biomass of the abyssal grenadier in the eastern north Pacific is clearly food limited, and the same is as likely true for the rough abyssal grenadier at even greater depths, facts supporting Priede et al.'s (1990) hypothesis.

Practically nothing is known of the reproductive biology and early life history of abyssal grenadier from any of the world's oceans. Females with ripe ovaries are rarely seen (Stein and Pearcy, 1982; Stein, 1985) despite extensive collections. No early developmental stages or alevins have been reported for the abyssal grenadier but have been for the ghostly grenadier in which development is pelagic and transformation to the alevin occurs by 15.2 mm head length (HL) (Stein, 1980). Catches from bottom trawls suggest that the youngest juveniles, as in other deep slope fishes, "settle" near the shallow end of the depth range (*ca.* 2,000 m) near 80 mm TL (50 mm TL for ghostly), moving to greater depths with growth (Stein and Pearcy, 1982; Merrett, 1992). However, recent submersible observations made between 2,000 and 3,700 m depth in the Charlie-Gibbs Fracture Zone revealed that such small *C. armatus* overwhelmingly reside 1 to 2 m above the sediment, rather than directly on it, and were indeed abundant near 2,000 m. That layer of the water column has probably not been well sampled with trawls, accounting for the relatively few fish of that size in collections (e.g., Stein and Pearcy, 1982).

The rough abyssal grenadier is the ecological (depth) replacement of the abyssal grenadier deeper than about 4,300 m in the basin of the north Pacific Ocean (Wilson and Waples, 1983; Endo and Okamura, 1992). It ranges across the North Pacific from the continental rise of western North America (Wilson and Waples, 1983) to the rim of the Japan Trench (Endo and Okamura, 1992) and is probably the deepest-dwelling grenadier in the world's oceans with records to 6,450 m along the Japan Trench (Endo and Okamura, 1992). It possibly ranges beyond the Pacific Ocean basin, but no published record of occurrence outside the North Pacific exists except for an H.M.S. *Challenger* record barely south of the central Pacific equator (Wilson and Waples, 1983). The species is not reported from either the north or south Atlantic, or Indian, ocean basins where the Atlantic form of the abyssal grenadier dominates trawl catches below 2,000 m at temperate latitudes (Wilson, 1984; Middelton and Musick, 1986; Merrett, 1992). Somewhere in the abyssal basin of the western south Pacific Ocean, the rough abyssal grenadier most likely yields the basin habitat to the Atlantic form of abyssal grenadier. Thus, over much of the world, the North Atlantic form occupies the entire depth range that uniquely in the north Pacific is shared between two grenadiers. Perhaps the rough abyssal grenadier will prove to be a species with a Pacific plate distribution (Springer, 1982). If so, one would not expect to find this species in its depth range (ca. 3,800 to $>$ 6,000 m) on the Nazca Plate between the east Pacific Rise and the Peru-Chile Trench. Only the abyssal grenadier has been collected from there (Wilson and Waples, 1983; Iwamoto and Sazonov, 1988), but sampling has apparently been shallower than 4,000 m.

Rough abyssal and abyssal grenadiers are closely related genetically ($I = 0.74$, Wilson and Waples, 1983), are very similar morphologically (Iwamoto and Stein, 1974; Endo and Okamura, 1992), and are probably true sister taxa among macrourids (Morita, 1999, Wilson and Attia, 2003). Compared to specimens from the eastern Pacific, rough abyssal grenadier of the central Pacific show significant allelic frequency differences at one genetic locus, significant morphometric differences in interorbital width and upper jaw length, a slightly lower average heterozygosity from 27 loci (0.028 *vs.* 0.033), and slightly smaller sagittae (Wilson and Waples, 1983; Wilson, 1985). This vast basin-wide population of rough abyssal grenadier might prove not to be genetically homogeneous over its range (e.g., Creasy and Rogers, 1999).

As with abyssal grenadier, virtually nothing is known of reproduction and early life history of the rough abyssal grenadier. Between about 3,600 and 3,800 m in the eastern Pacific Ocean off southern California individuals are mostly between about 270 and 460 mm TL. At greater depths (e.g., 4,800 m) but still relatively near the continent, individuals are mostly $>$ 700 mm TL. In the central north Pacific basin near 5,900 m, this size segregation is less evident with both small and large individuals occurring together (Wilson, pers. obser.).

Thus, the ontogeny and early life history of the rough abyssal grenadier differ from that of its slope-dwelling congeners and perhaps even the abyssal grenadier as settlement within a narrow inshore-offshore interval of distance over the slope or rise would no longer be necessary. A different set of life conditions for the central basin population might explain the apparent genetic and morphological differences.

Wilson (1988) studied thin-sectioned otoliths of rough abyssal grenadier in the sagittal plane and found ostensible growth zones including evident daily growth increments. As the deepest dwelling grenadier in the Pacific Ocean, it has the smallest otoliths (Wilson, 1985). The finest-scale growth increments, interpreted as daily, were much more closely spaced (2 µm or less) in otoliths of specimens from the central basin than in otoliths of specimens from the eastern north Pacific, where increment spacing was nearly the same as that seen for the abyssal grenadier (Wilson, 1988). Confirmation by others that such growth zones are in fact deposited periodically, even annually, in deep-sea fishes (Andrews et al., 1999; Cailliet et al., 2001; Swan and Gordon, 2001) implies that the central basin fishes are growing more slowly than conspecifics inhabiting shallower depths near the continent—perhaps only half as fast. This disparity in growth would be consistent with Priede et al.'s (1990) observation and explanation of long staying times at bait drops among the rough abyssal grenadiers of the central basin. The relative scarcity of food in the central Pacific basin is reflected both in an evident slowing of growth as seen in otolith increments and in foraging behavior conforming to predictions from optimal foraging theory.

The Future

Many aspects of the ecology of deep-sea fishes of the eastern Pacific Ocean remain of general interest. For example, how might species composition vary in numbers or biomass within and between years? Are bathymetric distributions generally stratified by size, sex, and degree of gonadal maturity? What drives ontogenetic changes in diet and feeding times and places? How might competition and predation structure communities or function as limiting factors for population size and species diversity? Where and when does spawning occur among the species of most interest; what are the cues? How much population and genetic exchange takes place among populations in different areas such as among the various borderland basins, latitudinally along the slope, or across the Pacific abyss? Are there seasonal or other types of periodic long migrations?

Answering the above questions and probably many others must continue to include development and application of new and advanced technologies. Ultimately, progress and discovery in science, all science, is technology dependent, be it from the advent of SONAR, multiple opening and closing nets (e.g., MOCNESS), thermally-protected cod-ends and pressure-insulated traps, ROVs and AUVs (autonomous underwater vehicles), manned submersibles and accessories, *in situ* respirometry, *in situ* acoustic tracking and telemetry, radiometric ageing, molecular genetics (and systematics), or advanced computational methods.

Each stand-alone technology eventually reaches a point where little more that is truly new is produced, and much more of the same inevitably results. Integration of advanced technologies raises the chances for progress. For example, increased sampling with MOCNESS, large benthic trawls, submersibles, and ROVs/AUVs might answer questions regarding bathymetric distribution and vertical stratification by size or sex, but probably not about population or genetic exchange among areas, or periodic migration, unless joined with molecular genetics or acoustic tracking. In the future, sampling and *in situ* observation in the deep sea should be even more thoughtfully integrated with other methods with the aim of hypothesis testing through experimentation.

Acknowledgments

The first author would like to thank the Natural History Museum of Los Angeles County and Christine E. Thacker for access to the resources of the Section of Fishes, as well as Richard F. Feeney, Michael H. Horn, and Jeffrey A. Seigel for comments on a draft of the chapter. Larry G. Allen's development and final execution of the figures are also appreciated.

Literature Cited

Ahlstrom, E.H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish. Bull. 161:107–146.

Alexander, R. McN. 1971. Swimbladder gas secretion and energy expenditure in vertically migrating fishes, p. 74–82. In: Proceedings of an international symposium on biological sound scattering in the ocean. G. B. Farquhar (ed.). U.S. Gov. Printing Office, Washington, DC

———. 1972. The energetics of vertical migration by fishes. Symp. Soc. Exp. Biol. 26: 273–294.

Ambrose, D.A. 1996. Platytroctidae: tubeshoulders, p. 234–239. In: The early stages of fishes in the California Current region. Calif. Coop. Oceanic Fish. Invest. Atlas No. 33. H. G. Moser (ed.). Allen Press. Lawrence, KS.

Andersen, N.R., and B.J. Zahuranec (eds.) 1977. Oceanic sound scattering prediction. Plenum Press, New York, 859 pp.

Anderson, M.E., G.M. Cailliet, and B.S. Antrim. 1979. Notes on some uncommon deep-sea fishes from the Monterey Bay area, California. Calif. Fish Game 65:256–264.

Andrews, A.H., G.M. Cailliet, and K.H. Coale. 1999. Age and growth of the Pacific grenadier (*Coryphaenoides acrolepis*) with age estimate validation using an improved radiometric ageing technique. Can. J. Fish. Aquat. Sci. 56:1339–1350.

Angel, M. V. 1997. What is the deep sea? p. 1–41. In: Deep-sea fishes. D.J. Randall and A.P. Farrell (eds.). Academic Press, San Diego, CA.

Aron, W. 1962. The distribution of animals in the eastern North Pacific and its relationship to physical and chemical conditions. J. Fish. Res. Bd. Can. 19:271–314.

Atsatt, L.H., and R.R. Seapy. 1974. An analysis of sampling variability in replicated midwater trawls off Southern California. J. Exp. Mar. Biol. Ecol. 14:261–273.

Aughtry, R.H. 1953. The biology and ecology of *Cyclothone signata* Garman in the Monterey Bay area. Unpubl. Master's thesis, Stanford University, Stanford, CA, 72 pp.

Badcock, J. 1969. Colour variation in two mesopelagic fishes and its correlation with ambient light conditions. Nature 221:383–385.

Bailey, D.M., and I.G. Priede. 2002. Predicting fish behaviour in response to abyssal food falls. Mar. Biol. 141:831–840.

Bailey, T.G. 1984. Distribution, abundance, and aspects of the life histories of midwater fishes from three regions of the eastern North Pacific. Unpubl. Ph. D. diss., University of California, Santa Barbara, 150 pp.

Bailey, T.G., and B.H. Robison. 1986. Food availability as a selective factor on the chemical compositions of midwater fishes in the eastern North Pacific. Mar. Biol. 91:131–141.

Baird, R.C., and G.Y. Jumper. 1993. Olfactory organs in the deep sea hatchetfish *Sternoptyx diaphana* (Stomiiformes, Sternoptychidae). Bull. Mar. Sci. 53:1163–1167.

Baird, R.C., N.P. Thompson, T.L. Hopkins, and W.R. Weiss. 1975. Chlorinated hydrocarbons in mesopelagic fishes of the eastern Gulf of Mexico. Bull. Mar. Sci. 25:473–481.

Balanov, A.A., and E.N. Il'inskii. 1992. Species composition and biomass of mesopelagic fishes in the Sea of Okhotsk and the Bering Sea. J. Ichthyol. 32(4):85–93.

Barham, E.G. 1971. Deep-sea fishes: lethargy and vertical orientation, p. 100–116. *In:* Proceedings of an international symposium on biological sound scattering in the ocean. G. B. Farquhar (ed.). U.S. Gov. Printing Office, Washington, DC.

Beamish, R.J., K.D. Leask, O.A. Ivanov, A.A. Balanov, A. M. Orlov, and B. Sinclair. 1999. The ecology, distribution, and abundance of midwater fishes of the Subarctic Pacific gyres. Prog. Oceanogr. 43:399–442.

Belman, B.W., and M.E. Anderson. 1979. Aquarium observations on feeding by *Melanostigma pammelas* (Pisces: Zoarcidae). Copeia 1979:366–369.

Belman, B.W., and M.S. Gordon. 1979. Comparative studies on the metabolism of shallow-water and deep-sea marine fishes. V. Effects of temperature and hydrostatic pressure on oxygen consumption in the mesopelagic zoarcid *Melanostigma pammelas*. Mar. Biol. 50:275–281.

Benoit-Bird, K.J., and W.W.L. Au. 2001. Target strength measurements of Hawaiian mesopelagic boundary community animals. J. Acoust. Soc. Am. 110:812–819.

Berry, F.H., and H.C. Perkins. 1966. Survey of pelagic fishes of the California Current area. U.S. Fish. Bull. 65:625–682.

Best, E.A., and J.G. Smith. 1965. Fishes collected by midwater trawling from California coastal waters, March 1963. Calif. Fish Game 51:248–251.

Blaxter, J.H.S., and P. Tytler. 1978. Physiology and function of the swimbladder. Adv. Comp. Physiol. Biochem. 7:311–367.

Blaxter, J.H.S., C.S. Wardle, and B.L. Roberts. 1971. Aspects of the circulatory physiology and muscle systems of deep-sea fish. J. Mar. Biol. Ass. U.K. 51: 991–1006.

Bolin, R.L. 1956. Age and growth of the myctophid fish *Lampanyctus leucopsarus* (Eigenmann and Eigenmann). Proc. XIV Int. Congr. Zool.*,* 1953. p. 541.

Bone, Q. 1973. A note on the buoyancy of some lantern-fishes (Myctophoidei). J. Mar. Biol. Ass. U.K. 53:619–633.

Brewer, G.D. 1973. Midwater fishes from the Gulf of California and the adjacent eastern tropical Pacific. Nat. Hist. Mus. Los Angeles Cty. Contrib. Sci. 242:1–47.

Brown, D.W. 1974. Hydrography and midwater fishes of three contiguous oceanic areas off Santa Barbara, California. Nat. Hist. Mus. Los Angeles Cty. Contrib. Sci. 261:1–30.

Bruun, A.F. 1955. Life and life-conditions of the deepest deep sea. Proc. Eighth Pacific Sci Congress 1: 399–408.

Burton, E.J. 1999. Radiometric age determination of the giant grenadier (*Albatrossia pectoralis*) using ^{210}Pb:^{226}Ra disequilibria. Unpubl. Master's thesis, San Francisco State University, 90 pp.

Butler, J.L., and W.G. Pearcy. 1972. Swimbladder morphology and specific gravity of myctophids off Oregon. J. Fish. Res. Bd. Canada 29:1145–1150.

Cailliet, G.M., A.H. Andrews, E.J. Burton, D.L. Watters, D.E. Kline, and L. A. Ferry-Graham. 2001. Age determination and validation studies of marine fishes: do deep-dwellers live longer? Exper. Geron. 36:739–764.

Cailliet, G.M., and A.W. Ebeling. 1990. The vertical distribution and feeding habits of two common midwater fishes (*Leuroglossus stilbius* and *Stenobrachius leucopsarus*) off Santa Barbara. Calif. Coop. Oceanic Fish. Invest. Rep. 31:106–123.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish. Biol. 59:197–242.

Capen, R.L. 1967. Swimbladder morphology of some mesopelagic fishes in relation to sound scattering. U.S. Navy Electronics Laboratory Res. Rept. 1447. San Diego, CA.

Case, J.F., J. Warner, A.T. Barnes, and M. Lowenstine. 1977. Bioluminescence of lantern fish (Myctophidae) in response to changes in light intensity. Nature 265:179–181.

Castro, P. and M.E. Huber. 1997. Marine Biology, Second Edition. Wm. C. Brown/Time-Mirror, Dubuque, IA, 450 pp.

Childress, J.J., A.T. Barnes, L.B. Quetin, and B.H. Robison. 1978. Thermally protecting cod ends for the recovery of living deep-sea animals. Deep-Sea Res. 25:419–422.

Childress, J.J., and R.P. Meek. 1973. Observations on the feeding behavior of a mesopelagic fish (*Anoplogaster cornuta*: Beryciformes). Copeia 1973:602–603.

Childress, J.J., and M.H. Nygaard. 1973. The chemical composition of midwater fishes as a function of depth of occurrence off southern California. Deep-Sea Res. 20:1093–1109.

Childress, J.J., M.H. Price, J. Favuzzi, and D. Cowles. 1990. Chemical composition of midwater fishes as a function of depth of occurrence off the Hawaiian Islands: food availability as a selective factor? Mar. Biol. 105:235–246.

Childress, J.J., S.M. Taylor, G.M. Cailliet, and M.H. Price. 1980. Patterns of growth, energy utilization and reproduction in some meso- and bathypelagic fishes off Southern California. Mar. Biol. 61:27–40.

Clarke, G.L., and E.J. Denton. 1962. Light and animal life, p. 456–468 In: The Sea, vol. 1. M.N. Hill (ed.). Interscience Publishers, New York, London.

Clarke, T.A. 1972. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. U. S. Fish. Bull. 71:401–434.

Collard, S.B., 1970. Forage of some eastern Pacific midwater fishes. Copeia 1970:348–354.

Cox, J.L. 1970. Accumulation of DDT residues in *Triphoturus mexicanus* from the Gulf of California. Nature 227:192–193.

Creasey, S.S., and A.D. Rogers. 1999. Population genetics of bathyal and abyssal organisms. Adv. Mar. Biol. 35:3–151.

Crescitelli, F. 1989. The visual pigments of a deep-water malacosteid fish. J. Mar. Biol. Ass. U.K. 69: 43–51.

D'Aoust, B.G. 1971. Physiological constraints on vertical migration by mesopelagic fishes, p. 86–97. In: Proceedings of an international symposium on biological sound scattering in the ocean. G. B. Farquhar (ed.). U.S. Gov. Printing Office, Washington, DC.

Denton, E.J. 1970. Review lecture: On the organization of reflecting surfaces in some marine animals. Phil. Trans, R. Soc. Lond. 258B:285–313.

————. 1990. Light and vision at depths greater than 200 metres, p. 127–148 In: Light and life in the sea. P. J. Herring, A. K. Campbell, M. Whitfield, and L. Maddock (eds). Cambridge University Press, Cambridge.

Denton, E.J., J.B. Gilpin-Brown, and P. G. Wright. 1972. The angular distribution of the light produced by some mesopelagic fish in relation to their camouflage. Proc. R. Soc. Lond. B. 182:145–158.

Denton, E.J., P.J. Herring, E.A. Widder, M.F. Latz, and J. F. Case. 1985. The roles of filters in the photophores of oceanic animals and their relation to vision in the oceanic environment. Proc. Roy. Soc. Lond. B 225:63–97.

Denton, E.J. and N.B. Marshall. 1958. The buoyancy of bathypelagic fishes without a gas-filled swimbladder. J. Mar. Biol. Ass. U.K. 37:753–767.

DeWitt, F.A., Jr. 1972. Bathymetric distributions of two common deep-sea fishes, *Cyclothone acclinidens* and *C. signata*, off southern California. Copeia 1972:88–96.

DeWitt, F.A., and G.M. Cailliet. 1972. Feeding habits of two bristlemouth fishes, *Cyclothone acclinidens* and *C. signata* (Gonostomatidae). Copeia 1972: 868–871.

Donnelly, J., J.J. Torres, T.L. Hopkins, and T.M. Lancraft. 1990. Proximate composition of Antarctic mesopelagic fishes. Mar. Biol. 106:12–23.

Douglas, R.H., J.C. Partridge, and N.J. Marshall. 1998. The eyes of deep-sea fish I: lens pigmentation, tapeta and visual pigments. Prog. Retinal Eye Res. 17: 597–636.

Drazen, J.C. 2002. Energy budgets and feeding rates of *Coryphaenoides acrolepis* and *C. armatus*. Mar. Biol. 140:677–686.

Drazen, J.C., T.W. Buckley, and G.R. Hoff. 2001. The feeding habits of slope dwelling macrourid fishes in the eastern North Pacific. Deep-Sea Res. I 48:909–935.

Duxbury, A.C. 1971. The earth and its oceans. Addison-Wesley, Reading, MA, 381 pp.

Ebeling, A.W., and G.M. Cailliet. 1974. Mouth size and predator strategy of midwater fishes. Deep-Sea Res. 21:959–968.

Ebeling, A.W., R.M. Cailliet., Ibara, F. A. DeWitt, Jr., and D. W. Brown. 1971. Pelagic communities and sound scattering off Santa Barbara, California, p. 1–19. In: Proceedings of an international symposium on biological sound scattering in the ocean. G. B. Farquhar (ed.). U.S. Gov. Printing Office, Washington, DC.

Ebeling, A.W., G.M. Cailliet., R.M. Ibara, R. J. Lavenberg, and F. J. Rohlf. 1970. Ecological groups of deep-sea animals off southern California. Bull. Los Angeles Cty. Mus. Nat. Hist. Sci. 6:1–43.

Emery, K.O. 1954. Source of water in basins off southern California. J. Mar. Res. 13:1–21.

———. 1960. The sea off southern California, a modern habitat of petroleum. John Wiley and Sons, Inc., NY, 366 pp.

Endo, H., and O. Okamura. 1992. New records of the abyssal grenadiers *Coryphaenoides armatus* and *C. yaquinae* from the western North Pacific. Jpn. J. Ich. 38:433–438.

Endo, H., M. Yabe, and K. Amaoka. 1993. Occurrence of the macrourid alevins genera *Albatrossia* and *Coryphaenoides* in the northern North Pacific Ocean. Jpn. J. Ichthyol. 40:219–226.

Eschmeyer, W.N. (ed.) 1998. Catalog of fishes. Special Pub. No. 1, Center for Biodiversity Research and Information. California Academy of Sciences, San Francisco, CA. 1–3:1–2905.

Falk-Petersen, I.-B., S. Falk-Petersen, and J. R. Sargent. 1986. Nature, origin and possible roles of lipid deposits in *Maurolicus muelleri* (Gmelin) and *Benthosema glaciale* (Reinhart) from Ullsfjorden, northern Norway. Polar Biol. 5:235–240.

Farquhar, G.B. (ed.) 1971. Proceedings of an international symposium on biological sound scattering in the ocean. U.S. Gov. Printing Office, Washington, DC, 629 pp.

Fast, T.N. 1960. Some aspects of the natural history of *Stenobrachius leucopsarus* Eigenmann and Eigenmann. Unpubl. Ph. D. diss., Stanford University. Stanford, CA, 107 pp.

Fitch, J.E., and R.J. Lavenberg. 1968. Deep-water teleostean fishes of California. University. California Press, Berkeley, 155 pp.

Froese, R., and D. Pauly (eds.) 2003. FishBase. World Wide Web electronic publication. www.fishbase.org.

Frost, B.W., and L.E. McCrone. 1979. Vertical distribution, diel vertical migration, and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer. U.S. Fish. Bull. 76: 751–770.

Gartner, J.V., Jr. 1991a. Life histories of three species of lanternfishes (Pisces: Myctophidae) from the eastern Gulf of Mexico. I. Morphological and microstructural analysis of sagittal otoliths. Mar. Biol. 111:11–20.

———. 1991b. Life histories of three species of lanternfishes (Pisces: Myctophidae) from the eastern Gulf of Mexico. II. Age and growth patterns. Mar. Biol. 111:21–27.

———. 1993. Patterns of reproduction in the dominant lanternfish species (Pisces: Myctophidae) of the eastern Gulf of Mexico, with a review of reproduction among tropical-subtropical Myctophidae. Bull. Mar. Sci. 52:721–750.

Gartner, J.V., R.E. Crabtree, and K.J. Sulak. 1997. Feeding at depth, p. 115–193. In: Deep-sea fishes. D. J. Randall and A. P. Farrell (eds.). Academic Press, San Diego, CA.

Gartner, J.V., T.L. Hopkins, R.C. Baird, and D.M. Milliken. 1987. The lanternfishes (Pisces: Myctophidae) of the eastern Gulf of Mexico. U.S. Fish. Bull. 85:81–98.

Gee, J.H. 1983. Ecologic implications of buoyancy control in fish, p. 141–176. In: Fish biomechanics. P.W. Webb and D. Weihs (eds.). Praeger Publishers, New York.

Gjøsæter, J., and S. Tilseth. 1988. Spawning behaviour, egg and larval development of the myctophid fish *Benthosema pterotum*. Mar. Biol. 98:1–6.

Gorbatenko, K.M., and E.N. Il'inskii. 1992. Feeding behavior of the most common mesopelagic fishes in the Bering Sea. J. Ichthyol. 32(2):52–60.

Greely, T.M., J.V. Gartner, Jr., and J.J. Torres. 1999. Age and growth of *Electrona antarctica* (Pisces: Myctophidae), the dominant mesopelagic fish of the Southern Ocean. Mar. Biol. 133:145–158.

Günther, A.E. 1887. Report on the deep-sea fishes collected by H.M.S. *Challenger* during the years 1873–1876. Zoology 22:1–335.

Hart, J.L. 1973. Pacific fishes of Canada. Fish. Res. Bd. Can. Bull. 180, 740 pp.

Hedgpeth, J.W. 1957. Classification of marine environments. In: Treatise on marine ecology and paleoecology. J. Hedgpeth (ed.). Mem. Geol. Soc. Amer. 67, 1:17–27.

Helfman, G.S., B.B. Collette, and D.E. Facey. 1997. The diversity of fishes. Blackwell Science, MA, 528 pp.

Herring, P.J. 1972. Bioluminescence of searsid fishes. J. Mar. Biol. Ass. U.K. 56:879–887.

———. 1977. Oral light organs in *Sternoptyx*, with some observations on the bioluminescence of hatchet-fishes, p. 553–567. In: A voyage of discovery: George Deacon 70th anniversary volume. M. Angel (ed.). Pergamon Press Ltd., Oxford.

———. 2000. Species abundance, sexual encounter and bioluminescent signalling in the deep sea. Phil. Trans. R. Soc. Lond. B 355: 1273–1276.

———. 2002. The biology of the deep ocean. Oxford University Press. Oxford, New York, 314 pp.

Herring, P.J., and J.G. Morin. 1978. Bioluminescence in fishes, p. 273–329. In: Bioluminescence in action. P.J. Herring (ed.). Academic Press, London.

Hickey, B.M. 1979. The California Current system–hypotheses and facts. Prog. Oceanog. 8:191–279.

————. 1993. Physical oceanography, p. 19–70. *In:* Ecology of the Southern California Bight. A synthesis and interpretation. M.D. Dailey, D.J. Reish, and J. W. Anderson (eds.). University of California Press, Berkeley.

Hølmer, G. 1989. Triglycerides, pp. 139–173. In: Marine biogenic lipids, fats, and oils. Vol I. R. G. Ackman (ed.). CRC Press, Boca Raton, FL.

Holton, A.A. 1969. Feeding behavior of a vertically migrating lanternfish. Pac. Sci. 23:325–331.

Hopkins, T.L., and R.C. Baird. 1985. Feeding ecology of four hatchetfishes (Sternoptychidae) in the eastern Gulf of Mexico. Bull. Mar. Sci. 36:260–277.

Hopkins, T.L., and J.V. Gartner, Jr. 1992. Resource-partitioning and predation impact of a low-latitude myctophid community. Mar. Biol. 114:185–197.

Hopkins, T.L., and T.M. Lancraft. 1984. The composition and standing stock of mesopelagic micronekton at 27°N 86°W in the eastern Gulf of Mexico. Cont. Mar. Sci 27:143–158.

Hopkins, T.L., and T.T. Sutton. 1998. Midwater fishes and shrimps as competitors and resource partitioning in low latitude oligotrophic ecosystems. Marine Ecol. Prog. Ser. 164:37–45.

Hopkins, T.L., T.T. Sutton., and T.M. Lancraft. 1996. The trophic structure and predation impact of a low latitude midwater fish assemblage. Prog. Oceanogr. 38:205–239.

Hulley, P.A. 1992. Upper-slope distributions of oceanic lanternfishes (family: Myctophidae). Mar. Biol. 114: 365–383.

Imsand, S. 1981. Comparison of the food of *Triphoturus mexicanus* and *T. nigrescens*, two lanternfishes of the Pacific Ocean. Mar. Biol. 63:87–100.

————. 1982. Abundance in space and time of lanternfishes of the genus *Triphoturus* (Myctophidae) in the Pacific Ocean. Unpubl. Ph. D. diss., University of California, San Diego, 251 pp.

Isaacs, J.D., and R. Schwartzlose. 1975. Active animals of the deep-sea floor. Scien. Amer. 233:85–91.

Iwamoto, T., and Y.I. Sazonov. 1988. A review of the southeastern Pacific *Coryphaenoides* (sensu lato) (Pisces: Gadiformes, Macrouridae). Proc. Calif. Acad. Sci. 45(3): 35–82.

Iwamoto, T., and D.L. Stein. 1974. A systematic review of the rattail fishes (Macrouridae: Gadiformes) from Oregon and adjacent waters. Occ. Pap. Calif. Acad. Sci. 111:1–79.

Janssen, J., G.R. Harbison, and J. E. Craddock. 1986. Hatchetfishes hold horizontal attitudes during diagonal descents. J. Mar. Biol. Ass. U.K. 66: 825–833.

Jumper, G.Y., Jr., and R.C. Baird. 1991. Location by olfaction: a model and application to the mating problem in the deep-sea hatchetfish *Argyropelecus hemigymnus*. Am. Nat. 138:1431–1458.

Kalish, J.M., C.F. Greenlaw, W.G. Pearcy, and D. Van Holliday. 1986. The biological and acoustical structure of sound scattering layers off Oregon. Deep-Sea Res. 33:631–653.

Kanwisher, J., and A. Ebeling. 1957. Composition of the swim-bladder gas in bathypelagic fishes. Deep-Sea Res. 4:211–217.

Kashkin, N.I. 1995. Vertical distribution of *Cyclothone* (Gonostomatidae) in the Pacific Ocean (brief review). J. Ichthyol. 35(8):53–60.

Kaufmann, R.G., and R.R. Wilson, Jr. 1991. A summary and bibliography of seamount biota. SIO Reference Series, University of California, Scripps Institution of Oceanography, 91–98, 79 pp.

Kayama, M., and Y. Ikeda. 1975. Studies on the lipids of micronektonic fishes caught in Sagami and Suruga Bays, with special reference to their wax esters. Yukagaku 24:435–440 (in Japanese).

Kayama, M., and J.C. Nevenzel. 1974. Wax ester biosynthesis by midwater marine animals. Mar. Biol. 24:279–285.

Kleckner, R.C., and R.H. Gibbs, Jr. 1972. Swimbladder structure of Mediterranean midwater fishes and a method of comparing swimbladder data with acoustic profiles. Mediterranean Biological Studies Final Report, Rept. To U.S. Navy Office of Naval Research, Contract # N00014–67-A-0399–0007, 1:230–281.

Kline, D.E. 1996. Radiochemical age verification for two deep-sea rockfishes, *Sebastolobus altivelis* and *S. alascanus*. Unpubl. Master's thesis, San Jose State University, CA.

Kobayashi, B.N. 1973. Systematics, zoogeography, and aspects of the biology of the bathypelagic fish genus *Cyclothone* in the Pacific

Ocean. Unpubl. Ph.D. diss., University of California, San Diego, 487 pp.

Koefoed, E. 1927. Fishes from the sea bottom. Rep. Sci. Res. Michael Sars North Atlantic Deep-Sea Exped. 4:1–148.

Krause, D.C. 1965. Tectonics, bathymetry, and geomagnitism of the southern continental borderland west of Baja California, Mexico. Geol. Soc. Am. Bull. 76:617–650.

Lapko, V.V. 1995. Role of mesopelagic fishes in the ichthyocene of the epipelagic zone of the Sea of Okhotsk. J. Ichthyol. 35(9):273–280.

Lauth, R.R. 1999. The 1997 Pacific west coast upper continental slope trawl survey of groundfish resources off Washington, Oregon, and California: estimates of distribution, abundance, and length composition. NOAA Technical Memorandum, NMFS-AFSC-98.

Lavenberg, R.J., and A.W. Ebeling. 1967. Distribution of midwater fishes among deep-water basins of the southern California shelf, p. 185–201. In: Proceedings of the symposium on the biology of the California Islands. R. N. Philbrick (ed.). Santa Barbara Botanic Garden, Santa Barbara, CA.

Lavenberg, R.J., and J.E. Fitch. 1966. Annotated list of fishes collected by midwater trawl in the Gulf of California, March-April 1964. Calif. Fish Game. 52:92–110.

Lawry, J.V., Jr. 1974. Lantern fish compare downwelling light and bioluminescence. Nature 247: 155–157.

Lee, R.F., and J. Hirota. 1973. Wax esters in tropical zooplankton and nekton and the geographical distribution of wax esters in marine copepods. Limnol. Oceanogr. 18:227–239.

Lee, R.F., J. Hirota, and A.M. Barnett. 1971. Distribution and importance of wax esters in marine copepods and other zooplankton. Deep-Sea Res. 18:1147–1165.

Lee, R.F., and J.S. Patton. 1989. Alcohol and waxes, p. 73–102. In: Marine biogenic lipids, fats, and oils. Vol. I. R.G. Ackman (ed.). CRC Press, Boca Raton, FL.

Lewis, R.W. 1970. The densities of three classes of marine lipids in relation to their possible role as hydrostatic agents. Lipids 5:151–153.

Longhurst, A. 1998. Ecological geography of the sea. Academic Press, San Diego, CA, 398 pp.

MacGregor, J.S. 1974. Changes in the amount and proportions of DDT and its metabolites, DDE and DDD, in the marine environment off southern California, 1949–72. U.S. Fish. Bull. 72:275–293.

Marshall, N.B. 1954. Aspects of deep sea biology. Philosophical Library, NY, 380 pp.

————. 1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. Discovery Repts. 31:1–122.

————. 1965. Systematic and biological studies of the macrourid fishes (Anacanthini-Teleosteii). Deep-Sea Res. 12:299–322.

————. 1967. The olfactory organs of bathypelagic fishes. Symp. Zool. Soc. Lond. 19:57–70.

————. 1971a. Explorations in the life of fishes. Harvard Univ. Press, Cambridge, MA, 204 pp.

————. 1971b. Swimbladder development and the life of deep-sea fishes, p. 69–73. In: Proceedings of an international symposium on biological sound scattering in the ocean. G.B. Farquhar (ed.). U.S. Gov. Printing Office, Washington, DC

————. 1972. Swimbladder organization and depth ranges of deep-sea teleosts. Soc. exp. Biol. Symp. 26: 261–272.

————. 1979. Developments in deep-sea biology. Blandford Press, Poole, Dorset. 566 pp.

————. 1980. Deep-sea biology, developments and perspectives. Garland STPM Press, NY, 566 pp.

Marshall, N.B., and N.R. Merrett. 1977. The existence of a benthopelagic fauna in the deep-sea, p. 483–497. In: A voyage of discovery: George Beacon 70th anniversary volume. M.V. Angel (ed.). Pergamon Press, Oxford, New York.

Marshall, N. J. 2000. Communication and camouflage with the same bright colours in reef fishes. Phil. Trans. R. Soc. Lond. B 355:1243–1248.

Matsui, T., S. Kato, and S.E. Smith. 1990. Biology and potential use of Pacific grenadier, *Coryphaenoides acrolepis*, off California. Mar. Fish. Rev. 52:1–17.

McCosker, J.E., and M.E. Anderson. 1976. Aquarium maintenance of mesopelagic animals: a progress report. Bull. So. Calif. Acad. Sci. 75:211–219.

McFall-Ngai, M. 1990. Crypsis in the pelagic environment. Amer. Zool. 30:175–188.

McFall-Ngai, M., F. Crescitelli, J. Childress, and J. Horwitz. 1986. Patterns of pigmentation in the eye lens of the deep-sea hatchetfish, *Argyropelecus affinis* Garman. J. Comp. Physiol. A 159:791–800.

McNulty, J. A. 1976. A comparative study of the pineal complex in the deep-sea fishes *Bathylagus wesethi* and *Nezumia liolepis*. Cell Tiss. Res. 172:205–225.

McNulty, J.A., and B.G. Nafpaktitis. 1976. The structure and development of the pineal complex in the lanternfish *Triphoturus mexicanus* (family Myctophidae). J. Morphol. 150:579–606.

————. 1977. Morphology of the pineal complex in seven species of lanternfishes (Pisces: Myctophidae). Am. J. Anat. 150:509–530.

Mead, G.W., and S.A. Earle. 1970. Notes on the natural history of snipe eels. Proc. Calif. Acad. Sci. 38:99–103.

Mensinger, A.F., and J.F. Case. 1997. Luminescent properties of fishes from nearshore California basins. J. Exp. Mar. Biol. Ecol. 210:75–90.

Merrett, N.R. 1989. The elusive macrourid alevin and its seeming lack of potential in contributing to intrafamilial systematics, p. 175–185. In: Papers on the systematics of gadiform fishes. D.M. Cohen (ed). Nat. Hist. Mus. Los Angeles Co. Science Series No. 32, Los Angeles.

————. 1992. Demersal ichthyofaunal distribution in the abyssal eastern North Atlantic, with special reference to *Coryphaenoides (Nematonurus) armatus* (Macrouridae). J. Mar. Biol. Ass. U.K. 72:5–24.

Middleton, R.W., and J.A. Musick. 1986. The abundance and distribution of the family Macrouridae (Pisces: Gadiformes) in the Norfolk Canyon area. U.S. Fish. Bull. 84:35–62.

Miller, D. J., and R. N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dept. Fish Game Fish Bull. No. 157, 235 pp.

Miya, M., and T. Nemoto. 1991. Comparative life histories of the meso- and bathypelagic fishes of the genus *Cyclothone* (Pisces: Gonostomatidae) in Sagami Bay, central Japan. Deep-Sea Res. 38:67–89.

Moku, M., K. Kawaguchi, H. Watanabe, and A. Ohno. 2000. Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. Mar. Ecol. Prog. Ser. 207:129–140.

Montgomery, J., and N. Pankhurst. 1997. Sensory physiology, p. 325–349. In: Fish Physiology, v. 16, Deep-sea fishes. W. S. Hoar, D.J. Randall, and A.P. Farrell (eds.), Academic Press, San Diego, CA.

Moore, J.A. 2002. Upside-down swimming behavior in a whipnose anglerfish (Teleostei: Ceratioidei: Gigantactinidae). Copeia 2002: 1144–1146.

Morita, T. 1999. Molecular phylogenetic relationships of the deep-sea fish genus *Coryphaenoides* (Gadiformes: Macrouridae) based on mitochondrial DNA. Mol. Phylogen. Evol. 13:447–454.

Morris, R.J., and F. Culkin. 1989. Fish, p. 145–178. In: Marine biogenic lipids, fats, and oils. Vol. II. R.G. Ackman (ed.). CRC Press, Boca Raton, FL.

Moser, H.G. 1974. Development and distribution of larvae and juveniles of *Sebastolobus altivelis* (Pisces; Family Scorpaenidae). U.S. Fish. Bull. 72:865–884.

————. (ed.). 1996a. The early stages of fishes in the California Current region. Calif. Coop. Oceanic Fish. Invest. Atlas No. 33. Allen Press. Lawrence, KS, 1505 pp.

————. 1996b. Astronesthidae: snaggletooths. p. 305–307. In: The early stages of fishes in the California Current region. H.G. Moser (ed.). Calif. Coop. Oceanic Fish. Invest. Atlas No. 33. Allen Press. Lawrence, KS.

Moser, H.G., and E. H. Ahlstrom. 1996. Myctophidae: lanternfishes. p. 387–475. In: The early stages of fishes in the California Current region. H.G. Moser (ed.). Calif. Coop. Oceanic Fish. Invest. Atlas No. 33. Allen Press. Lawrence, KS.

Moser, H.G., R.L. Charter, P.E. Smith, D.A. Ambrose, S.R. Charter, C.A. Meyer, E.M. Sandknop, and W. Watson. 1993. Distributional atlas of fish larvae and eggs in the California Current region: taxa with 1000 or more total larvae, 1951 through 1984. Calif. Coop. Oceanic Fish. Invest. Atlas No. 31. 233pp.

————. 1994. Distributional atlas of fish larvae in the California Current region: Taxa with less than 1000 total larvae, 1951 through 1984. Calif. Coop. Oceanic Fish. Invest. Atlas No. 32. 181pp.

Muntz, W.R.A. 1976. On yellow lenses in mesopelagic animals. J. Mar. Biol. Ass. U.K. 56:963–976.

Neighbors, M.A. 1988. Triacylglycerols and wax esters in the lipids of deep midwater teleost fishes of the Southern California Bight. Mar. Biol. 98:15–22.

————. 1992. Occurrence of inflated swimbladders in five species of lanternfishes (family Myctophidae) from waters off southern California. Mar. Biol. 114:355–363.

Neighbors, M.A., and B.G. Nafpaktitis. 1982. Lipid compositions, water contents, swimbladder morphologies and buoyancies of nineteen species of midwater fishes (18 myctophids and 1 neoscopelid). Mar. Biol. 66:207–215.

Nevenzel, J.C., and N.K. Menon. 1980. Lipids of midwater marine fish: family Gonostomatidae. Comp. Biochem. Physiol. 65B:351–355.

Nevenzel, J.C., W. Rodegker, J.S. Robinson, and M. Kayama. 1969. The lipids of some lantern fishes (family Myctophidae). Comp. Biochem. Physiol. 31: 25–36.

Newman, J.B., and B.H. Robison. 1992. Development of a dedicated ROV for ocean science. Mar. Tech. Soc. J. 26(4):46–53.

Nicol, J.A.C. 1978. Bioluminescence and vision, p. 367–398. In: Bioluminescence in action. P.J. Herring (ed.). Academic Press, New York.

Novikov, N.P. 1970. Biology of *Chalinura pectoralis* in the North Pacific, p. 304–331 In: Soviet fisheries investigations in the northwestern Pacific, Part V (In Russian), P.A. Moiseev (ed). Proc. All Union Sci. Res. Inst. Mar. Fish. Ocean (VINRO), vol. 70, and Pac. Sci. Res. Inst. Fish. Ocean. (TINRO), vol. 72 (Translated by the Israel Program for Scientific Translations, Jerusalem, 1972).

O'Day, W.T. 1973. Luminescent silhouetting in stomiatoid fishes. Nat. Hist. Mus. Los Angeles Co. Cont. Sci. 246:1–8.

————. 1974. Bacterial luminescence in the deep-sea anglerfish *Oneirodes acanthias* (Gilbert, 1915). Nat. Hist. Mus. Los Angeles Co. Cont. Sci. 255:1–11.

O'Day, W.T., and H.R. Fernandez. 1974. *Aristostomias scintillans* (Malacosteidae): a deep-sea fish with visual pigments apparently adapted to its own bioluminescence. Vision Res. 14:545–550.

Partridge, J.C., and R. H. Douglas. 1995. Far-red sensitivity of dragon fish. Nature 375:21–22.

Paxton, J.R. 1967a. A distributional analysis for the lanternfishes (Family Myctophidae) of the San Pedro Basin, California. Copeia 1967:422–440.

————. 1967b. Biological notes on southern California lanternfishes (family Myctophidae). Calif. Fish Game 53:214–217.

————. 1972. Osteology and relationships of the lanternfishes (family Myctophidae). Bull. Nat Hist. Mus. Los Angeles Co. Sci 13:1–81.

Pearcy, W.G. 1964. Some distributional features of mesopelagic fishes off Oregon. J. Mar. Res. 22:83–102.

Pearcy, W.G., and J. Ambler. 1974. Food habits of deep-sea macrourid fishes of the Oregon coast. Deep-Sea Res. 21:745–759.

Pearcy, W.G., E.E. Krygier, R. Mesecar, and F. Ramsey. 1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24:223–245.

Pearcy, W.G., and R. M. Laurs. 1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153–165.

Pearcy, W.G., H.V. Lorz, and W. Peterson. 1979. Comparison of the feeding habits of migratory and non-migratory *Stenobrachius leucopsarus* (Myctophidae). Mar. Biol. 51:1–8.

Pearcy, W.G., and R.S. Mesecar. 1971. Scattering layers and vertical distribution of oceanic animals off Oregon, p. 381–394. In: Proceedings of an international symposium on biological sound scattering in the ocean. G.B. Farquhar (ed.) U.S. Gov. Printing Office, Washington, DC.

Phleger, C.F. 1991. Biochemical aspects of buoyancy in fishes, p. 209–247. In: Biochemistry and molecular biology of fishes, Vol. I, Phylogenetic and biochemical perspectives. P.W. Hochachka and T. P. Mommsen (eds.). Elsevier, Amsterdam.

————. 1998. Buoyancy in marine fishes: direct and indirect role of lipids. Amer. Zool. 38: 321–330.

Phleger, C.F., M.M. Nelson, B.D. Mooney, and P.D. Nichols. 1999. Wax esters versus triacylglycerols in myctophid fishes from the Southern Ocean. Antarctic Sci. 11:436–444.

Phleger, C.F., P.D. Nichols, and P. Virtue. 1997. The lipid, fatty acid and fatty alcohol composition of the myctophid fish *Electrona antarctica*: high level of wax esters and food-chain implications. Antarctic Sci. 9:258–265.

Phleger, C.F., and A. Soutar. 1971. Free vehicles and deep-sea biology. Amer. Zool. 11:409–418.

Pieper, R.E. 1967. Final Report, Mesopelagic faunal discontinuities in the eastern North Pacific. AC Electronics—Defense Res. Labs., General Motors Corporation, Santa Barbara, CA. Sea Operations Dept. Tech. Rept. TR67-19.

Pieper, R.E., and B.G. Bargo. 1980. Acoustic measurements of a migrating layer of the Mexican lampfish, *Triphoturus mexicanus*, at 102 kilohertz. U.S. Fish. Bull 77:935–942.

Pietsch, T.W. 1976. Dimorphism, parasitism and sex: reproductive strategies among deepsea ceratioid anglerfishes. Copeia 1976:781–793.

Priede, I.G., and P.M. Bagley. 2000. *In situ* studies on deep-sea demersal fishes using autonomous unmanned lander platforms, p. 357–392. In: Oceanography and marine biology. R.N. Gibson and M. Barnes (eds.). Allen & Unwin, London.

Priede, I.G., P.M. Bagley, J.D. Armstrong, K.L. Smith, and N.R. Merrett. 1991. Direct measurement of active dispersal of food-falls by deep-sea demersal fishes. Nature 351:647–649.

Priede, I.G., and N.R. Merrett. 1998. The relationship between numbers of fish attracted to baited cameras and population density: Studies on demersal grenadiers *Coryphaenoides (Nematonurus) armatus* in the abyssal NE Atlantic Ocean. Fish. Res. 36:133–137.

Priede, I.G., K.L. Smith, and J.D. Armstrong. 1990. Foraging behaviour of abyssal grenadier fish: inferences from acoustic tagging and tracking in the North Pacific Ocean. Deep-Sea Res. 37:81–101.

Rainwater, C.L. 1975. An ecological study of midwater fishes in Santa Catalina Basin, off southern California, using cluster analysis. Unpubl. Ph. D. diss., University. of Southern California, Los Angeles, 159 pp.

Reid, J.L., Jr., G.I. Roden, and J.G. Wyllie. 1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Inv. Prog. Rept. 5:27–57.

Reinhardt, S.B., and E.S. Van Vleet. 1986. Lipid composition of twenty-two species of Antarctic midwater zooplankton and fish. Mar. Biol. 91:149–159.

Robertson, D.A. 1977. Planktonic eggs of the lanternfish, *Lampanyctodes hectoris* (family Myctophidae). Deep-Sea Res. 24: 849–852.

Robison, B.H. 1972. Distribution of midwater fishes of the Gulf of California. Copeia 1972:448–461.

————. 1973a. A system for maintaining midwater fishes in captivity. J. Fish. Res. Bd. Canada 30:126–128.

————. 1973b. Distribution and ecology of midwater fishes of the eastern North Pacific Ocean. Unpubl. Ph.D. diss., Stanford University. Stanford, CA, 175 pp.

————. 1992. Midwater research methods with MBARI's ROV. Mar. Technol. Soc. J. 26(4):32–39.

————. 1999. Shape change behavior by mesopelagic animals. Mar. Fresh. Behav. Physiol. 32:17–25.

————. 2003. What drives the diel vertical migrations of Antarctic midwater fish? J. Exp. Mar. Biol. Ass. U.K. 83:639–642.

————. 2004. Deep pelagic biology. J. Mar. Biol. Ecol. 300: 253–272.

Robison, B.H., and T.G. Bailey. 1981. Sinking rates and dissolution of midwater fish fecal matter. Mar. Biol. 65:135–142.

————. 1982. Nutrient energy flux in midwater fishes, p. 80–87. In: Gutshop '81. Proc. third Pacific workshop on fish food habits studies. G.M. Cailliet and C.A. Simenstad (eds.) University of Washington Press, Seattle.

Ross, L.G. 1976. The permeability to oxygen of the swimbladder of the mesopelagic fish *Ceratoscopelus maderensis*. Mar. Biol. 37:83–87.

Saito, H., and M. Murata. 1998. Origin of the monoene fats in the lipid of midwater fishes: relationship between the lipids of myctophids and those of their prey. Mar. Ecol. Prog. Ser. 168:21–33.

Sargent, J.R. 1976. The structure, metabolism and function of lipids in marine organisms. p. 149–212. In: Biochemical and biophysical perspectives in marine biology, Vol. 3. D.C. Malins and J.R. Sargent (eds.). Academic Press, London.

————. 1978. Marine wax esters. Sci. Prog., Oxf. 65:437–458.

Sargent, J.R., R.F. Lee, and J. C. Nevenzel. 1976. Marine waxes. p. 49–91. In: Chemistry and biochemistry of natural waxes. P.E. Kolattukudy (ed.). Elsevier, Amsterdam.

Seo, H.-S., Y. Endo, K. Fujimoto, H. Watanabe, and K. Kawaguchi. 1996. Characterization of lipids in myctophid fish in the subarctic and tropical Pacific Ocean. Fisheries Sci. 62:447–453.

Seo, H.-S., Y. Endo, M. Moku, K. Kawaguchi, and K. Fujimoto. 2001. Wax ester biosynthesis in the liver of myctophid fishes. Lipids 36:389–393.

Siebenaller, J.F. 1978. Genetic variability in deep-sea fishes of the genus *Sebastolobus* (Scorpaenidae), p. 95–122. In: Marine organisms. B. Battaglia and J. Beardmore (eds.). Plenum Press, New York.

Sinclair, E.H., A.A. Balanov, T. Kubodera, V.I. Radchenko, and Y.A. Fedorets. 1999. Distribution and ecology of mesopelagic fishes and cephalopods, p. 485–508. In: Dynamics of the Bering Sea. T.R. Loughlin and K. Ohtani (eds.). Univ. of Alaska Sea Grant, Fairbanks, AK.

Smith, C.R., and S.C. Hamilton. 1983. Epibenthic megafauna of a bathyal basin off southern California: patterns of abundance, biomass, and dispersion. Deep-Sea Res. 30:907–928.

Smith, D.G., and J.G. Nielsen. 1976. Preliminary note on sexual dimorphism in the Nemichthyidae and the identity of *Avocettinops* and *Paravocettinops* (Pisces, Anguilliformes). Steenstrupia 4:1–5.

Smith, K.L., Jr. 1978. Metabolism of the abyssopelagic rattail *Coryphaenoides armatus* measured in situ. Nature 274:362–364.

————, and N.O. Brown. 1983. Oxygen consumption of pelagic juveniles and demersal adults of the deep-sea fish *Sebastolobus altivelis*, measured at depth. Mar. Biol. 76:325–332.

Smith, K.L., and R.R. Hessler. 1974. Respiration of benthopelagic fishes: *In-situ* measurements at 1230 meters. Science 184:72–73.

Smith, K.L., and M.B. Laver. 1981. Respiration of the bathypelagic fish *Cyclothone acclinidens*. Mar. Biol. 61:261–266.

Smith, K.L., M.B. Laver, and N.O. Brown. 1983. Sediment community oxygen consumption and nutrient exchange in the central and eastern North Pacific. Limnol. Oceanogr. 28:882–898.

Smith, K.L., G.A. White, M.B. Laver, R.R. McConnaughey, and J.P. Meador. 1979. Free vehicle capture of abyssopelagic animals. Deep-Sea Res. 26:57–64.

Smith-Beasley, L. 1992. A study of the vertical distribution of upper mesopelagic animals in the Monterey Submarine Canyon, California. Unpubl. Master's thesis, Moss Landing Marine Labs., San Jose State University, CA, 62 pp.

Smoker, W., and W.G. Pearcy. 1970. Growth and reproduction of the lanternfish *Stenobrachius leucopsarus*. J. Fish. Res. Bd. Can. 27:1265–1275.

Somiya, H. 1976. Functional significance of the yellow lens in the eyes of *Argyropelecus affinis*. Mar. Biol. 34:93–99.

Springer, V.G. 1982. Pacific plate biogeography with special reference to shore fishes. Smithson. Contr. Biol. 367:1–182.

Stein, D.L. 1980. Description and occurrence of macrourid larvae and juveniles in the northeastern Pacific Ocean off Oregon. Deep-Sea Res. 27:889–900.

————. 1985. Towing large nets by single warp at abyssal depths: methods and biological results. Deep-Sea Res. 32:183–200.

Stein, D.L., and J. Butler. 1972. First records of *Bathysaurus mollis* (Pisces: Bathysauridae) from the Northeast Pacific Ocean. J. Fish. Res. Bd. Can. 29:1093–1094.

Stein, D.L., and W. G. Pearcy. 1982. Aspects of reproduction, early life history, and biology of macrourid fishes off Oregon, U.S.A. Deep-Sea Res. 29:1313–1329.

Stepien, C.A., A.K. Dillon, and A.K. Patterson. 2000. Population genetics, phylogeography, and systematics of the thornyhead rockfishes (*Sebastolobus*) along the deep continental slopes of the North Pacific Ocean. Can. J. Fish. Aquat. Sci. 57:1701–1717.

Stickney, D.G., and J.J. Torres. 1989. Proximate composition and energy content of mesopelagic fishes from the eastern Gulf of Mexico. Mar. Biol. 103:13–24.

Sulak, K.J., C.A. Wenner, G.R. Sedberry, and L. van Guelpen. 1985. The life history and systematics of deep-sea lizard fishes, genus *Bathysaurus* (Synodontidae). Can. J. Zool. 63:623–642.

Sutton, T.T., and T.L. Hopkins. 1996a. Species composition, abundance, and vertical distribution of the stomiid (Pisces: Stomiiformes) fish assemblage of the Gulf of Mexico. Bull. Mar. Sci. 59:530–542.

————. 1996b. Trophic ecology of the stomiid (Pisces: Stomiidae) fish assemblage of the eastern Gulf of Mexico: strategies, selectivity and impact of a top mesopelagic predator group. Mar. Biol. 127:179–192.

Sutton, T.T., T.L. Hopkins., and T.M. Lancraft. 1995. Trophic diversity of a mesopelagic fish community, p. 353–351. In: Pelagic biogeography ICoPBII. Proc. 2nd intl. conference. IOC Workshop Report No. 142. A.C. Pierrot-Bults and S. van der Spoel (eds.). UNESCO.

Sverdrup, H.U., M.W. Johnson, and R. H. Fleming. 1942. The oceans: their physics, chemistry and general biology. Prentice-Hall, Inc., Englewood Cliffs, NJ, 1060 pp.

Swan, S.C., and J.D.M. Gordon. 2001. A review of age estimation in macrourid fishes with new data on age validation of juveniles. Fish. Res. 51:177–195.

Takahashi, S., S. Tanabe, and K. Kawaguchi. 2000. Organochlorine and butyltin residues in mesopelagic myctophid fishes from the western North Pacific. Environ. Sci. Technol. 34:5129–5136.

Talbot, J.J. 1973. Some aspects of the ecology and bathymetric distribution of *Cyclothone acclinidens* in the Santa Catalina Basin. Copeia 1973:600–601.

Taylor, H.F. 1922. Deductions concerning the air bladder and the specific gravity of fishes. Bull. Bureau Fish. 38:121–126.

Thompson, D.R., R.W. Furness, and L.R. Monteiro. 1998. Seabirds as biomonitors of mercury inputs to epipelagic and mesopelagic marine food chains. Science Total Env. 213:299–305.

Torgersen, T., and S. Kaartvedt. 2001. *In situ* swimming behaviour of individual mesopelagic fish studied by split-beam echo target tracking. ICES J. Mar. Sci. 58:346–354.

Torres, J.J., B.W. Belman, and J.J. Childress. 1979. Oxygen consumption rates of midwater fishes as a function of depth of occurrence. Deep-Sea Res. 26A:185–197.

Tyler, H.R., Jr., and W.G. Pearcy. 1975. The feeding habits of three species of lanternfishes (family Myctophidae) off Oregon, USA. Mar. Biol. 32:7–11.

Uchupi, E., and K.O. Emery. 1963. The continental slope between San Francisco, California and Cedros Island, Mexico. Deep-Sea Res. 10:397–447.

Vent, R.J., and G.V. Pickwell. 1977. Acoustic volume scattering measurements with related biological and chemical observations in the northeastern tropical Pacific, p. 697–716. In: Oceanic sound scattering prediction. N.R. Andersen and B.J. Zahuranec (eds.). Plenum Press, NY.

Vetter, R.D., and E.A. Lynn. 1997. Bathymetric demography, enzyme activity patterns, and bioenergetics of deep-living scorpaenid fishes (genera *Sebastes* and *Sebastolobus*): paradigms revisited. Mar. Ecol. Prog. Ser. 155:173–188.

Wagner H.-J., E. Fröhlich, K. Negishi, and S.P. Collin. 1998. The eyes of deep-sea fish II. functional morphology of the retina. Prog. Retinal Eye Res. 17: 637–685.

Wakefield, W.W., and A. Genin. 1987. The use of a Canadian (perspective) grid in deep-sea photography. Deep-Sea Res. 34:469–478.

Wakefield, W.W., and K.L. Smith, Jr. 1990. Ontogenetic vertical migration in *Sebastolobus altivelis* as a mechanism for transport of particulate organic matter at continental slope depths. Limnol. Oceanogr. 36:1314–1328.

Warrant, E. 2000. The eyes of deep-sea fishes and the changing nature of visual scenes with depth. Phil. Trans. R. Soc. Lond. B 355: 1155–1159.

Watanabe, H., M. Moku, K. Kawaguchi, K. Ishimaru, and A. Ohno. 1999. Diel vertical migration of myctophid fishes (Family Myctophidae) in the transitional waters of the western North Pacific. Fish. Oceanogr. 8:115–127.

Watson, W. 1996. Anoplogastridae: fangtooths, p. 683–685. In: The early stages of fishes in the California Current region. Calif. Coop. Oceanic Fish. Invest. Atlas No. 33. H.G. Moser (ed.). Allen Press. Lawrence, KS.

Weitzman, S.H. 1997. Systematics of deep-sea fishes, p. 43–77, In: Deep-sea fishes. D.J. Randall and A.P. Farrell (eds.). Academic Press, San Diego.

Widder, E.A., M.I. Latz, P.J. Herring, and J.F. Case. 1984. Far red bioluminescence from two deep-sea fishes. Science 225: 512–514.

Willis, J.M. 1984. Mesopelagic fish faunal regions of the northeast Pacific. Biol. Oceanogr. 3:167–185.

Willis, J.M., and W.G. Pearcy. 1980. Spatial and temporal variations in the population size structure of three lanternfishes (Myctophidae) off Oregon, USA. Mar. Biol. 57:181–191.

Wilson, R.R., Jr. 1982. A comparison of ages estimated by the polarized light method with ages estimated by vertebrae in females of *Coryphaenoides acrolepis* (Pisces:Macrouridae), Deep-Sea Res. 29:1373–1379.

————. 1984. Taxonomic and biological studies on the abyssal grenadiers *Coryphaenoides armatus* and *C. yaquinae* in the eastern and central North Pacific, with special reference to otoliths. Unpubl. Ph.D. diss., University of California, San Diego. 194 pp.

————. 1985. Depth-related changes in sagitta morphology in six species of macrourid fishes of the Pacific and Atlantic oceans. Copeia 1985:1011–1017.

———. 1988. Analysis of growth zones and microstructure in otoliths of two macrourids from the North Pacific abyss. Environ. Biol. Fish. 21:251–261.

———. 1994. Interrelationships of the subgenera of *Coryphaenoides* (Gadiformes: Macrouridae): comparison of protein electrophoresis and peptide mapping. Copeia 1994:42–50.

———. 2001. A new species of *Nezumia* from Fieberling Guyot, eastern North Pacific Ocean. Rev. Biol. Trop. 49 (Suppl.1):29–37.

Wilson, R.R. Jr., and P. Attia. 2003. Interrelationships of the subgenera of *Coryphaenoides* (Teleostei: Gadiformes: Macrouridae): synthesis of allozyme, peptide mapping, and DNA sequence data. Mol. Phylogen. Evol. 27:343–347.

Wilson, R.R. Jr., and K.L. Smith, Jr. 1984. Effect of near-bottom currents on detection of bait by the abyssal grenadier fishes (*Coryphaenoides* spp.) recorded *in situ* with a video camera on a free vehicle. Mar. Biol. 84:83–91.

———. 1985. Live capture, maintenance, and partial decompression of a deep-sea grenadier fish (*Coryphaenoides acrolepis*) in a hyperbaric trap-aquarium. Deep-Sea Res. 32:1571–1582.

Wilson, R.R. Jr., and R.S. Waples. 1983. Distribution, morphology, and biochemical genetics of *Coryphaenoides armatus* and *C. yaquinae* (Pisces:Macrouridae) in the central and eastern North Pacific. Deep-Sea Res. 30:1127–1145.

———. 1984. Electrophoretic and biometric variability in the abyssal grenadier *Coryphaenoides armatus* of the western North Atlantic, eastern South Pacific and eastern North Pacific Oceans. Mar. Biol. 80:227–237.

Wisner, R.L. 1962. Midwater trawl surveys. Limnol. Oceanogr. 7 suppl.:xxxix–xli.

———. 1976. The taxonomy and distribution of lanternfishes (Family Myctophidae) of the Eastern Pacific Ocean. NORDA Rept. 3. Navy Ocean Res. Dev. Activity. Bay St. Louis, MS.

Yancey, P.H., T. Kulongoski, M.D. Usibelli, R. Lawrence-Berrey, and A. Pedersen. 1992. Adaptations in mesopelagic fishes-II. Protein contents of various muscles and actomyosin contents and structure of swimming muscle. Comp. Biochem. Physiol. 103B: 691–697.

Yancey, P.H., R. Lawrence-Berrey, and M.D. Douglas. 1989. Adaptations in mesopelagic fishes. I. Buoyant glycosaminoglycan layers in species without diel vertical migrations. Mar. Biol. 103:453–459.

Young, R.E., E.M. Kampa, S.D. Maynard, F. M. Mencher, and C.F.E. Roper. 1980. Counterillumination and the upper depth limits of midwater animals. Deep-Sea Res. 27A:671–691.

Young, R.E., and C.F.E. Roper. 1977. Intensity regulation of bioluminescence during countershading in living midwater animals. U.S. Fish. Bull. 75:239–252.

Young, R.E., C.F.E. Roper., and J.F. Walters. 1979. Eyes and extraocular photoreceptors in midwater cephalopods and fishes: their roles in detecting downwelling light for counterillumination. Mar. Biol. 51:371–380.

Zahuranec, B.J., and W.L. Pugh. 1971. Biological results from scattering layer investigations in the Norwegian Sea, p. 360–379. In: Proceedings of an international symposium on biological sound scattering in the ocean. G.B. Farquhar (ed.). U.S. Gov. Printing Office, Washington, DC.

Zdanowicz, V.S., B. Sharack, S.L. Cunneff, T.W. Finneran, B. Leimburg, and M. C. Ingham. 1996. Metal concentrations in midwater fish and plankton from the 106-mile dumpsite. J. Mar. Env. Eng. 1:131–148.