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CHAPTER 11

Ichthyoplankton

H.G. MOSER AND W. WATSON

Historic Overview

The term ichthyoplankton is applied to fish eggs and larvae that are found among the other planktonic organisms drifting with the currents in the upper part of the water column. Fish eggs are immotile, whereas larvae swim feebly after hatching and become more motile as they develop toward the juvenile stage. Ichthyoplankters are further classified as meroplankton (temporary plankton), the early, planktonic ontogenetic stages of aquatic organisms that develop into juveniles and adults and ultimately occupy a variety of pelagic and demersal habitats.

Plankton research began in the nineteenth century when British and German scientists, experimenting with fine-mesh nets of various designs, began to describe the vast array of small organisms captured in the sea. In 1865, the Norwegian scientist, G.O. Sars discovered that the eggs of cod and other species in Norwegian seas are pelagic; this marked the beginning of ichthyoplankton research, which accelerated at the turn of the twentieth century with the realization that quantitative ichthyoplankton sampling could be a means of estimating the size and extent of commercial fish stocks (Hempel, 1979; Ahlstrom and Moser, 1981; Kendall, 2000).

As in the North Atlantic, fisheries concerns generated the first ichthyoplankton studies off California. The Pacific sardine (*Sardinops sagax*) fishery expanded rapidly in the 1920s and by the mid-1930s had become one of the largest world fisheries, with annual landings exceeding 700 thousand tons. During the rapid expansion of the fishery, California Department of Fish and Game (CDFG) biologists realized that catch and life-history information essential to rational management of the fishery were lacking (Clark, 1982). A system for monitoring landings was established and research on sardine early life history began with a series of plankton-oceanographic surveys during 1920 to 1932. These surveys, conducted by scientists from CDFG and the Hydrobiological Survey of the Hopkins Marine Station, provided the first information on sardine eggs and larvae in an area extending from northern California to Cabo San Lucas, Mexico, and marked the beginning of ichthyoplankton research in the California Current region (Scofield and Lindner, 1930; Scofield, 1934).

By the 1930s, the sardine population had expanded northward to British Columbia, its management had become international in scope, and scientists of the U.S. Fish and Wildlife Service Bureau of Commercial Fisheries (BCF) joined the group of fishery biologists and managers dealing with the sardine fishery. This consortium included two scientists who were especially important to the development of ichthyoplankton research in the California Current region: Oscar E. Sette and Elbert H. Ahlstrom. Sette (1943) was the principal designer of a cooperative research plan for sardine that emphasized the importance of ichthyoplankton surveys in attacking the problems of recruitment, trophic dynamics, and biomass estimation. Sette, along with Ahlstrom, oceanographers from Scripps Institution of Oceanography (SIO), and scientists from CDFG, developed a plan to monitor the early life stages of sardine, associated planktonic organisms, and the ocean environment. A series of 24 cruises was conducted during 1937 to 1941 to establish the boundaries, station placement, and sampling frequency needed to meet key requirements of Sette's research plan, principally to collect sardine eggs and larvae over the entire areal and seasonal spawning range of the species.

In 1949, under the sponsorship of the Marine Research Committee of the State of California, the consortium of BCF, SIO, and CDFG scientists that would eventually be known as the California Cooperative Oceanic Fisheries Investigations (CalCOFI) began the annual biological-oceanographic surveys. At this time, the sardine population had declined to a small fraction of its former size during the mid-1920s (Ahlstrom, 1966; Hewitt, 1988; Kawasaki, 1991; Moser et al., 1993, 1994a, 2001a; Smith and Moser, 2003). During the past half-century, these surveys have produced a wealth of data on the biology, chemistry, and physics of the California Current, in addition to the information on sardine early life history originally sought by the CalCOFI founders. Ahlstrom was in charge of CalCOFI ichthyoplankton investigations from the beginning of the program and, although the focus was on sardine, he attempted to identify all fish larvae captured in each CalCOFI tow. His "faunal" approach formed the basis for advances in our knowledge of ichthyoplankton ecology in the CalCOFI survey area (Ahlstrom, 1959, 1960, 1965, 1966, 1969, 1972; Orton 1953a,b, 1955a,b, 1962, 1963; Orton and Limbaugh, 1953; Kramer, 1970; Moser et al., 1974, 1984, 1987, 1993, 1994a, 2001a, 2002; Ahlstrom and Moser, 1975; Ahlstrom and Stevens, 1976; Ahlstrom et al., 1976, 1978; Sumida and Moser, 1980, 1984; Gruber et al., 1982; Loeb et al., 1983a,b,c; MacCall and Prager, 1988; Smith and Moser, 1988, 2003; Moser and Watson, 1990; Moser and Boehlert, 1991; Moser and Smith, 1993; Moser, 1996; Moser and Pommeranz, 1999). The southern region of the California Current off Mexico was an integral part of the CalCOFI surveys until 1985 when coverage was limited to the Southern California Bight region (SCB: a region between the major upwelling centers off central California and the central Baja California peninsula, approximately Point Conception, California, to Point Baja, Baja California, Mexico; Bakun, 1996). Centro Interdisciplinario de Ciencias Marinas (CICIMAR), Instituto Politecnico Nacional's marine laboratory in La Paz, Baja California Sur, continued limited ichthyoplankton surveys in the Magdalena Bay region during the 1980s and early 1990s (Funes-Rodriguez et al., 2001), and in 1997, a collaboration of CICIMAR and Centro de Investigacion Cientifica de Educacion Superior de Ensenada (CICESE) reinstituted biological-oceanographic surveys off Baja California, following CalCOFI station placement and standard protocols (Baumgartner et al., 2000).

The CalCOFI survey design has an offshore emphasis because, at the inception of the program, sardines spawned over a broad expanse of the California Current region (fig. 11-1); however, with the decline of the population, spawning contracted to a narrow coastal band by the 1960s. Since the mid 1980s, sardine spawning has expanded rapidly to reoccupy a large portion of the California Current region, as far north as British Columbia (McFarlane et al., 2000). During this period, human impact on coastal fish communities stimulated numerous nearshore ichthyoplankton programs along the California coast. A primary concern has been the use of seawater to cool reactors at nuclear power plants and the effect this may have on nearshore fish populations and other marine life. This resulted in a number of monitoring programs that have greatly advanced our knowledge of the taxonomy, distribution, and abundance of nearshore ichthyoplankton in the SCB region (Brewer et al., 1981, 1984; Brewer and Smith, 1982; Schlotterbeck and Connally, 1982; Watson, 1982, 1992; Allen et al., 1983; Barnett et al., 1984; Brewer and Kleppel, 1986; Jahn and Lavenberg, 1986; Lavenberg et al., 1986; Walker et al., 1987; Jahn et al., 1988; Watson and Davis, 1989; McGowen, 1993).

Ichthyoplankton studies at San Onofre Nuclear Generating Station ended in 1986; however, ichthyoplankton sampling and analysis at the Diablo Canyon nuclear power plant in central California continued through 1999 (Ehrler et al., 2002). Other ichthyoplankton studies off central and northern California have focused largely on the declining populations of nearshore fishes, especially the rockfishes (Eldridge and Bryan, 1972; Misitano, 1976; Eldridge, 1977; Icanberry et al., 1978; Laidig et al., 1991; Laidig and Sakuma, 1998; Lenarz et al., 1991; Ralston and Howard, 1995; Sakuma and Laidig, 1995; Sakuma and Ralston, 1995; Laidig et al., 1996; Ralston et al., 1996; Yoklavich et al., 1992, 1996; Sakuma et al., 1999; Ralston et al., 2003). In recent years, the growing popularity of the live-fish restaurant trade has generated an intense nearshore fishery that targets shallow water rockfishes (*Sebastes*), e.g., copper (*S. caurinus*), grass (*S. rastrelliger*), gopher (*S. carnatus*), brown (*S. auriculatus*), and kelp (*S. atrovirens*) rockfishes, and other associated reef fishes such as cabezon (*Scorpaenichthys marmoratus*), greenlings (family Hexagrammidae), lingcod (*Ophiodon elongatus*), and California sheephead (*Semicossyphus pulcher*) (Pattison and Vejar, 2000; Moser et al., 2001b; Walters, 2001).

Ichthyoplankton surveys in Pacific northwest waters were conducted by CalCOFI and its precursors in 1939, 1949, 1950, 1955, 1972, and 1989 (Hewitt, 1988; Moser et al., 1994a). LaBrasseur (1970) published a checklist of fish larvae collected in >3000 zooplankton samples from the northeast Pacific from 1956 to 1959. Although most of these samples were taken in the Gulf of Alaska, a substantial number also were taken in the California Current region as far south as northern California. In the 1970s, ichthyoplankton studies were initiated at Oregon State University (OSU) and at the Alaska Fisheries Science Center. At OSU, the collaboration of William G. Pearcy and Sally L. Richardson and their students generated an ichthyoplankton program that ranged from Yaquina Bay to offshore waters of the Oregon and Washington coasts and included studies on seasonal and interannual distribution and abundance, recruitment, and larval taxonomy and systematics (Richardson, 1973, 1977, 1980, 1981a,b; Pearcy and Meyers, 1974; Pearcy et al., 1977; Richardson and Pearcy, 1977; Richardson and Stephenson, 1978; Laroche and Richardson, 1979, 1980, 1981; Richardson and Laroche, 1979; Richardson and Washington, 1980; Richardson et al., 1980a,b; Stein, 1980; Brodeur et al., 1985; Shenker, 1988). After the departure of Dr. Richardson from OSU, ichthyoplankton research at the Hatfield Marine Science Center in Newport, Oregon, continued with George W. Boehlert and his students and research group and included physiological as well as field studies (Boehlert and Yoklavich, 1984, 1985; Boehlert et al., 1985; Boehlert and Mundy, 1987, 1988). Another center of ichthyoplankon research in the region is the Resource Assessment and Conservation Engineering Division (RACE) of the Alaska Fisheries Science Center, National Marine Fisheries Service, in Seattle, Washington. Although their field surveys and research are focused on the Gulf of Alaska and Bering Sea, they have made extensive contributions to our knowledge of the northern California Current region. An early survey sampled a station grid extending from Vancouver Island to northern California, from the coast to several hundred miles offshore (Waldron, 1972). Comprehensive ichthyoplankton investigations began under the direction of Arthur W. Kendall, Jr., who conducted a series of 10 biological/oceanographic surveys off the coasts of Washington, Oregon, and northern California from 1980 to 1987 (Doyle, 1992a). These collections provided information on the distribution and abundance of Pacific northwest fish eggs and larvae (Doyle, 1992a,b; Doyle et al., 1993) and formed the basis for an ichthyoplankton laboratory guide (Matarese et al., 1989) and numerous other contributions (e.g., Matarese et al., 1981; Kendall and Vinter, 1984; Kendall and Matarese, 1987, 1994; Kendall, 1993; Busby, 1998; Busby et al., 2000; Orr and Matarese, 2000).

Ichthyoplankton Sampling

A primary reason for conducting ichthyoplankton surveys is to determine the distribution and abundance of the eggs and/or larvae of fishes in a region of the ocean, usually to detect interannual changes in the size and scope of one or more populations. Indexes of relative abundance derived from these surveys often are the only fishery-independent information available to scientists who have the task of estimating the biomass of a stock from catch-at-age fishery data. In addition to indexes of larval abundance, ichthyoplankton surveys can provide valuable information on spawning seasons and temperatures, larval dispersion and mortality, and a great many other aspects

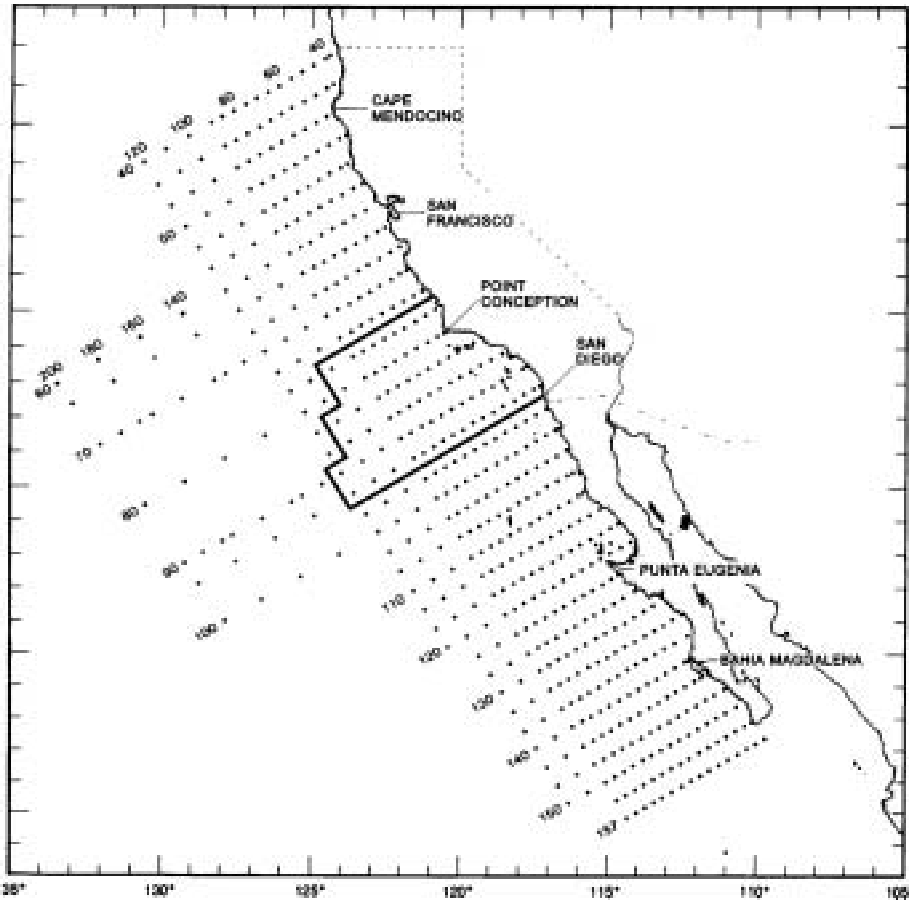

FIGURE 11-1 The CalCOFI survey pattern extending from the California-Oregon border (line 40) to the south of Cabo San Lucas, Baja California Sur, Mexico (line 157). Numbers at the ends of the onshore-offshore lines indicate survey lines; station numbers are shown along line 40; present (since 1985) survey area outlined.

of fish life history and ecology. Ichthyoplankton surveys designed to estimate spawning biomass must encompass the geographic limits of target spawning stock(s). For species such as the Pacific sardine, this may involve thousands of square kilometers and require multiship surveys (Ahlstrom, 1966), whereas shorefish species may require a sampling area that extends only to the edge of the continental shelf or to the mouth of a bay in the case of some estuarine species. Another requirement for a quantitative survey is the need to encompass the vertical extent of the ichthyoplankton target species. Most ichthyoplankters live in the upper water column and are adequately sampled by a plankton tow to 212 m depth, the target depth for the standard CalCOFI oblique plankton tow (Ahlstrom, 1959; Moser and Smith, 1993; Moser and Pommeranz, 1999). For stations over the shelf, the target depth of the tow is determined by bottom depth, usually as close to the bottom as possible without endangering the sampling gear.

Quantitative plankton sampling began with Hensen's (1895) "egg net," a conical net with a three-lead bridle that became the archetype for ichthyoplankton samplers until the development of the bongo net (McGowan and Brown, 1966). The bongo net has the advantage of being able to take two adjacent simultaneous samples during a single tow with a bridleless frame that presents fewer avoidance signals to organisms in front of the net. In the standard CalCOFI 1-m diameter ring net used from 1949 to 1977, a cylindrical section preceded the conical section to improve filtration efficiency (Ahlstrom, 1954; Smith et al., 1968). Nylon mesh (0.505 mm) replaced the original silk mesh (0.55 mm) in 1969, and the 71-cm bongo net frame came into use in 1977 (Smith and Richardson, 1977; Moser et al., 1993; Ohman and Smith, 1995). The bongo net, with mouth diameters of either 60 or 71 cm, has gained international acceptance as the preferred sampler for ichthyoplankton surveys. Usually, double oblique tows are employed on ichthyoplankton surveys. During a CalCOFI tow, for example, 300 m of wire are paid out at a constant rate of 50 m/minute (35 m of depth/minute) to reach the target depth of 212 m; then, after fishing at depth for 30 seconds, the net is retrieved at a constant rate of 20 m/minute (14 m of depth/minute), with the wire held at a constant angle of 45° by adjusting the ship speed and course (see Kramer et al., 1972 and Smith and Richardson, 1977 for detailed descriptions of gear and methods). If the tow is quantitative, i.e., the vertical range of the target species has been encompassed and the net has filtered an equal amount of water in each stratum of the water column, the numbers of specimens of any species captured in the tow can be converted to the number of organisms under a unit surface area (subsequently denoted as number/unit area) by multiplying the number per unit volume of water filtered during the tow (measured by the flowmeter at the mouth of each net) by the depth of the tow. The abundance at each station in a grid can be expanded to the area represented by each station and then summed to obtain the abundance for the entire area encompassed by the grid.

Oblique tows taken with the research vessel underway, usually at a speed of ~1.5 knots, have a better chance of capturing fish larvae compared to vertical tows taken with the ship stopped on station; however, vertical tows employing a bongo or ring net are appropriate for sampling fish eggs which drift passively and lack the ability to avoid the approaching net. Surveys designed to measure the daily egg production of large spawning stocks use vertical tows with a small-mouth net (e.g., 0.25 m diameter) that is cast and retrieved rapidly (~70 m/minute retrieval speed), thus allowing high station density and improved sampling precision (Lasker, 1985). This net also has been used successfully in shallow coastal waters (Lavenberg et al., 1987), and vertical tows with bongo nets, primarily for sampling fish eggs, have proved useful in shallow waters as well (Watson et al., 1999).

Although oblique net tows are designed to sample the entire vertical distribution of target taxa, they are relatively poor samplers for species whose eggs and larvae are concentrated exclusively in the near-surface zone, which, during a typical oblique tow, is sampled for only a few seconds (Zaitsev, 1970; Hempel and Weikert, 1972; Doyle, 1992b; Moser et al., 2002). Some of these are valuable fisheries species and/or are important ecologically. Specialized "neuston" samplers such as the Manta net (Brown and Cheng, 1981) and the Sameoto neuston net (Sameoto and Jaroszynski, 1969) that can take a quantitative sample from the surface stratum have become part of the standard protocol for ichthyoplankton surveys where target species have obligate neustonic larvae (Doyle, 1992b; Moser et al., 2002). Another important feature of neuston nets is their tendency to capture specimens at the upper ends of larval size distributions; such specimens are relatively rare in catches from oblique nets (Ahlstrom and Stevens, 1976; Doyle, 1992a,b; Moser et al., 2002).

Ichthyoplankton studies in shelf and bay waters have shown that larvae of some species descend from the water column to the epibenthos as early as the yolk-sac stage (e.g., some sciaenids) and are inadequately sampled with standard oblique tows (Schlotterbeck and Connally, 1982; Barnett et al., 1984; Jahn and Lavenberg, 1986). Epibenthic sled plankton samplers have been used effectively for these larvae (Eldridge and Bryan, 1972; Walker et al., 1987), and the Auriga net, a specialized, wheel-mounted epibenthic sampler, also has been used successfully in coastal waters (Schlotterbeck and Connally, 1982; Barnett et al., 1984). Another coastal zone sampler, a bongo net mounted between wheels and used to make oblique tows that include the epibenthos, has been used as well (Lavenberg et al., 1986).

The need for information on the vertical distribution of ichthyoplankton and micronekton has stimulated the invention of numerous devices for sampling discrete depth strata, beginning with simple messenger-actuated devices that constrict and close the net immediately behind the mouth (Nansen, 1915; Leavitt, 1935; Motoda, 1962) and pressure-actuated devices at the cod end of the net that divert the sample from one collecting bucket to another (Foxton, 1963). Multiple-net samplers include the Tucker net, and modified versions of it, which consists of one or more nets attached to bars, forming a rectangular mouth, that can be opened and closed mechanically or acoustically (Tucker, 1951; Davies and Barham, 1969; Baker et al., 1973; Hodell et al., 2000). Another sampler, the MOCNESS (Multiple Opening-Closing Nets/Environmental Sampling System), consists of a rectangular frame with sequentially opening/closing nets attached to horizontal bars that are released electronically via signals from a shipboard computer (Weibe et al., 1985). The MOCNESS can be configured as paired 0.5-m^2 nets, or in 1-m^2, 10-m^2, or 20-m^2 versions. A conductivity-temperature-depth sensor attached to the frame relays environmental data to the deck unit throughout each tow, and other sensors (e.g., pH, O_2) can be added.

Sampler avoidance can be reduced by increasing towing speed; however, water pressure increases rapidly with towing speed which can result in increased extrusion of eggs and larvae through the mesh, specimen damage, and damage to the net itself. Many approaches have been used to overcome this problem, usually by reducing the mouth diameter of the net and encasing the net in a streamlined housing (Aron et al., 1965; Fraser, 1968). One series of high-speed nets, the "Gulf" samplers, has appeared in numerous versions (Gehringer, 1952; Bridger, 1958; Nellen and Hempel, 1969), including a model capable of taking discrete depth samples (Moser and Pommeranz, 1999).

Shipboard pumps have been used extensively to sample zooplankton (Lasker, 1975; Mullin and Brooks, 1970; Jahn and Lavenberg, 1986); however, their utility in capturing ichthyoplankton is limited to eggs and weakly swimming newly hatched larvae, although in some applications pumps may be superior to plankton nets (Leitheiser et al., 1979). Until recently, most shipboard pumps have been used with the research vessel drifting or at anchor (Mullin et al., 1985), but the invention of a system (CUFES: Continuous Underway Fish Egg Sampler) that can be operated while the research vessel is underway has provided new opportunities for measuring egg production over a large area (Checkley et al., 1997, 2000; Van der Lingen et al., 1998; Lo et al., 2001).

Anchored and buoyed net arrays (Graham and Venno, 1968; Graham and Davis, 1971; Graham, 1972) and other fixed nets (Eldridge, 1977; Boehlert and Mundy, 1987; Witting et al., 1999) have been used effectively in estuaries to sample ichthyoplankton during tidal flows. Another collecting technique is to dip-net fish larvae that are attracted to lights either aboard ship or from piers (Busby et al., 2000). Although highly selective, dip-netting is a relatively inexpensive means of developing a time series of larval fish that may not be attainable by other means. In shallow estuarine and bay waters, dropbox enclosures have been used, and small-mesh beach seines have been used to collect late larval and juvenile stages of fishes (Allen et al., 1983; Kramer, 1991). Diver-operated samplers consisting of a small plankton net attached to a diver propulsion vehicle (Ennis, 1972) or a small diver-steered, towed plankton net (Marliave, 1986), have been used to sample very close to substrates (e.g., rocks, kelp). A wide variety of other plankton samplers has been used elsewhere, but little or not at all in Californian waters. Examples of some of these are the push-net surface sampler (Miller, 1973; Miller et al., 1973); the plankton purse seine (Murphy and Clutter, 1972); the multiple opening-closing net sampler related to the MOCNESS, the BIONESS (Bedford Institute of Oceanography Net and Environmental Sampling System: Sameoto et al., 1980; Sameoto, 1983); an automated high-speed sampler, the Hardy Plankton Recorder (Hardy, 1936) and a variant, the Longhurst-Hardy Plankton Recorder (Longhurst et al., 1966); and light traps, which are highly selective and difficult to quantify, but are effective in capturing larger fish larvae that are taken rarely by plankton nets (Thorrold, 1992, 1993; Choat et al., 1993; Brogan, 1994).

Ontogenetic Stages

During ontogeny, an animal proceeds from the fertilized egg stage through a series of developmental processes that lead to the formation of a reproducing adult. In a large proportion of

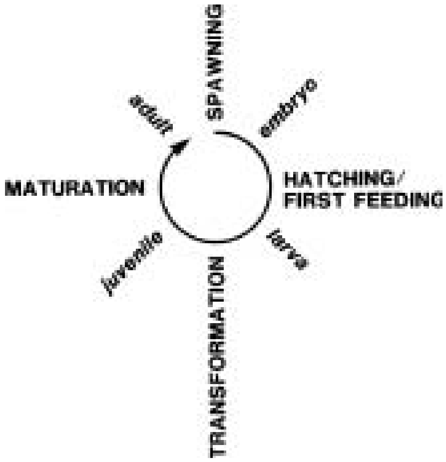

FIGURE 11-2 Major events (in capitals) and stages (lower case) in the ontogeny of fishes.

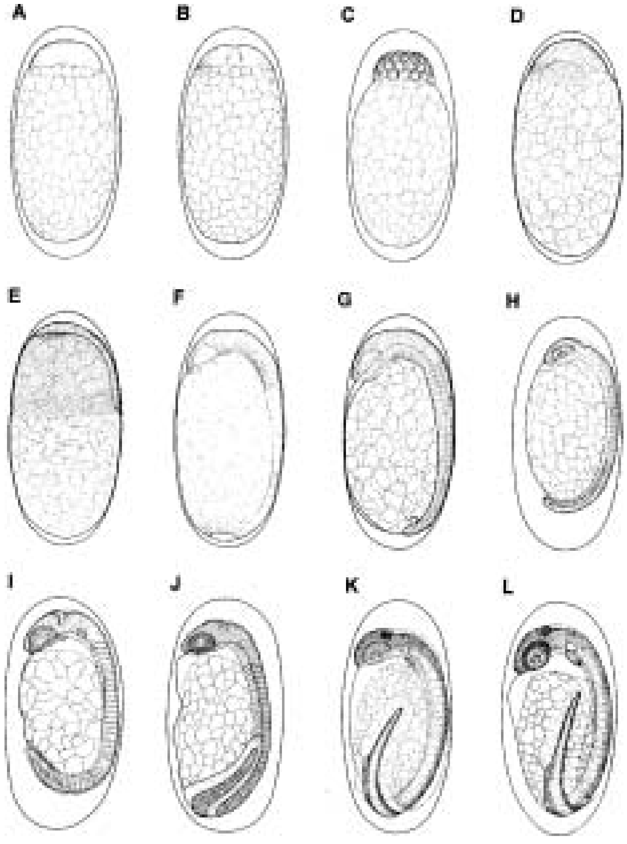

FIGURE 11-3 Developmental stages of northern anchovy (*Engraulis mordax*) eggs (modified from Moser and Ahlstrom, 1985). A: Stage I; B: early Stage II; C: Stage II; D: Stage III; E: Stage IV; F: Stage V; G: Stage VI; H: Stage VII; I: Stage VIII; J: Stage IX; K: Stage X; L: Stage XI. A–D are "early stage"; E–F are "middle stage"; G–L are "late stage."

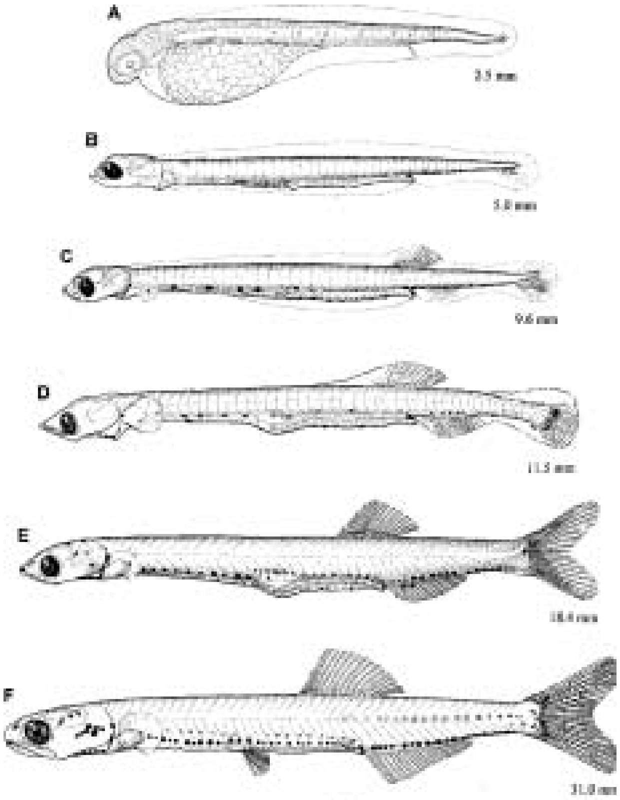

FIGURE 11-4 Developmental stages of northern anchovy (*Engraulis mordax*) larvae. A: yolk-sac stage, 2.5 mm; B: preflexion stage, 5.0 mm; C: early flexion stage, 9.6 mm; D: late flexion stage, 11.5 mm; E: postflexion stage, 18.4 mm; F: transformation stage, 31.0 mm. Illustrations from Kramer and Ahlstrom (1968).

marine fishes, the eggs are free-floating after spawning and develop into planktonic larvae that inhabit the productive upper region of the water column. Although developmental processes are continuous, it is helpful to subdivide the ontogenetic process from egg to juvenile into a series of stages or periods that are punctuated by critical life-history events (fig. 11-2). The "events" in fig. 11-2 are emphasized to suggest their critical place in the dynamics of fish populations. Kendall et al. (1984) presented terminology that generally is used in ichthyoplankton research and compared it with alternate terminologies; ontogenetic stages have been described and discussed further by a number of authors, for example, Fahay (1983), Matarese et al. (1989), Moser (1996), and Leis and Carson-Ewart (2000). Here we present illustrations of developmental stages of northern anchovy, *Engraulis mordax* (fig. 11-3 and 11-4). Typical teleost egg development may be subdivided into three stages as follows: early stage, from extrusion and fertilization to the formation of an advanced blastodisc (fig. 11-3A–D); middle stage, from the beginning to the end of epiboly, essentially the gastrulation process (fig. 11-3E,F); and late stage, from the end of epiboly and "blastopore" closure to hatching (fig. 11-3G–L). Early-stage eggs of many teleosts are similar in size and morphology and are difficult to identify; however, the state of development and the appearance of organs, structures, and pigmentation in middle and late-stage eggs provide a suite of taxonomic characters that are helpful in identifying species (Ahlstrom and Moser, 1980; Matarese and Sandknop, 1984). Further subdivision of egg development is needed when samples of eggs are staged for biomass estimation using the daily egg production method (DEPM) (Lasker, 1985; Lo et al., 2001). The set of 11 stages for northern anchovy was based on structural criteria chosen from the sequence of morphological changes that occur during embryogenesis (Moser and Ahlstrom, 1985). Once stage criteria are established, temperature-specific stage-to-age keys can be obtained by laboratory studies from which mortality curves can be derived for egg samples from field surveys. They form the basis for estimating daily egg production (Lasker, 1985; Lo et al., 2001). The stages of egg development described for northern

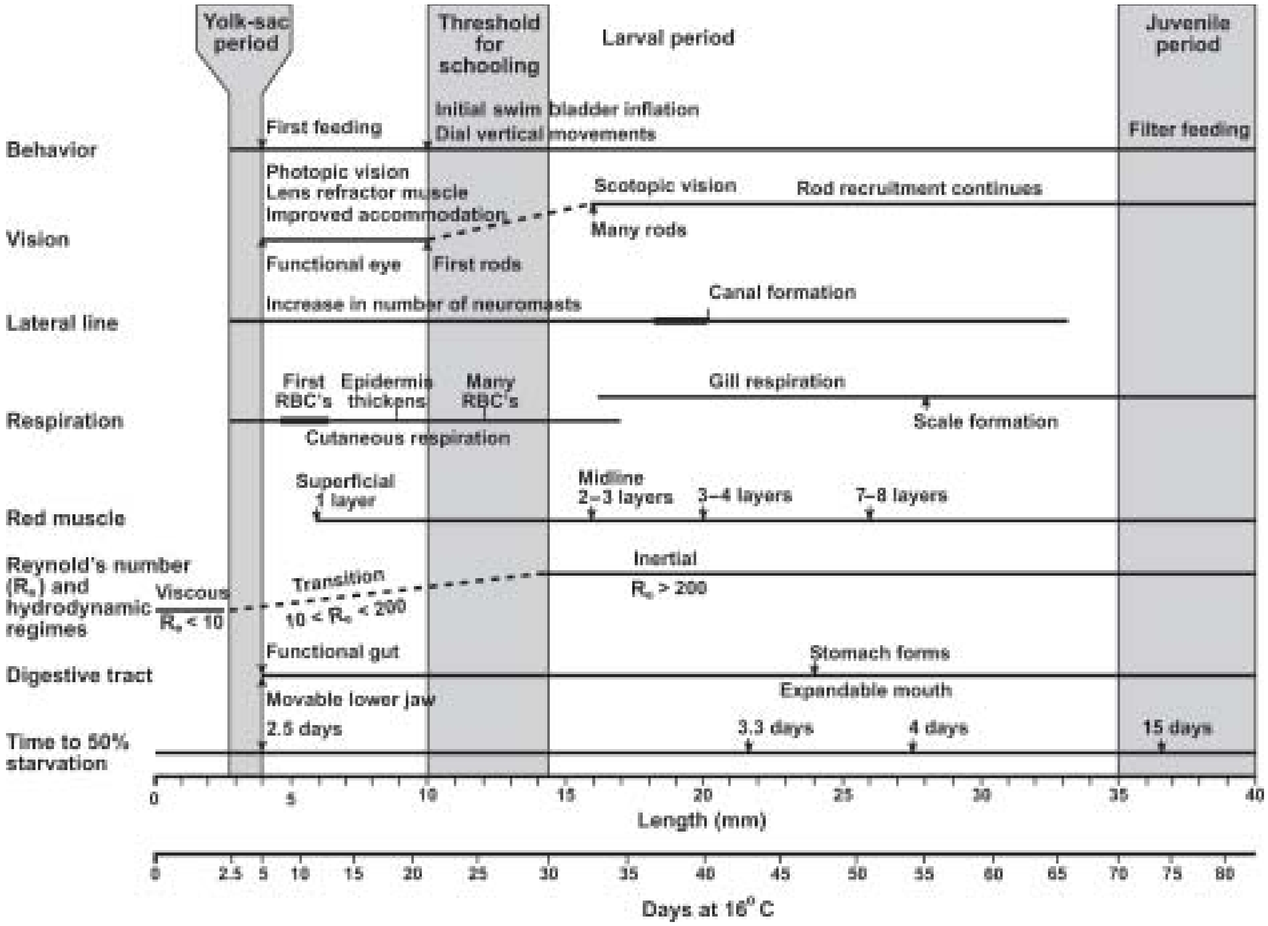

FIGURE 11-5 Developmental processes and events in northern anchovy, *Engraulis mordax*, from Hunter and Coyne (1982).

anchovy have been used with slight modification for other species (e.g., Pacific sardine, Pacific hake, Dover sole, croakers) and are applicable to a wide variety of teleosts.

In the majority of fish species with planktonic eggs, the larvae hatch at a non-feeding yolk-sac stage of development typically characterized by a large yolk sac, unpigmented or only partially pigmented eyes, nonfunctional mouth, and no fin rays or bony fin supports (fig. 11-4A). Larvae that hatch from larger planktonic eggs (≥ ~2–3 mm diameter) may be more developed at hatching, and larvae that hatch from demersal eggs typically are more developed, with little or no yolk remaining and with pigmented eyes, a functional mouth, and commonly with fin rays forming in one or more fins. Exhaustion of the yolk reserve and acquisition of functional eyes, mouth, and digestive tract in preparation for the commencement of feeding marks the end of the yolk-sac stage.

Subdivision of the post yolk-sac larval period into three stages based on the state of notochord flexion during caudal-fin development (preflexion-fig. 11-4B; flexion-fig. 11-4C,D; postflexion-fig. 11-4E) effectively defines the early, middle, and late stages of larval development. Organogenesis and behavioral development in fish larvae involves a complicated orchestration of processes and events that lead to transformation (fig. 11-4F) into the juvenile stage. In the well-studied northern anchovy, for example, the process of notochord flexion that takes place at a body length of ~10–13 mm coincides with the appearance of rods in the retina, the formation of multiple red muscle layers, the proliferation of red blood cells, initial swim bladder development and diel vertical movement, the threshold for schooling, and the transition from viscous to inertial hydrodynamic regimes (fig. 11-5) (Hunter and Coyne, 1982). Also, in anchovy and typically in other teleosts, the formation of dorsal and anal fin rays begins during caudal fin formation (Moser, 1996). Margulies (1989) found that notochord flexion in white sea bass (*Atractoscion nobilis*) larvae coincided with an improvement in their ability to escape juvenile white sea bass predators; this was related, in part, to major developmental events during this stage (e.g., rapid improvement in visual acuity, visual accommodation to distant objects, growth and stratification of the optic tectum, and large increases in the number of free neuromasts on the head and body) (fig. 11-6). Although other information on the coordination of developmental events in teleosts is scanty, where this has been studied (O'Connell, 1981; Blaxter, 1984; Fuiman, 1997; Fuiman et al., 1998), notochord flexion typically coincides with the development of an array of structures and functional capabilities critical to larval survival and serves as a meaningful and practical milestone with which to divide the larval period. At the end of this period, larvae undergo a transformation process during which larval characters are lost and juvenile/adult characters are acquired (Moser, 1996). This process may be abrupt and involve morphological changes that require rapid differentiation and allometric growth (e.g., changes in shape and general morphology, development of a stomach, and formation of a thick, solidly pigmented integument invested with scales and, in some, a silvery guanine layer,

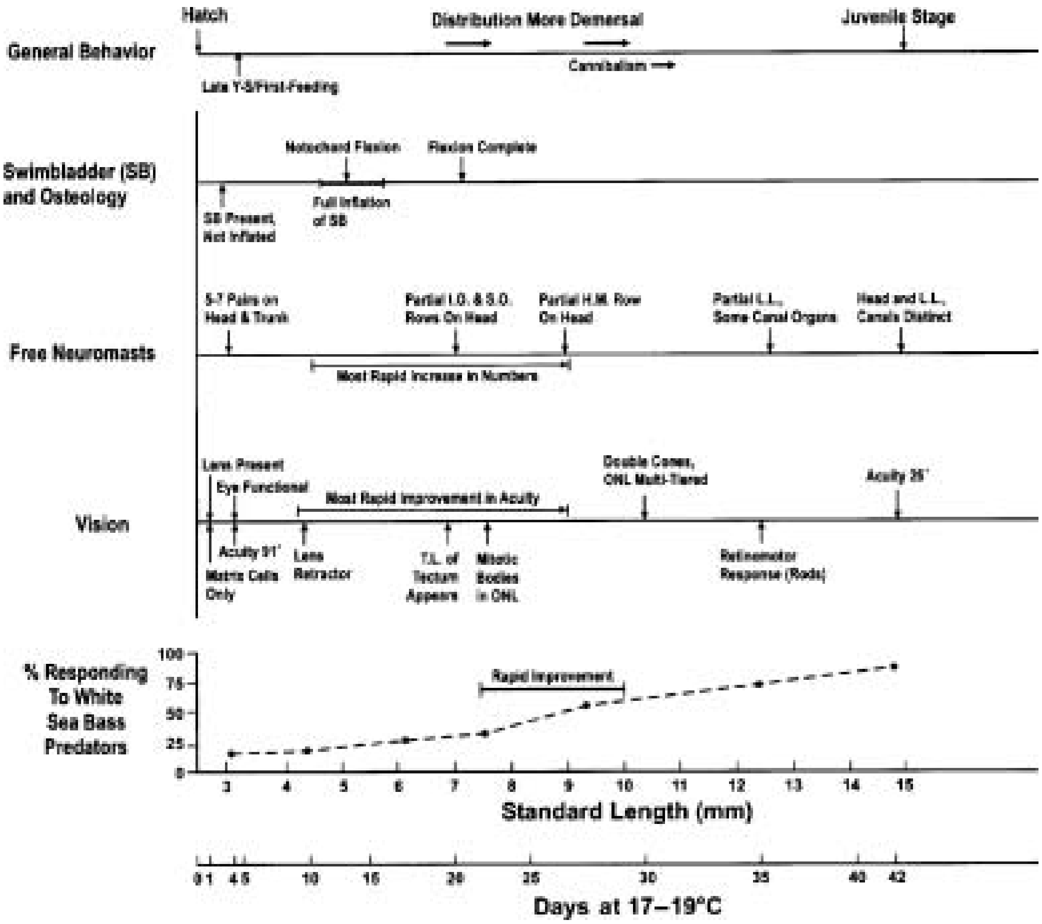

FIGURE 11-6 Developmental processes and events in white sea bass, *Atractoscion nobilis*, modified from Margulies (1989). I.O. = infraorbital; H.M. = hyomandibular; L.L. = lateral line; ONL = outer nuclear layer of retina; S.O. = supraorbital; T.L. = torus longitudinalis. Values for acuity refer to minutes of arc.

photophores, or other luminous tissue). Full complements of fin rays are present and specialized larval structures (see below) are lost. At the end of this process, epipelagic species may remain in the same habitat or move to inshore nursery areas, midwater species descend to juvenile depths, and demersal species settle in appropriate juvenile habitats. Some demersal species have specialized pelagic juvenile stages that may remain in the pelagic environment for a protracted period (Kendall et al., 1984; Moser, 1996; Leis and Carson-Ewart, 2000).

CalCOFI Larval Fish Assemblages

About 26 orders and 160 families of fishes are represented in the ichthyofauna of the California Current region. Among the families that produce planktonic larvae, the region has about 800 species. A guide to the ichthyoplankton of the region (Moser, 1996) included 25 orders, 158 families, and 586 species. Species whose larvae remain unidentified are primarily nearshore fishes (e.g., cottids, sticheoids, gobioids, blennioids) that are relatively poorly sampled by CalCOFI or other research programs. In CalCOFI oblique plankton tows, coastal pelagic fish larvae are the dominant category; about 70% of the total larvae is contributed by only 4% of the total taxa (Moser et al., 2001b). Midwater fish larvae have the most taxa (38%) and are second in abundance with 20% of the total larvae. Rocky-shore fishes contribute about one-fourth of the taxa but represent only 7% of the total larval abundance. In the Natural History Museum of Los Angeles County (LACM) nearshore larval surveys, bottom fish taxa constitute ~80% of the total taxa; about half belong to rocky-shore taxa (Moser et al., 2001b). Larvae of midwater species represent only 11% of the total taxa and ~1% of the total larval abundance. As in the CalCOFI surveys, larvae of coastal pelagic fishes dominate the LACM surveys; more than 70% of the total abundance is contributed by 8.5% of the taxa. In the LACM surveys, larvae of soft substrate fishes are 10 times more abundant than in CalCOFI surveys. Larval northern anchovy are dominant in CalCOFI and in LACM surveys. In CalCOFI oblique plankton samples northern anchovy are 3.5 times more abundant than the second ranking species, Pacific hake, *Merluccius productus* (table 11-1). California smoothtongue *Leuroglossus stilbius*, a bathylagid, ranks third in total abundance, and the importance of midwater fishes in the ecology of the California Current system is apparent from the fact that midwater fishes (e.g., bathylagids, phosichthyids, gonostomatids, myctophids) represent more than half of the 30 most abundant taxa taken in CalCOFI samples (table 11-1).

The overall CalCOFI survey pattern extends from the California-Oregon border to the southern tip of Baja California, Mexico, and offshore to the outer edge of the California Current (fig. 11-1); however, most annual surveys covered a

TABLE 11-1

Thirty Most Abundant Larval Fish in CalCOFI Surveys (Present Pattern) 1951–2000

			Number		*Occurrences*	
Taxon	*Common Name*	*Family*	*Rank*	*Total*	*Rank*	*Total*
Engraulis mordax	Northern anchovy	Engraulidae	1	2999304	1	6064
Merluccius productus	Pacific hake	Merlucciidae	2	850302	6	3464
Leuroglossus stilbius	California smoothtongue	Bathylagidae	3	371276	4	4579
Sebastes spp.	Rockfishes	Scorpaenidae	4	317355	2	5563
Vinciguerria lucetia	Panama lightfish	Phosichthyidae	5	247015	11	1975
Stenobrachius leucopsarus	Northern lampfish	Myctophidae	6	234471	3	4882
Sardinops sagax	Pacific sardine	Clupeidae	7	146602	25	1009
Trachurus symmetricus	Jack mackerel	Carangidae	8	82668	14	1810
Sebastes jordani	Shortbelly rockfish	Scorpaenidae	9	70374	19	1500
Bathylagus ochotensis	Popeye blacksmelt	Bathylagidae	10	53112	7	2831
Sciaenidae	Croakers	Sciaenidae	11	37904	36	668
Triphoturus mexicanus	Mexican lampfish	Myctophidae	12	37822	8	2390
Bathylagus wesethi	Snubnose blacksmelt	Bathylagidae	13	35442	13	1862
Protomyctophum crockeri	California flashlightfish	Myctophidae	14	32067	5	3686
Ceratoscopelus townsendi	Dogtooth lampfish	Myctophidae	15	24678	21	1212
Citharichthys stigmaeus	Spotted sanddab	Paralichthyidae	16	23655	12	1951
Nannobrachium ritteri	Broadfin lampfish	Myctophidae	17	21988	9	2134
Tarletonbeania crenularis	Blue lanternfish	Myctophidae	18	21649	10	1978
Diogenichthys atlanticus	Longfin lanternfish	Myctophidae	19	19941	15	1799
Citharichthys spp.	Sanddabs	Paralichthyidae	20	18755	18	1591
Scomber japonicus	Chub mackerel	Scombridae	21	18006	42	438
Sebastes paucispinis	Bocaccio	Scorpaenidae	22	17692	22	1161
Symbolophorus californiensis	California lanternfish	Myctophidae	23	17455	16	1790
Cyclothone signata	Showy bristlemouth	Gonostomatidae	24	16268	27	945
Nannobrachium spp.	Lampfishes	Myctophidae	25	16126	17	1725
Genyonemus lineatus	White croaker	Sciaenidae	26	14299	63	212
Citharichthys sordidus	Pacific sanddab	Paralichthyidae	27	13544	30	864
Diaphus spp.	Headlightfishes	Myctophidae	28	12945	24	1025
Cyclothone spp.	Bristlemouths	Gonostomatidae	29	11690	23	1040
Vinciguerria poweriae	Highseas lightfish	Phosichthyidae	30	9612	70	168

NOTE: "Number" is a standardized value adjusted for standard haul factor and fraction of the plankton sample sorted.

smaller area from San Francisco, California, to Bahia Magdalena, Baja California Sur, and seaward to include the California Current. Spatial and temporal coverage was most complete during the early years of the surveys (1951–1960) when multivessel cruises occupied much of the survey pattern at monthly intervals (Moser et al., 1993). A recurrent group analysis (Fager, 1957) of the CalCOFI larval fish assemblages for 1954 to 1960 (Moser et al., 1987) revealed nine recurrent groups with numerous associated taxa (fig. 11-7). These formed Northern and Southern Complexes, each containing four groups and their associated taxa, and a Southern Coastal Complex that included one group and its associated taxa. The major recurrent group in the Northern Complex, Leuroglossus, is formed by three midwater species, popeye blacksmelt (*Bathylagus ochotensis*), California smoothtongue, and northern lampfish (*Stenobrachius leucopsarus*), and two demersal taxa, Pacific hake and the speciose rockfish genus (fig. 11-8A). Tarletonbeania is composed of blue lanternfish (*Tarletonbeania crenularis*), a myctophid that migrates to surface waters at night, and the medusafish (*Icichthys lockingtoni*), an epipelagic species of the family Centrolophidae (fig. 11-8B). The other two groups in the Northern Complex, Sardinops and Citharichthys, are composed of coastal pelagic and demersal species. Sardinops includes Pacific sardine and chub mackerel (*Scomber japonicus*) (fig. 11-8C). Citharichthys is formed by northern anchovy, longfin sanddab (*Citharichthys xanthostigma)*, and Gulf sanddab (*C. fragilis*) (fig. 11-8D). Speckled sanddab (*C. stigmaeus*), though not a member of a recurrent group, has significant affinities with members of the Leuroglossus and the Citharichthys groups (fig. 11–7).

In the Southern Complex the largest group, Symbolophorus, is formed by five midwater species: snubnose blacksmelt (*Bathylagus wesethi*), bristlemouths (genus *Cyclothone* in the family Gonostomatidae), and three myctophids, California lanternfish (*Symbolophorus californiensis*), longfin lanternfish (*Diogenichthys atlanticus*), and broadfin lampfish (*Nannobrachium ritteri*) (fig. 11-9A). Snubnose blacksmelt and broadfin lampfish are endemic to the California Current region, whereas longfin lanternfish and two of the bristlemouth species, benttooth bristlemouth (*C. acclinidens*) and slender bristlemouth (*C. pseudopallida*), have worldwide distributions that include equatorial and central water masses. Showy bristlemouth (*Cyclothone signata*), the most common bristlemouth species in CalCOFI collections, is endemic to the eastern central Pacific. California lanternfish may range westward from the California Current to the Kuroshio. The three-member Triphoturus group includes two myctophids, Mexican lampfish (*Triphoturus mexicanus*) and California flashlightfish (*Protomyctophum crockeri*), and jack mackerel (*Trachurus symmetricus*) (fig. 11-9B). California flashlightfish is endemic to the

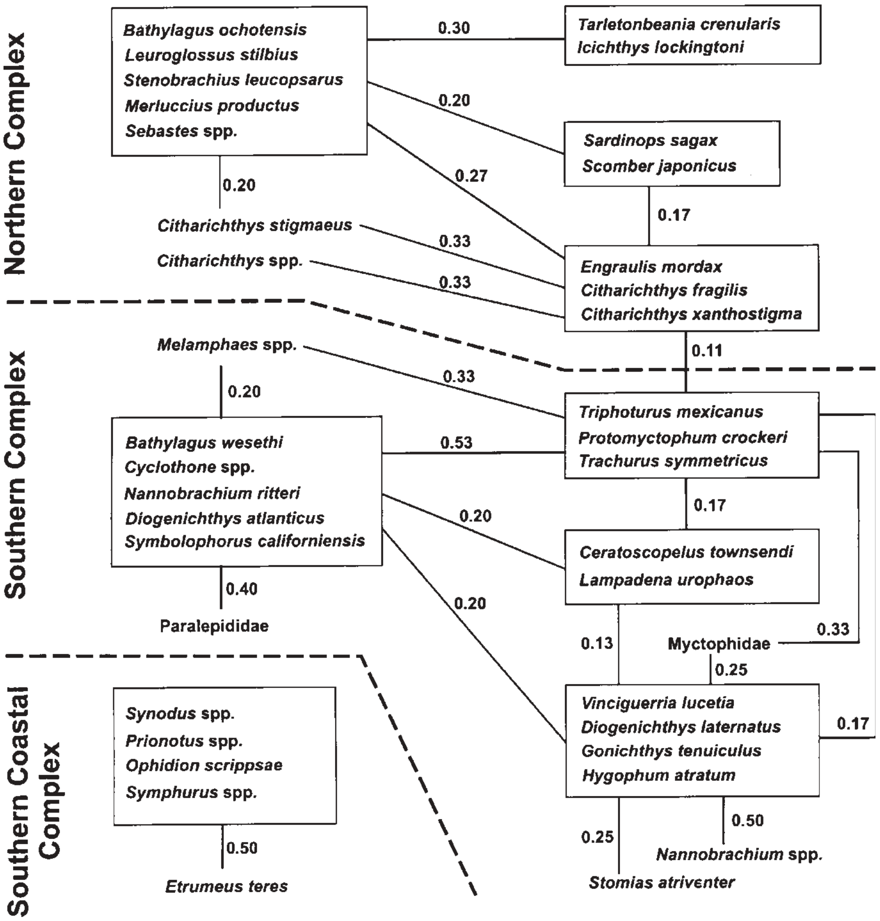

FIGURE 11-7 Recurrent groups and their associates in the CalCOFI survey area, 1954–1960. A line between two groups indicates that there are intergroup pairs with significant affinity indexes (≥ 0.3). The number associated with each line is the fraction of significant affinity pairs divided by the number of possible pairs. Northern, Southern, and Southern Coastal Complexes are separated by dashed lines (modified from Moser et al., 1987).

California Current region, and Mexican lampfish, the most abundant myctophid in the southern part of the California Current region, extends into the Gulf of California, and is replaced by a similar species, *T. oculeus*, southward along the mainland coast of Mexico and by highseas lampfish (*T. nigrescens*) westward of the California Current. Jack mackerel is a prominent pelagic species of the California and Baja California coasts. Two myctophids, dogtooth lampfish (*Ceratoscopelus townsendi*) and sunbeam lampfish (*Lampadena urophaos*), comprise Ceratoscopelus (fig. 11-9C). Sunbeam lampfish is a warm-water cosmopolite, whereas dogtooth lampfish is a California Current endemic (John Paxton, Australian Museum, pers. commun.). The Vinciguerria group (fig. 11-9D) is composed of four eastern tropical Pacific species whose ranges extend northward to the waters off southern California. Of the four species, the phosichthyid, Pacific lightfish (*Vinciguerria lucetia*), the most abundant off California, ranks fifth in total larval abundance, and its abundance increased sharply during the recent warm climate regime. Larvae of the other species, the myctophids Diogenes lanternfish (*Diogenichthys laternatus*), thickhead lanternfish (*Hygophum atratum*), and slendertail lanternfish (*Gonichthys tenuiculus*), are abundant off Baja California and occur rarely off southern California, typically during El Niño conditions when they are advected poleward by the strong coastal countercurrent (Moser et al., 2001a,b). The midwater genus *Melamphaes*, primarily highsnout bigscale (*M. lugubris*) and little bigscale (*M. parvus*), and the midwater predator family Paralepididae, primarily slender barracudina (*Lestidiops ringens*), are associates of Symbolophorus; *Melamphaes* also is an associate of Triphoturus. Blackbelly dragonfish (*Stomias atriventer*), a midwater predator in the family Stomiidae, is an associate of the Vinciguerria group.

The Southern Coastal Complex, Synodus, is composed of basketweave cusk-eel (*Ophidion scrippsae*) and three temperate-tropical genera, *Synodus*, *Prionotus*, and *Symphurus*, that inhabit soft-bottom shelf habitats (fig. 11-10). Each of these genera contains a species (California lizardfish, *S. lucioceps;* lumptail sea robin, *P. stephanophrys;* and California tonguefish, *S. atricaudus*), whose distribution extends northward into southern California waters and accounts for the largest proportion of the larvae of that genus in CalCOFI samples. The round herring (*Etrumeus teres*) is an associate of Synodus. The highest abundances of all of these species are in Bahia Sebastian Viscaino (the bay formed by the Punta Eugenia peninsula) and the region between Punta Eugenia and Bahia Magdalena (fig. 11-1). Together, these two regions have ~39,000 km^2 of shelf habitat (20,008 and 18,897 km^2, respectively), approximately 70% of the shelf habitat for the entire Baja California coast and ~4.6 times the amount of shelf habitat off southern California.

Geographic and Seasonal Distribution

The California Current region, including the coastal waters of California and Baja California, south to Cabo San Lucas, encompasses an area >1 million km^2 and includes three coastal zoogeographic provinces (the Oregonian, San Diegan, and Panamic), a coastal upwelling zone, and three oceanic water masses (Subarctic-Transitional, Central, and Eastern Tropical Pacific—the more or less distinct segment of Pacific equatorial

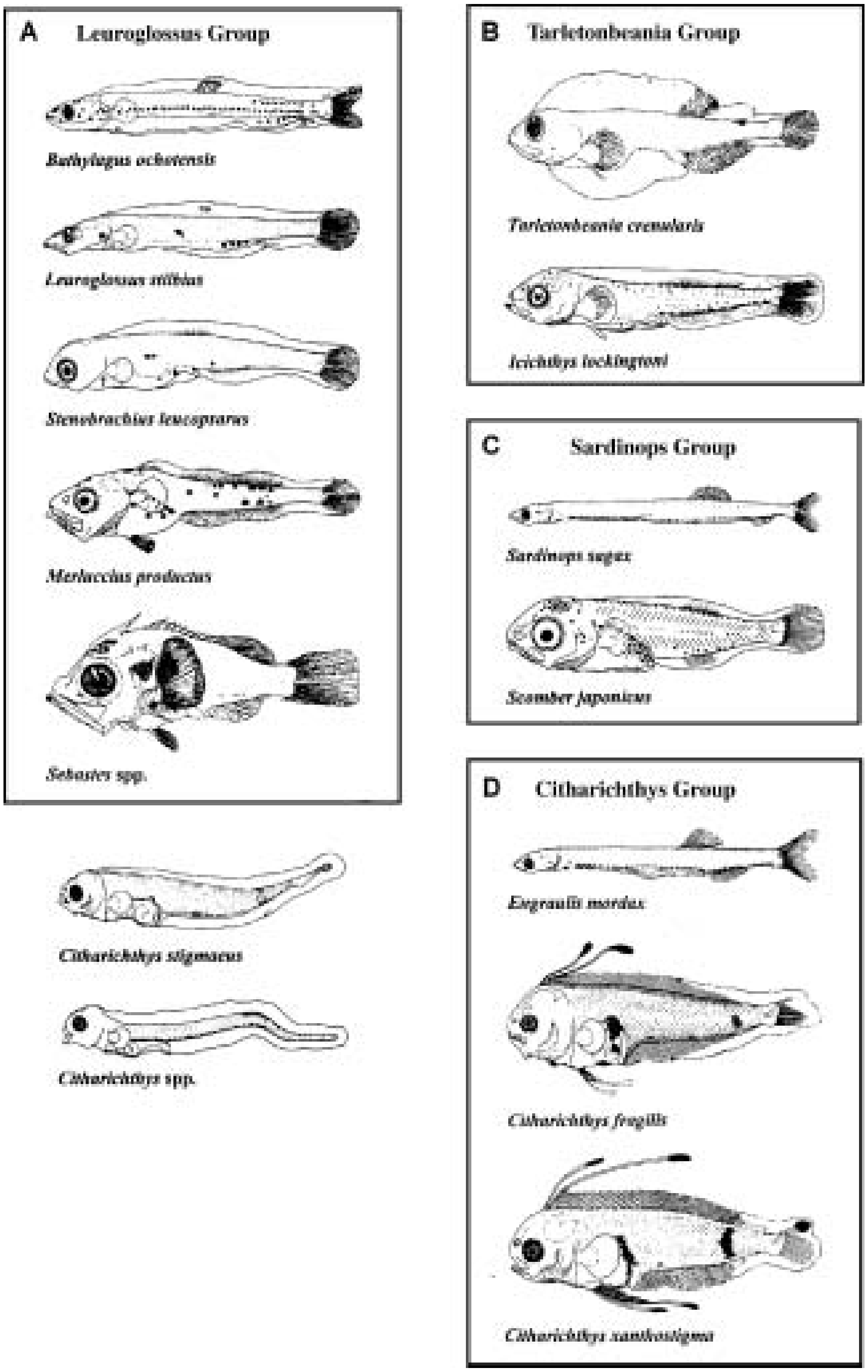

FIGURE 11-8 Members of the four recurrent groups of fish larvae of the Northern Complex in the CalCOFI survey area, 1954–1960. (A) Leuroglossus; (B) Tarletonbeania; (C) Sardinops; (D) Citharichthys. *Citharichthys stigmaeus* is an associate of Leuroglossus and Citharichthys; *Citharichthys* spp. is an associate of Citharichthys. All illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained.

water east of about 140°W) (fig. 11-11). Two of the three midwater members of Leuroglossus, northern lampfish (fig. 11-12A) and popeye blacksmelt (see Moser et al., 1993: CalCOFI Atlas 31, p.18), inhabit California Current waters south to northern Baja California and westward in the transition zone (Willis et al., 1988). The third midwater species, California smoothtongue, is a more southerly and coastal species with a center of distribution off southern California (CalCOFI Atlas 31, p.14). Larval abundance of the three species peaks in winter, and substantial numbers of larvae are present in spring. Pacific hake spawns off California and Baja California; the juveniles migrate north as they grow, reach maturity in the waters of the Pacific northwest and the Gulf of Alaska, and then migrate south to their spawning grounds. Spawning is concentrated during winter; off southern California, half the total larvae are produced in February and ~90% during January-March. The larval peak off southern Baja California (CalCOFI Atlas 31, p.8) is believed to represent a subpopulation distinct from the main population (Bailey et al., 1982). About sixty species of viviparous rockfishes occur off California and Baja California. Although rockfish larvae in aggregate rank fourth among all larvae captured on CalCOFI surveys (table 11-1), only seven species can be distinguished in CalCOFI samples. Most species release their larvae in winter, although parturition tends to shift to spring or summer at higher latitudes (CalCOFI Atlas 31, p.12). Some species have extended parturition seasons; for example, off southern California, aurora rockfish (*S. aurora*) releases larvae from November to August with a peak in June,

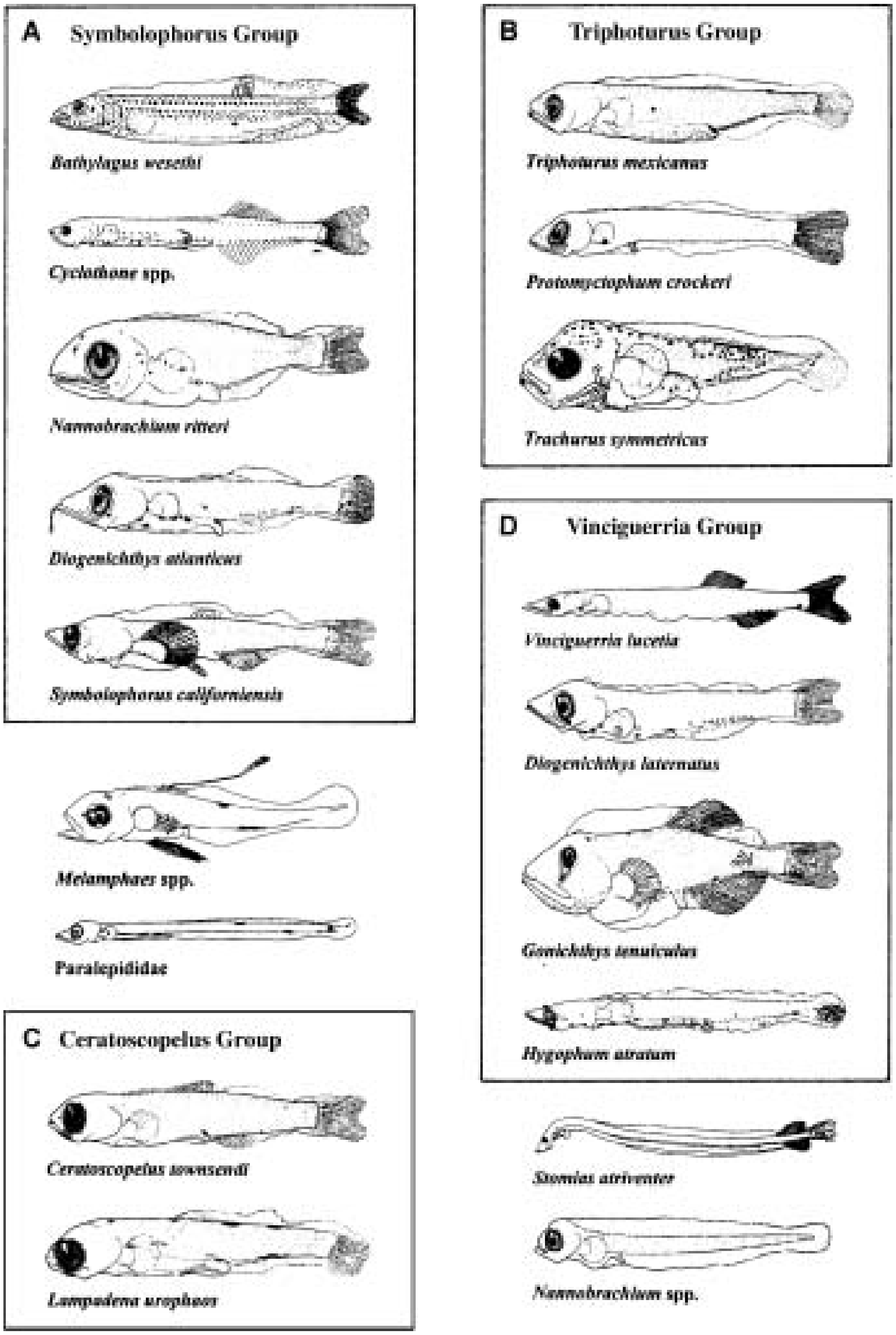

FIGURE 11-9 Members of four recurrent groups of fish larvae of the Southern Complex in the CalCOFI survey area, 1954–1960. (A) Symbolophorus; (B) Triphoturus; (C) Ceratoscopelus; (D) Vinciguerria. *Melamphaes* spp. is an associate of Symbolophorus and Triphoturus. Paralepididae is an associate of Symbolophorus; *Stomias atriventer* and *Nannobrachium* spp. are associates of Vinciguerria. All illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained.

and splitnose rockfish (*S. diploproa*) produces larvae year-round with a summer-fall peak (Moser and Boehlert, 1991; Moser et al., 2000). Slender sole (*Lyopsetta exilis*), a pleuronectid flatfish, is not a Leuroglossus group member but is the most abundant affiliate of the group (Moser et al., 1987). Slender sole larvae occur year-round off California and Baja California with a spring peak (CalCOFI Atlas 31, p. 86). The higher spring abundance of slender sole larvae off central California and in the Sebastian Viscaino Bay region, compared to regions between the two, probably reflects the amount of suitable habitat and relatively large spawning populations in the two regions.

The two Tarletonbeania species, blue lanternfish and medusafish, have a subarctic-transitional distribution ranging across the North Pacific and southward in the California Current to northern Baja California. Larvae are present year-round in the northern sector of the CalCOFI survey area with peak abundance of blue lanternfish during fall-winter (CalCOFI Atlas 31, p.38) and medusafish in spring–summer (CalCOFI Atlas 31, p.70). The two Sardinops group species, Pacific sardine (fig. 11-12B) and chub mackerel (CalCOFI Atlas 31, p.48), have broad spawning distributions that can extend from the Gulf of Alaska to the Gulf of California, depending on ocean conditions. During 1951 to 1984 their larvae were primarily south of Point Conception and most abundant off central and southern Baja California. Both species produce larvae year-round with winter and summer peaks off Baja California. Off southern California, chub mackerel larval abundance peaks during spring–summer (CalCOFI Atlas 31, p. 48).

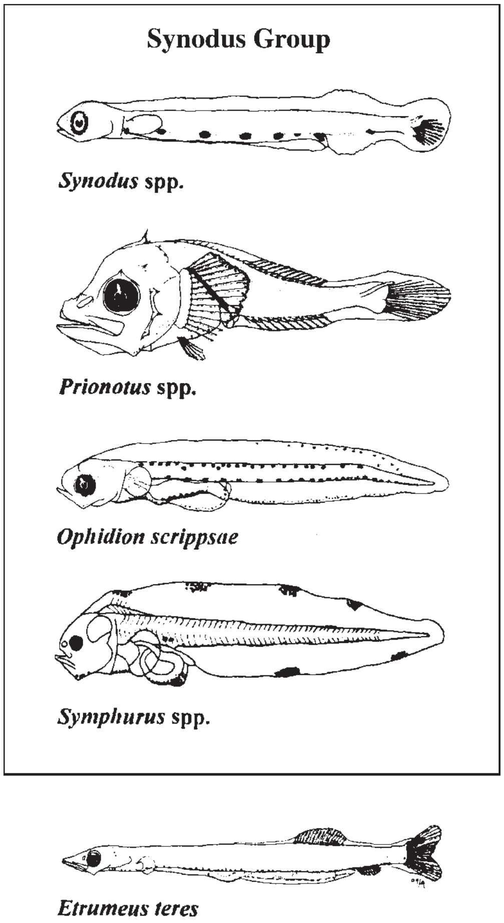

FIGURE 11-10 Members of the Synodus recurrent group of fish larvae that form the core of the Southern Coastal Complex in the CalCOFI survey area, 1954–1960. *Etrumeus teres* is an associate of Synodus. Most illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained. *Synodus* spp. from Okiyama (1984); *Prionotus* spp. from Richards (1996).

The Citharichthys group member, northern anchovy, was the most abundant species in the CalCOFI time series during 1951 to 1984 and accounted for almost half of the total fish larvae (Moser et al., 1993). Larval anchovy were ubiquitous seasonally, with a winter peak off southern California and northern Baja California (fig. 11-12C). The other two species in the group, longfin and Gulf sanddabs, also spawn year-round, but peak larval abundance is shifted to summer months in the Sebastian Viscaino Bay region (CalCOFI Atlas 31, pp. 60 and 50). Speckled sanddab, a Citharichthys associate species shared with the Leuroglossus group, spawns year-round with a fall peak off California and the Sebastian Viscaino Bay region (CalCOFI Atlas 31, p. 52). The Sebastian Viscaino Bay region provides optimum habitat for temperate–subtropical sanddabs; all three species had their highest average larval abundance there.

In Symbolophorus, larvae of California lanternfish (fig. 11-12D), snubnose blacksmelt (CalCOFI Atlas 31, p. 28), and broadfin lampfish (CalCOFI Atlas 31, p. 44) occur year-round with highest average larval abundances in the core of the central region of the California Current during spring–summer. Although a species similar to, and perhaps conspecific with, California lanternfish occurs in the western Pacific (Wisner, 1976; Willis et al., 1988), the rarity of larvae in the northern region of the California Current (Doyle, 1992a) suggests that the populations are disjunct. Showy bristlemouth accounts for >90% of bristlemouth larvae in CalCOFI samples, benttooth and slender bristlemouths contribute most of the remaining larvae, ~4 and 2%, respectively (Moser et al., 2001a). Larvae are present year-round with highest abundance in the core region of the California Current in summer and fall (CalCOFI Atlas 31, p. 34). The pattern of larval distribution for longfin lanternfish clearly demonstrates the protrusion of the population from the central water mass into the midregion of the California Current (fig. 11-12E). Slender barracudina, a Symbolophorus associate, is a California Current region endemic, replaced to the south by *L. neles* and to the west by *L. pacificum*. It spawns year-round with highest abundance in the California Current core (CalCOFI Atlas 31, p.112).

In Triphoturus, Mexican lampfish spawns year-round with peak larval abundance in summer off Northern and Central Baja California (CalCOFI Atlas 31, p.16). California flashlightfish spawns year-round in the core of the California Current with highest larval abundance in winter at the northern part of the CalCOFI survey pattern (CalCOFI Atlas 31, p. 36). Jack mackerel exhibits a seasonal south-to-north spawning progression, beginning in winter–spring and peaking off southern California in early summer (CalCOFI Atlas 31, p.24). An offshore segment of the population ranges to the western margin of the California Current and spawning progresses northward into the transition zone in summer and autumn. The Triphoturus associate genus, *Melamphaes,* spawns year-round with highest larval abundance from the core to the outer margins of the California Current (CalCOFI Atlas 31, p. 62). In Ceratoscopelus, dogtooth lampfish spawns year-round with highest larval abundance in the core and outer margin of the California Current (CalCOFI Atlas 31, p. 40). The high summer abundance in the outermost CalCOFI region probably represents larvae of the warm-water cosmopolite, *C. warmingii* (a species morphologically similar to dogtooth lampfish), an inhabitant of equatorial and central water masses. Larval abundance of the warm-water cosmopolite, sunbeam lampfish, is more seasonal, with a progression toward a summer–fall peak in the southern core of the California Current (CalCOFI Atlas 31, p. 134).

Larvae of the four Vinciguerria species are present year-round; only Pacific lightfish show high abundance as far north as southern California; in the CalCOFI time series for 1951 to 1984 the larval abundance of the Pacific lightfish peaked off northern Baja California in summer (fig. 11-12F). The abundance of Diogenes lanternfish larvae was consistently highest off southern Baja California without a seasonal peak (CalCOFI Atlas 31, p. 26). Larvae of the other two Vinciguerria members occurred primarily off southern Baja California; slendertail lanternfish larval abundance was highest in winter–spring (CalCOFI Atlas 31, p.108), whereas thickhead lanternfish showed little seasonality (CalCOFI Atlas 31, p.88). Larvae of the Vinciguerria associate, blackbelly dragonfish, are widespread off California and Baja California and present year-round, with highest abundance off California (CalCOFI Atlas 31, p.130). Spawning of *Ophidion scrippsae* (fig. 11-27E) and the other Synodus members, *Synodus* spp. (CalCOFI Atlas 31, p. 54), *Prionotus* spp. (CalCOFI Atlas 31, p. 68), and *Symphurus* spp. (CalCOFI Atlas 31, p.72), are distinctly seasonal with peak abundance during summer–fall in the extensive shelf habitats off central and southern Baja California.

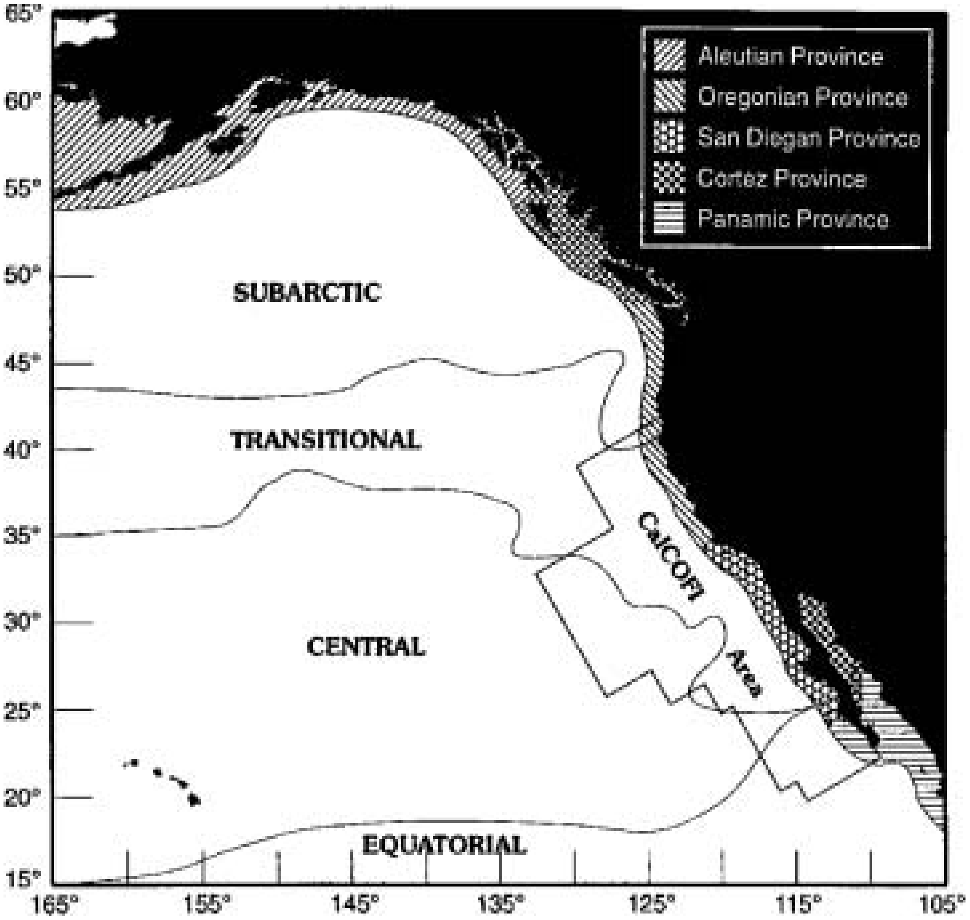

FIGURE 11-11 Water masses and zoogeographic Provinces of the northeast Pacific in relation to the CalCOFI survey area. The Eastern Tropical Pacific water mass referred to in the text is the wedge-shaped eastern limb of the equatorial water mass. From Brinton (1962), Allen and Smith (1988), and Moser (1996).

Interannual and Decadal Changes

Ichthyoplankton samples are dominated by eggs and early larval stages that reflect the reproductive output of adult stocks, thus providing useful indexes of relative population abundance. Consequently, the changes undergone by many fish populations off California and Baja California during the past half-century are evident in the CalCOFI ichthyoplankton time series. The most dramatic of these are the waxing and waning of the Pacific sardine and northern anchovy populations. CalCOFI surveys in 1954 showed that sardine and anchovy larvae extended from central California to Cabo San Lucas and offshore to the margin of the survey pattern occupied that year (~250 n. mi.); anchovy larvae were more concentrated coastally than sardine (fig. 11-13A). Eight years later, larval sardine abundance had plummeted and their distribution had contracted to semi-isolated patches along the shelf regions from southern California to central Baja California (Ahlstrom, 1966) (fig. 11-13B). In contrast, anchovy larval abundance increased markedly (Ahlstrom, 1966; Smith, 1972); areas of high concentration extended offshore to the margin of the survey pattern occupied in 1954 (fig. 11-13B). Average abundance of sardine larvae in the SCB region, the area covered by CalCOFI surveys since 1984, declined from ~10/10 m^2 of surface area in 1954 to ≤1/10 m^2 for a 20-year period from 1961 to 1981 (fig. 11-13C). Abundance increased sporadically from 1984 to 1995 and then abruptly to ~90/10 m^2 in 1997. Larval anchovy, however, showed a distinctly different trend, increasing from ~20/10 m^2 in 1951 to a maximum of ~800 larvae/10 m^2 in 1981, and declining to ≤100/10 m^2 in recent surveys (fig. 11-13C).

A fishing moratorium for Pacific sardine was in force during the years when the population was depressed and had retracted to bays and nearshore areas along the southern California and Baja California coast (Wolf and Smith, 1985; Wolf et al., 1987). An increase in larval sardine abundance was detected in nearshore habitats as early as 1981 (Watson, 1992), and subsequent ichthyoplankton surveys have shown extensive spawning offshore to the California Current and northward to central California, whereas anchovy spawning has contracted to nearshore areas of the SCB (fig. 11-14) (Checkley et al., 2000; Smith and Moser, 2003). The role that fisheries management has played in the resurgence of the Pacific sardine should be considered in the light of natural fluctuations in sardine and anchovy populations over a period of centuries. Deposition rates of sardine and anchovy scales in anaerobic sediments from the Santa Barbara Basin indicate that populations of both species varied cyclically over periods of about 60 years and that northern anchovy also varied over a 100-year period (fig. 11-13D; Baumgartner et al., 1992). Moreover, Pacific sardine has experienced nine major population collapses and recoveries during the past 1700 years with an average recovery time of about 30 years (Baumgartner et al., 1992). The importance of ocean climate in the regulation of Pacific sardine populations is highlighted by the fact that stocks underwent near-synchronous

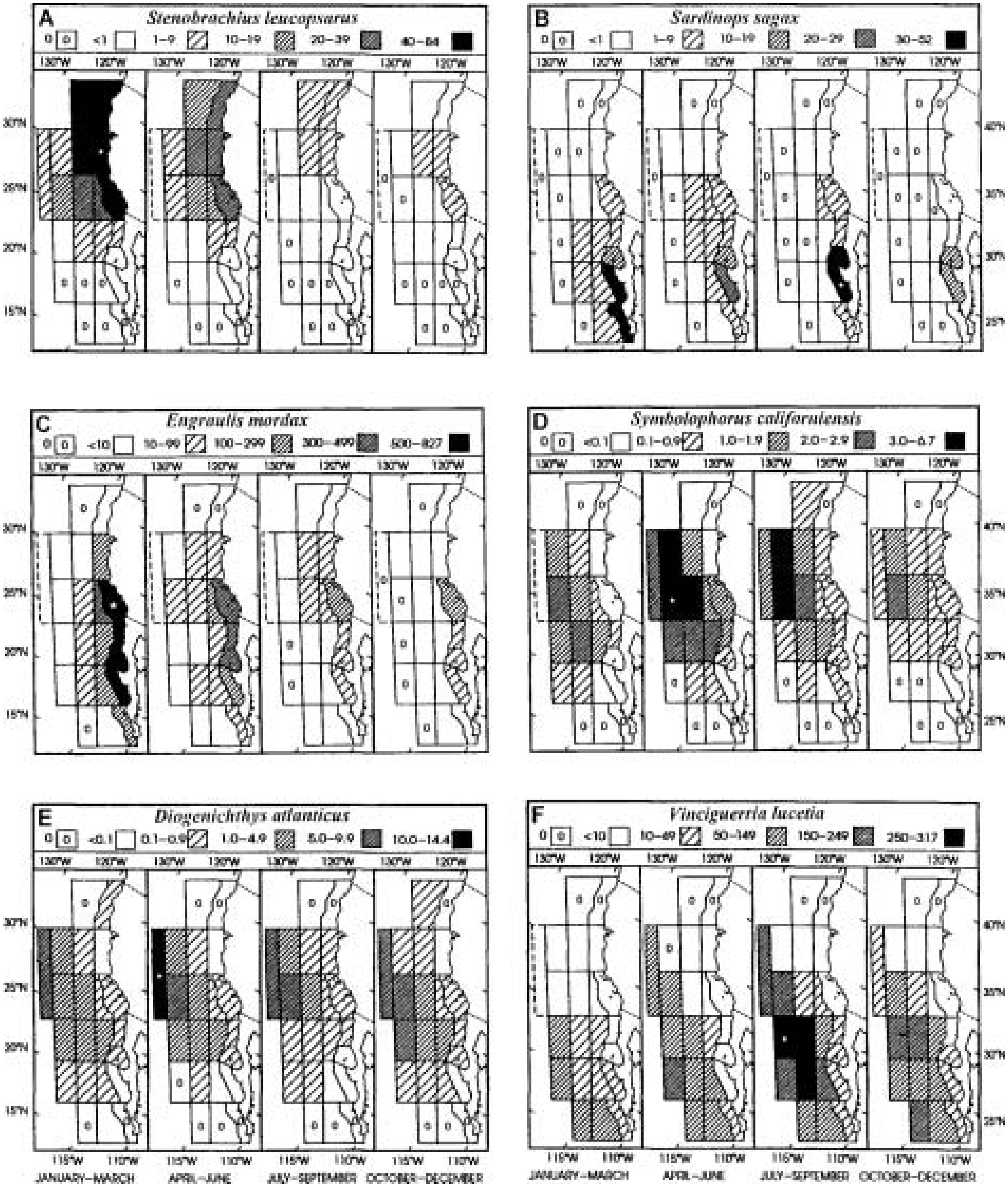

FIGURE 11-12 Quarterly maps showing mean larval abundance (number per 10 m^2) from 1951 to 1984 in each of 22 CalCOFI regions (Moser et al., 1993) for *Stenobrachius leucopsarus* (Leuroglossus recurrent group of the CalCOFI survey area), *Sardinops sagax* (Sardinops), *Engraulis mordax* (Citharichthys), *Symbolophorus californiensis* (Symbolophorus), *Diogenichthys atlanticus* (Symbolophorus), and *Vinciguerria lucetia* (Vinciguerria).

cycles of collapse and recovery in three separate regions of the Pacific (U.S. west coast, Japan, Chile-Peru) during the past century (Kawasaki, 1991) and that these cycles coincided with shifts in decadal-scale ocean climate regimes. Extensive records of population changes, such as those available for sardine and anchovy, are not available for other species in the California Current region; however, decadal-scale fluctuations in larval abundance are apparent in the CalCOFI time series for most of the teleost fishes of the region. CalCOFI oceanographic measurements made at each station provide the opportunity to examine the variation in larval distribution and abundance in the context of interannual and decadal environmental changes.

The cyclic warming and cooling of equatorial waters, known as the El Niño/Southern Oscillation (ENSO), produced

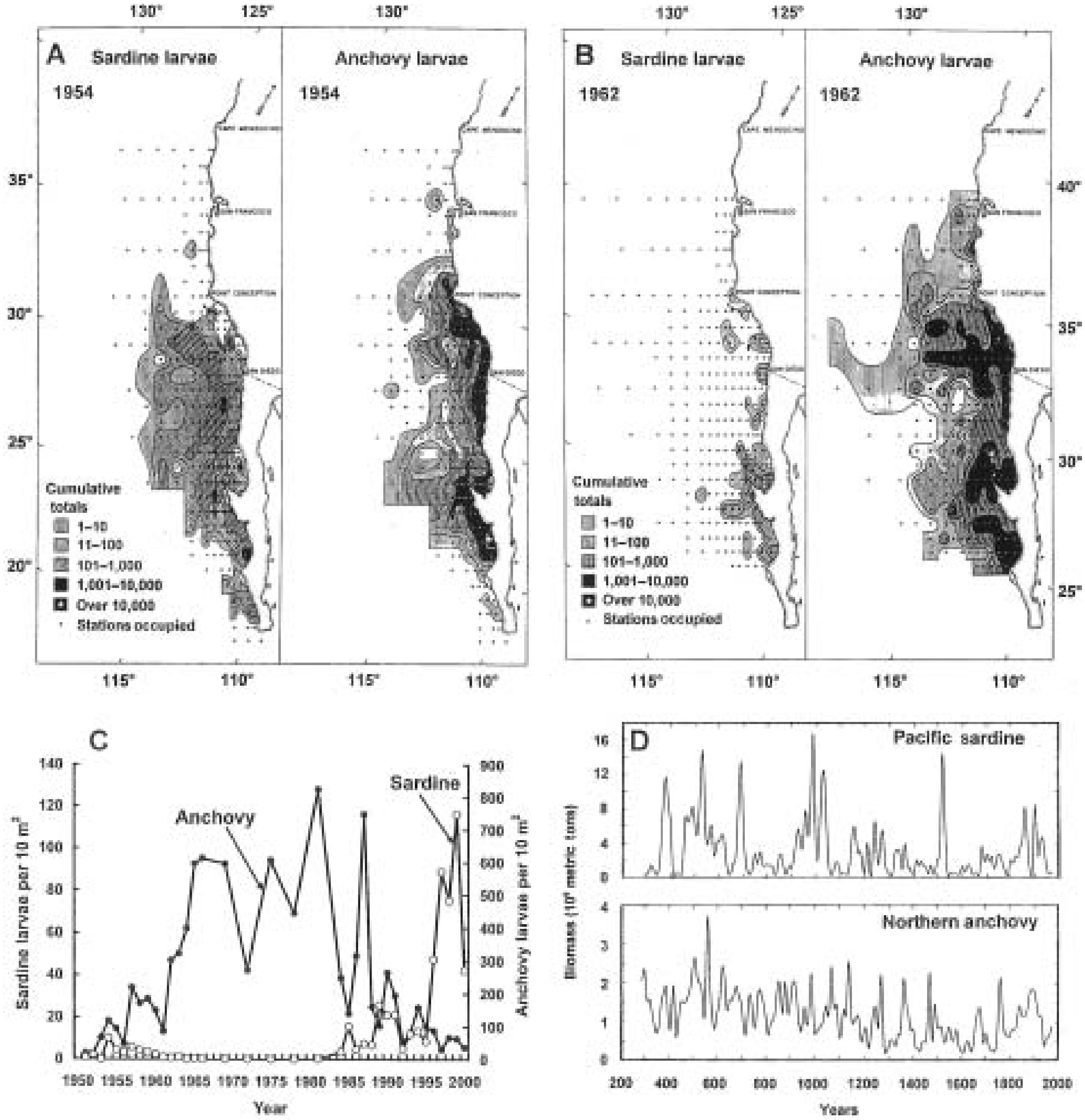

FIGURE 11-13 Interannual changes in abundances and distributions of Pacific sardine and northern anchovy. A: larval distributions in the CalCOFI survey area, 1954, from Ahlstrom (1966); B: larval distributions in the CalCOFI survey area, 1962, from Ahlstrom (1966); C: mean annual larval abundance (number per 10 m^2) in the Southern California Bight from 1951 to 2000; D: 1700-year series of estimated adult biomasses off California and Baja California based on scale deposition rates in ocean sediments, from Baumgartner et al. (1992).

a series of warm (1957–1958, 1963, 1982–1983, 1993, and 1997–1998) and cold (1954–1956, 1988–1989, 1998–1999) episodes in the California Current region during the past 50 years. Prolonged cold ocean conditions in the CalCOFI region during 1970 to 1976, produced by three closely spaced La Niñas, were followed abruptly by a shift to a warm ocean regime late in 1976. Ocean regimes in the North Pacific are generated by a 20–30 year oscillation (Pacific Decadal Oscillation or PDO) that is related to basin-scale changes in atmospheric pressure, particularly the intensification and position of the Aleutian low pressure system, and possibly to low latitude atmospheric teleconnections (Miller et al., 1994; Mantua et al., 1997; Hollowed et al., 1998; Schwing et al., 2002). The PDO produced two cool ocean regimes (1900 to 1924 and 1947 to 1976) and two warm regimes (1925 to 1946 and 1977 to at least 1998) during the past century. Primary and secondary production in the California Current region decreased dramatically after the regime shift of 1976 to 1977 (Brodeur and Ware, 1992; Roemmich and McGowan, 1995a,b; Ware, 1995; Hayward, 1997; McGowan et al., 1998). Major shifts occurred in the distributions of larval fishes in response to ENSO events and the PDO, as the boundaries between subarctic and equatorial water masses shifted latitudinally and intrusion of central water into the SCB region waxed and waned (Moser et al., 1987, 2001a; Smith and Moser, 1988, 2003).

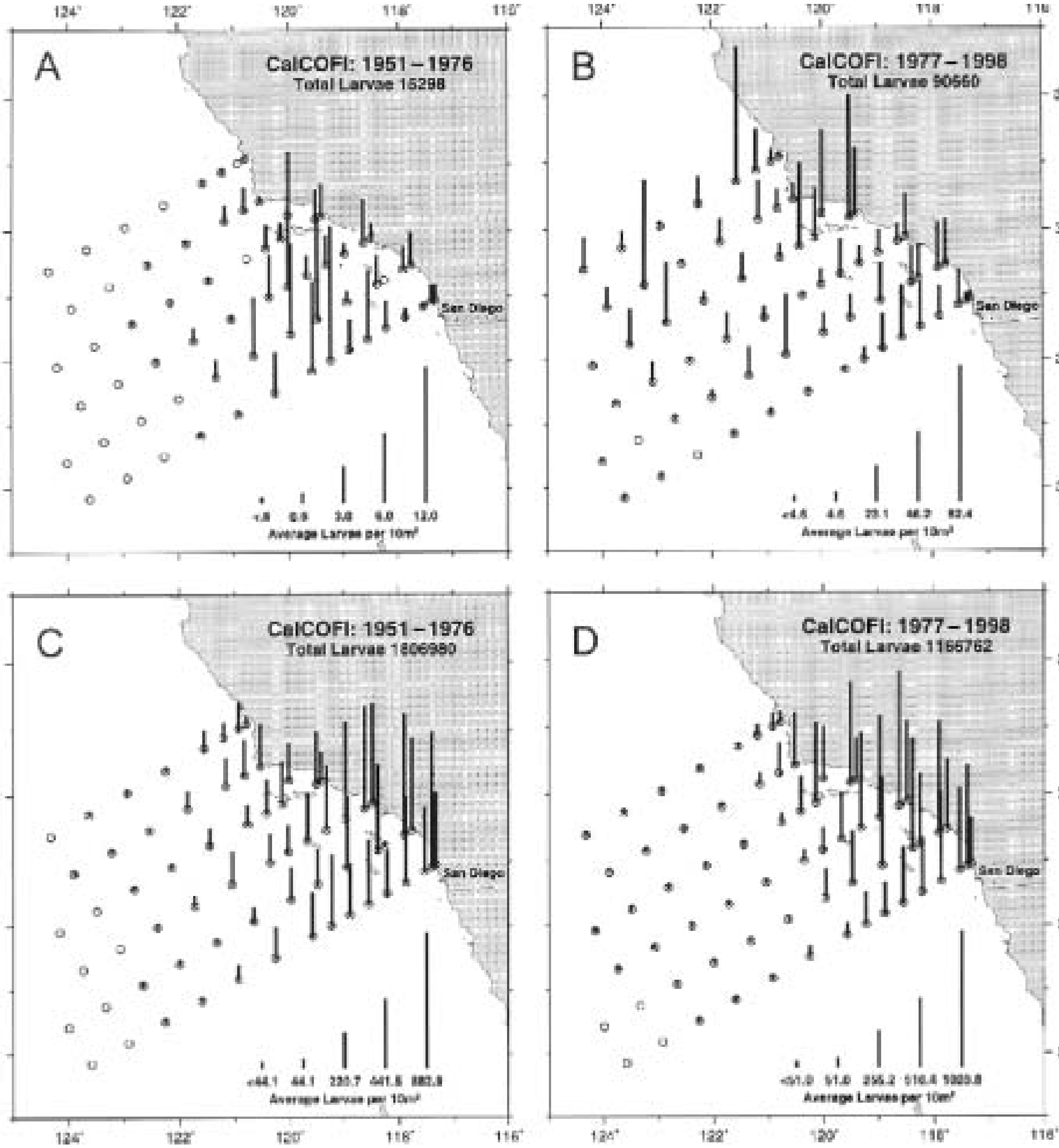

FIGURE 11-14 Mean abundance of Pacific sardine larvae at CalCOFI stations (present survey pattern) during cool (A) and warm (B) ocean regimes compared with mean abundance of northern anchovy larvae during cool (C) and warm (D) regimes, from Moser (2001a).

Northern lampfish, a subarctic-transitional species in the Leuroglossus recurrent group, demonstrates the effect that ENSO and the PDO have on larval fish distribution and abundance (fig. 11-15). The shoreward and northward contraction of the larval distribution in response to long-term offshore warming is apparent (fig. 11-15A,B); equally apparent are the abrupt decline in larval abundance associated with the El Niño episode in 1957 to 1959 and the trend of increasing relative abundance from 1960 to 1972. One would expect that the relative abundance would have declined during the three El Niño events after the regime shift and would have been relatively low, generally, during the warm regime; however, there was no obvious trend in relative abundance associated with the transition from cool to warm ocean regimes nor with ENSO events during the warm regime. A possible explanation may be found in the compression of spawning toward the continental borderland (fig. 11-15A,B) where generally higher production (Hayward and Venrick, 1998) could have compensated for reduced primary and secondary production during the warm regime. Also, reproduction in this species is essentially limited to the cold months of the year in the CalCOFI survey area, when the effect of warm ocean conditions might have been minimized (fig. 11-15D). The medusafish, a subarctic-transitional species in the Tarletonbeania group, showed a 4-fold decline in larval abundance between the two regimes (fig. 11-16A,B), relatively high abundance during the cold ocean episodes in the cool regime, and abrupt declines during El Niño episodes (fig. 11-16C). Larval production peaked during

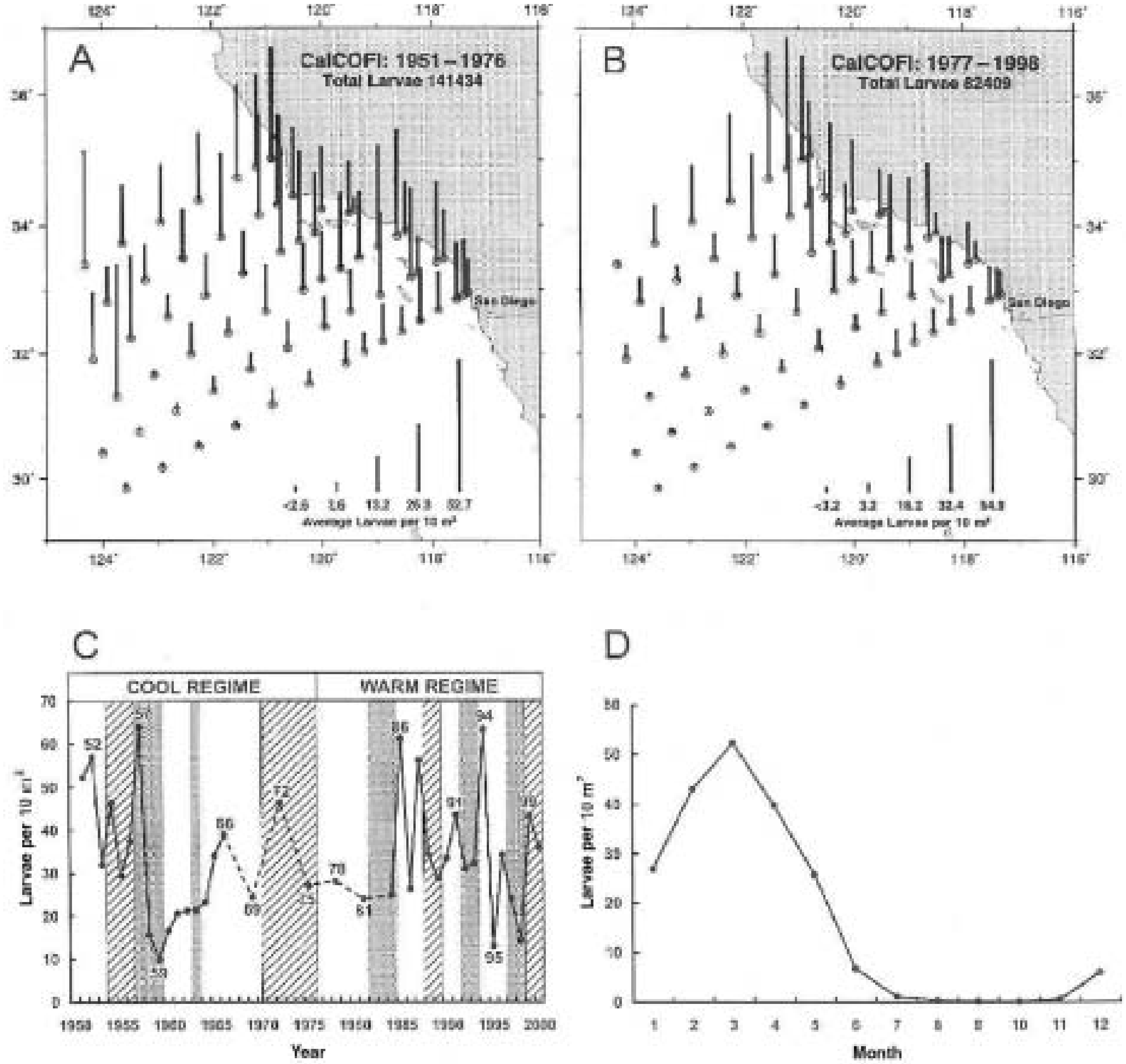

FIGURE 11-15 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Stenobrachius leucopsarus* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

March and June and declined sharply during summer months (fig. 11-16D).

Shortbelly rockfish (*Sebastes jordani*), an associate of the Leuroglossus group, showed little change in distribution pattern between the two regimes (fig. 11-17A,B); however, the generally elevated abundance during cold episodes and the abrupt declines in response to El Niños are apparent (fig. 11-17C). The marked peak in larval abundance (1988 to 1991) during the warm regime may be related to the appearance of an anomalously large year class in the late 1980s (Moser et al., 2000); rockfishes are well known for sporadic and unexplained production of large year classes. Like other species associated with the Leuroglossus group, shortbelly rockfish release their larvae during cold months (fig. 11-17D). In contrast to shortbelly rockfish, a noncommercial species, the cowcod (*S. levis*) is a heavily exploited species whose larvae declined precipitously at the regime shift and were nearly absent from CalCOFI samples during the warm regime, when their distribution receded to a few stations in the Santa Barbara Channel area (fig. 11-18). A recent population analysis of cowcod (Butler et al. 1999, 2003) used fishery data in combination with the CalCOFI larval time series to estimate changes in biomass during the past century. This study showed that the cowcod stock has declined to 7% of its biomass prior to 1940 and recommended a rebuilding program to include a Cowcod Conservation Area, where fishing is prohibited. Although the data are sparse, a continuance of the apparent trend of increasing larval abundance in 1999 and 2000 may indicate a reversal of the population decline (fig. 11-18C).

The larval distribution pattern of snubnose blacksmelt, a California Current endemic in the Symbolophorus group, changed little during the two regimes; however, the trend of

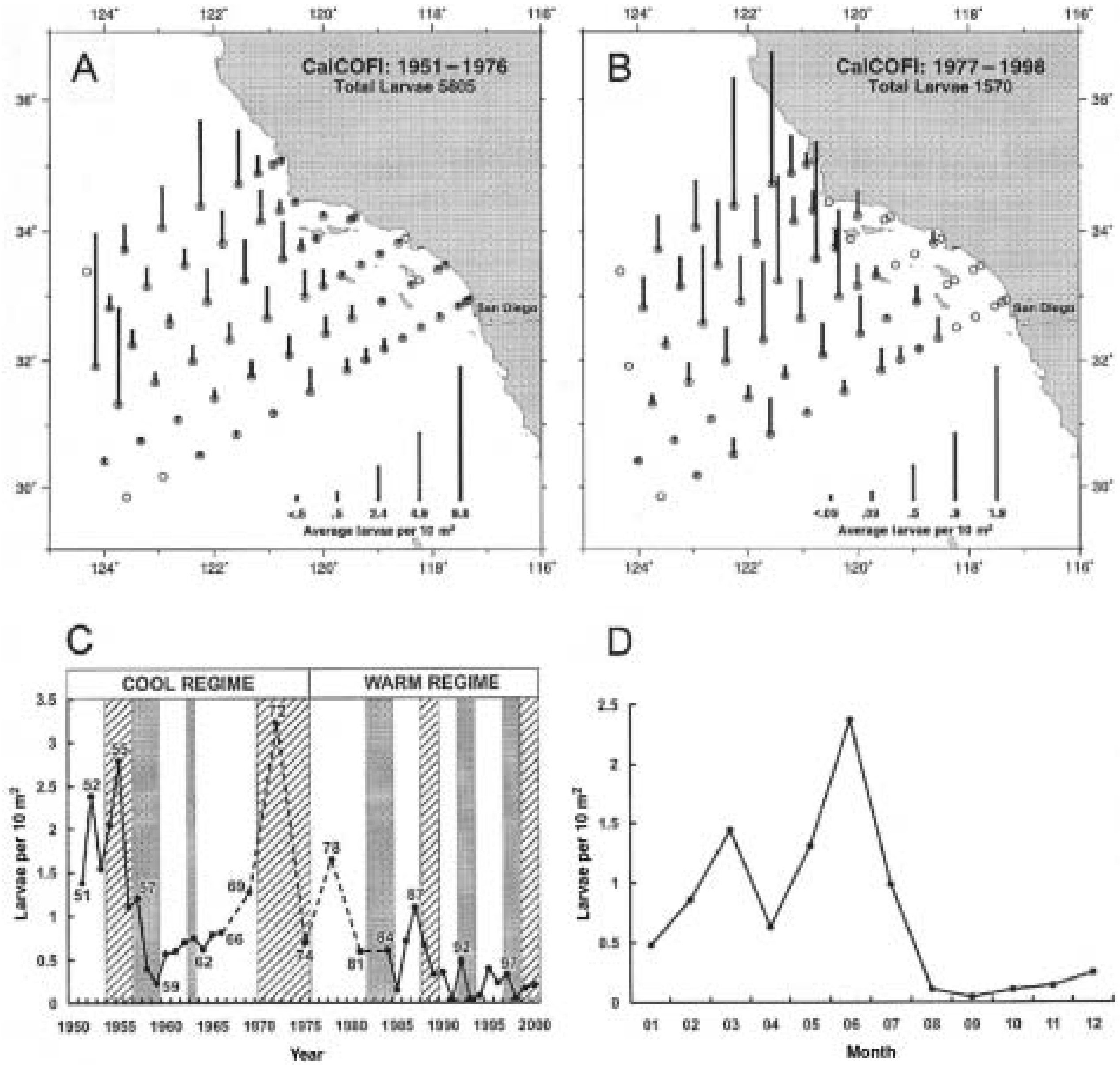

FIGURE 11-16 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Icichthys lockingtoni* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

increasing larval abundance during the 1980s and 1990s is apparent (fig. 11-19A–C). Consonant with this is the peak of larval production centered on the warm months (fig. 11-19D). The precipitous decline in larval abundance following the 1997 to 1998 El Niño (fig. 11-19C) may be indicative of a shift to a cool ocean regime. A positive reaction to warm conditions was even more apparent in longfin lanternfish, a warm-water cosmopolite in the Symbolophorus group. Larval abundance increased steadily throughout the time series with increased intrusion into the California Current from the central water mass (fig. 11-20A–C). As for snubnose blacksmelt, larval abundance declined sharply following the 1997 to 1998 El Niño. There was no apparent seasonality in larval production, as is typical of warm-water cosmopolites (fig. 11-20D). In the Triphoturus group, Mexican lampfish, an endemic species of the southern region of the California Current and Gulf of California, showed a northward shift in larval distribution during the warm regime, increases in larval abundance just before or during El Niño episodes, decreases during La Niña events (especially after the 1998 to 1999 La Niña), and peak spawning during the warmest ocean period in the SCB (fig. 11-21A–D).

Members of the eastern tropical Pacific recurrent group Vinciguerria show the largest response to ocean changes. The larval distribution of Panama lightfish shifted northward and coastward from the cool to warm regime, abundance increased markedly during the warm regime and episodically in response to El Niño conditions during both regimes (fig. 11-22A–C). As evident in the time series for Symbolophorus members, larval abundance declined precipitously following the 1998 to 1999 La Niña, possibly a trend signaling a shift to a cool ocean regime. Like Mexican lampfish, larval production in the SCB

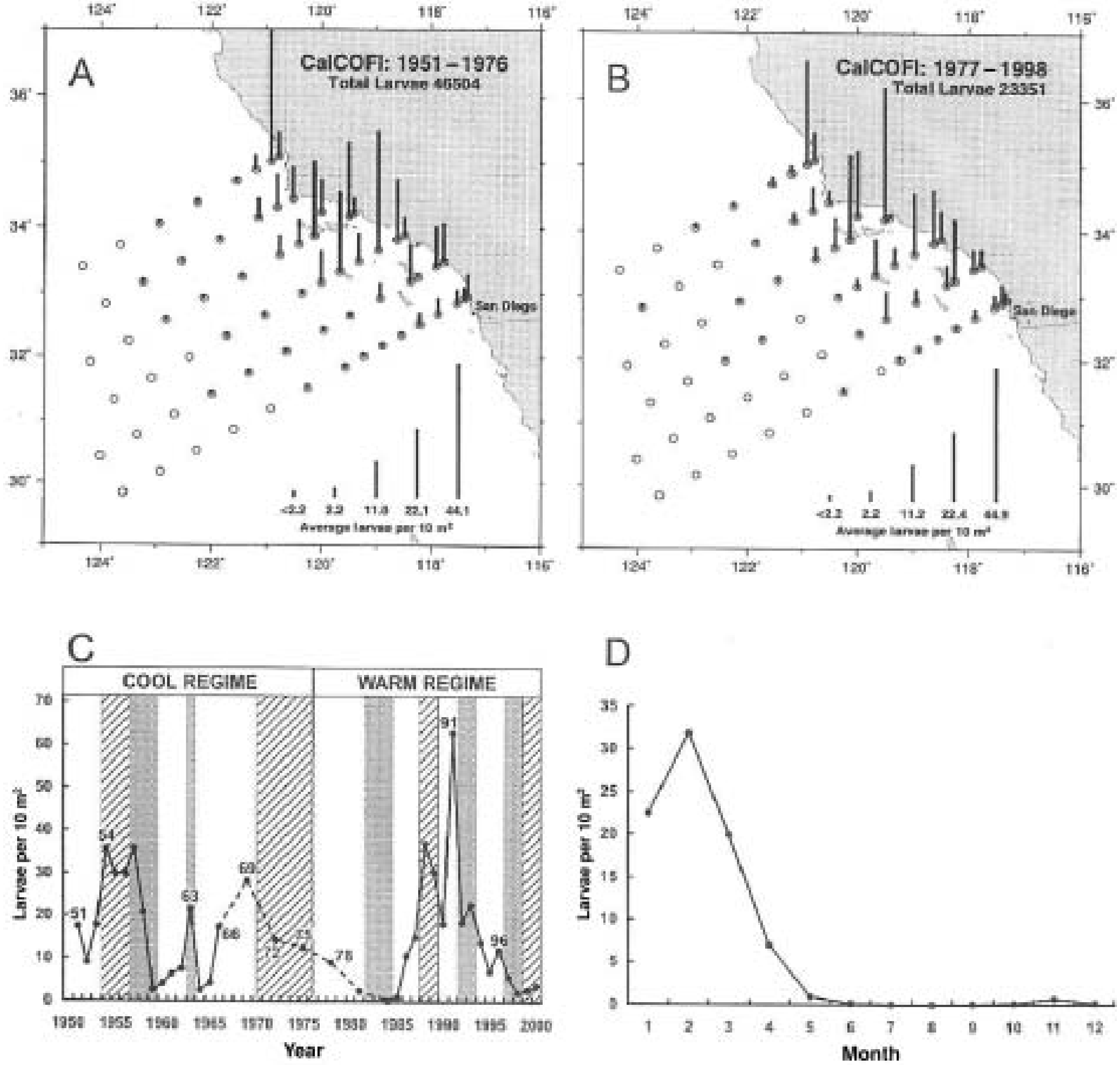

FIGURE 11-17 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Sebastes jordani* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

was highest during the months when the ocean was warmest (fig. 11-22D). Diogenes lanternfish larvae, in the Vinciguerria group, were rare in the SCB until 1997 when an unusually strong coastal countercurrent associated with the 1997 to 1998 El Niño advected relatively large numbers of them into the SCB from waters off Baja California (fig. 11-23A–D). After 1998, Diogenes lanternfish larvae were not taken on CalCOFI surveys, demonstrating the value of larval fish distributions as indicators of dynamic oceanographic events (Moser et al., 2001b; Smith and Moser, 2003).

The increased presence of early-stage larvae of midwater species from eastern tropical Pacific and central Pacific water masses during warm regimes in the California Current reflects shifts in the boundaries of these populations. This could result from intrusion of these water masses into the California Current, carrying these populations, or could be a result of modifications of the subarctic-transitional water of the California Current that are conducive to survival and reproduction of these populations in a region adjacent to their typical range. Perhaps these population boundary shifts are caused by a combination of both scenarios. One of the most fascinating questions in marine zoogeography is how oceanic midwater fish species are segregated by water mass boundaries (Ebeling, 1962; Johnson and Barnett, 1975, Miya and Nishida, 1996, 1997). The CalCOFI ichthyoplankton time series, spanning two ocean regimes and numerous ENSO episodes, offers an excellent opportunity to study the dynamics of fish populations and habitat variables at these water mass boundaries and could provide insight into the mechanisms underlying this fundamental zoogeographic question.

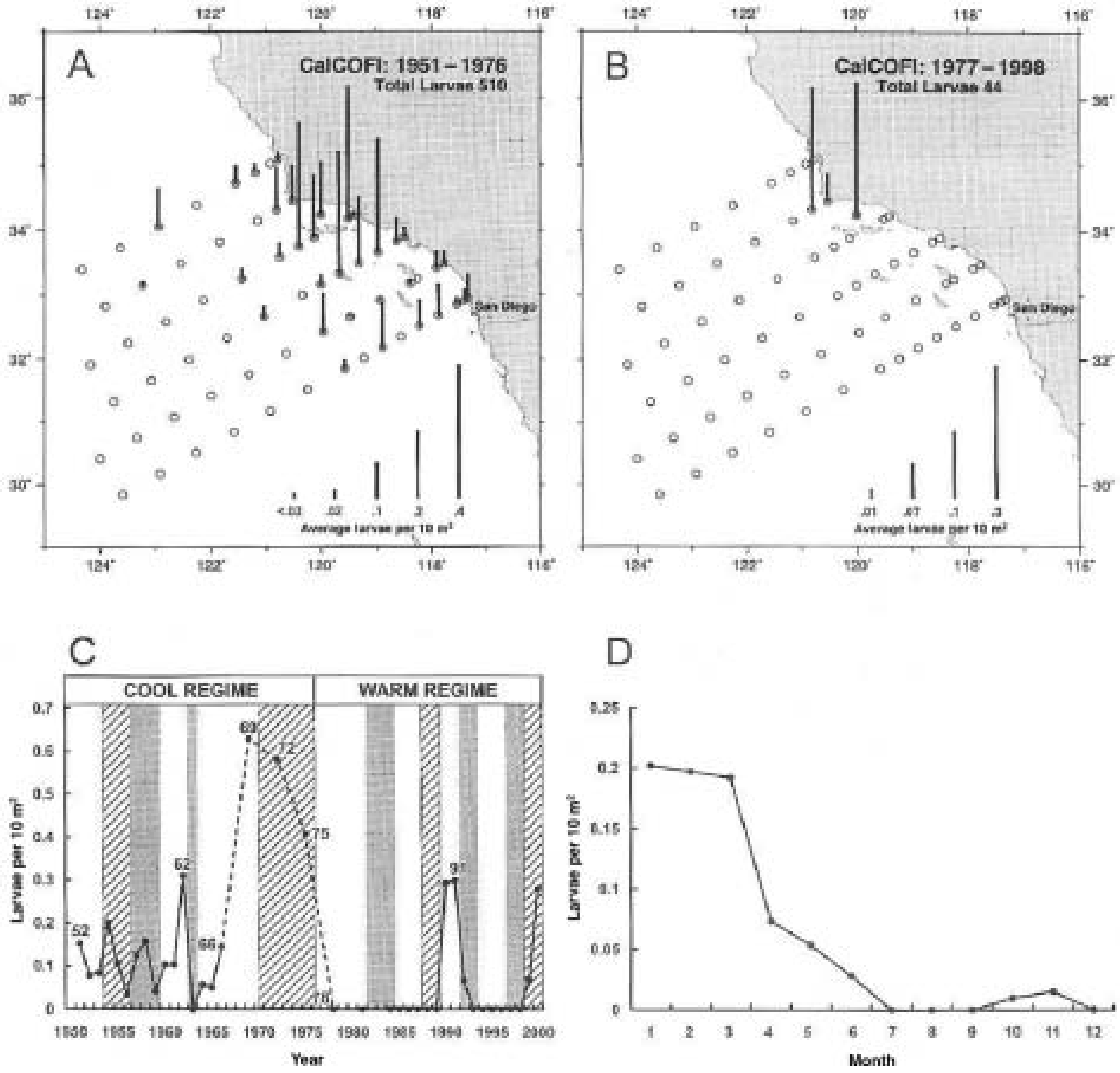

FIGURE 11-18 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Sebastes levis* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

CalCOFI Assemblages—Summary

Fisheries landings and ichthyoplankton surveys show that the epipelagic habitat of the California Current region is dominated by large coastal pelagic fish stocks (northern anchovy, Pacific sardine, jack mackerel, chub mackerel) and a demersal species, Pacific hake. Similar species of the same genera dominate the other major eastern boundary currents: the Peru, Canary, and Benguela Currents (Bakun, 1985, 1996). Relatively large interannual and interdecadal oscillations of stock sizes of these species present a challenging suite of scientific and social problems. Ichthyoplankton surveys designed to encompass the spawning distributions of these populations have become indispensable to scientists who study their dynamics and to fisheries managers given the task of conserving them. Additional benefits of these surveys are the vast amounts of information obtained on the physics and chemistry of the habitat, on the invertebrate zooplankton, and on the larvae of the other species that make up the ichthyofaunas of these regions. The larval fish assemblages in the California Current reflect the water masses of this complex region. The Northern Complex contains subarctic-transitional species that spawn primarily in the cold months. The Southern Complex consists of a relatively large group of California Current endemics and warm-water cosmopolites and another group of eastern tropical Pacific species. The Southern Coastal Complex consists of larvae of shorefishes that inhabit the large shelf areas of central and southern Baja California. Spawning in both southern complexes occurs primarily during warm months. The larval abundance of species in the Southern Complex increased during El Niño events and during the warm regime when their geographic distributions expanded northward and shoreward.

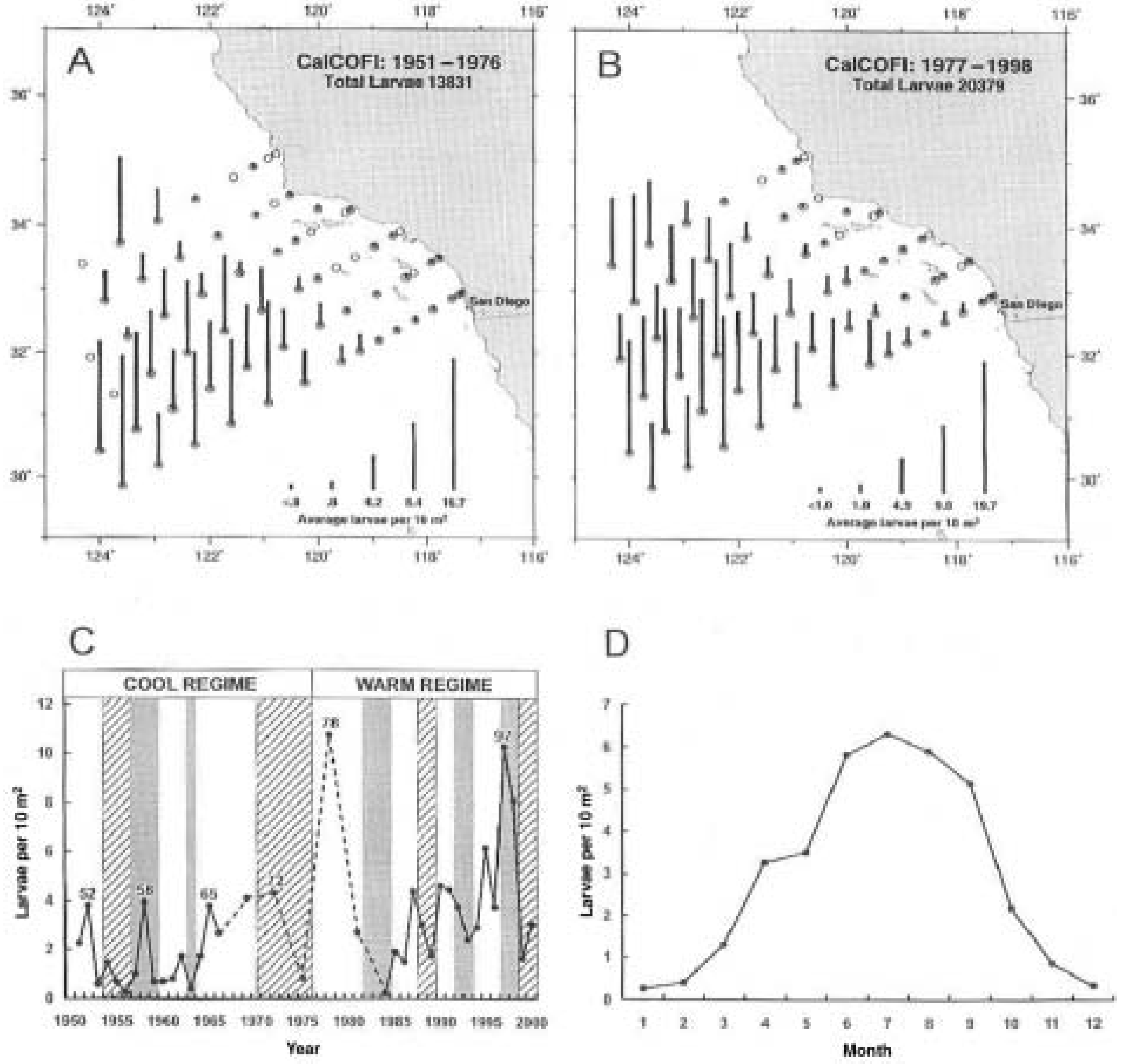

FIGURE 11-19 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Bathylagus wesethi* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

Continuing CalCOFI surveys will reveal whether or not the precipitous declines in larval abundances of Southern Complex species following the 1998 La Niña are harbingers of a shift from a warm to a cool ocean regime. Studies of the CalCOFI ichthyoplankton time series show the importance of midwater fishes to the ecology of the California Current region and suggest that they use a large proportion of the annual production of this system.

Nearshore Assemblages

The coastal fishes of California, species whose distributions are centered over the continental shelf (shoreward of 200 m depth), comprise more than 400 species representing well over 100 families (e.g., Miller and Lea, 1972). Somewhat more than 200 marine species of somewhat fewer than 100 families have been recorded from California's bays and estuaries (e.g., Horn and Allen, 1976). The coastal larval fish assemblage is dominated by Pacific sardine and herring (Family Clupeidae) and northern anchovy (Engraulidae); some other abundant coastal taxa are silversides (Atherinidae), croakers (Sciaenidae), and various flatfishes (Paralichthyidae and Pleuronectidae). Marine larval fish assemblages of the bays and estuaries are dominated by gobies (Gobiidae); examples of other common bay/estuarine taxa are herrings, several species of anchovies, silversides, sculpins (Cottidae), and blennies (Blenniidae, Chaenopsidae, and Labrisomidae).

The oceanic, coastal, and bay/estuarine zones do not exist in isolation from one another and although each is characterized

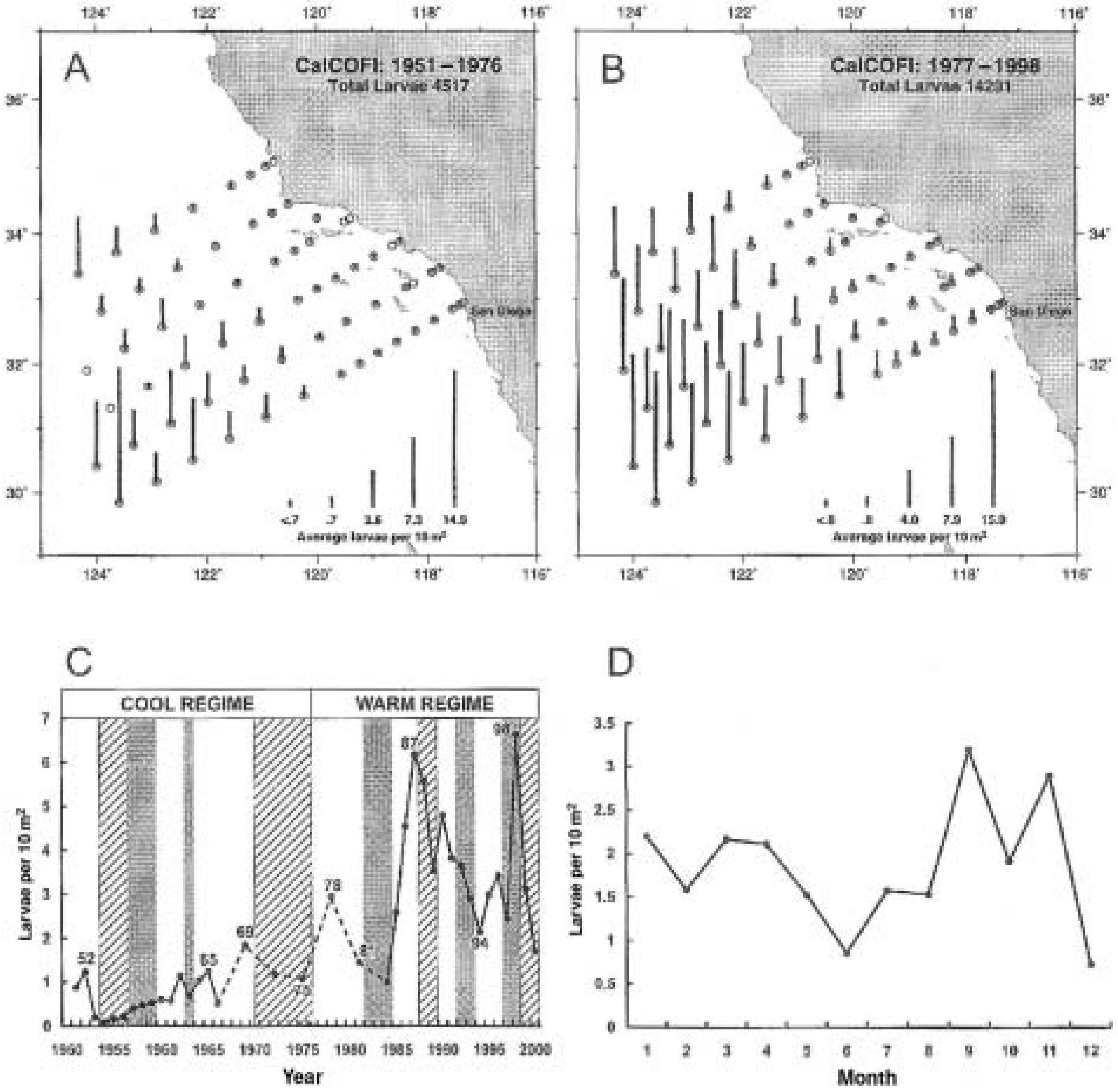

FIGURE 11-20 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Diogenichthys atlanticus* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

by a distinct ichthyoplankton assemblage, many taxa that are most abundant in one zone also occur in adjacent zone(s). For example, larvae of some oceanic taxa such as Mexican lampfish and several bristlemouth species, which are most abundant ~ 200 km and more than 400 km from shore, respectively (Moser et al., 1993), also occur relatively commonly in coastal waters (Walker et al., 1987; McGowen, 1993; Moser et al., 1993) and occasionally are taken in bays (Eldridge and Bryan, 1972). Eggs and larvae of northern anchovy are most abundant over the shelf but also occur in smaller numbers more than 400 km from shore (Moser et al., 1993) and may be moderately abundant in bays and estuaries as well (Eldridge, 1977; Allen et al., 1983; McGowen, 1993). Goby larvae such as the arrow goby, *Clevelandia ios*, among the most abundant of the bay/estuarine taxa (e.g., Eldridge, 1977; Leithiser, 1981; Allen et al., 1983), are relatively common along the open coast (Walker et al., 1987) but do not occur in the oceanic zone.

Coastal Assemblages

Most of the studies that have focused on the Californian coastal ichthyoplankton as a whole have been conducted since the mid-1970s (most in the 1970s and 1980s) in the SCB (e.g., Barnett et al., 1984; Lavenberg et al., 1986; Walker et al., 1987; McGowen, 1993; Watson et al., 1999); thus, the following description of coastal ichthyoplankton assemblages, based on McGowen (1993), has a southern bias. Using cluster analyses (Sokal and Michener, 1958; Boesch, 1977) of ichthyoplankton collections between the 6–75 m isobaths along four

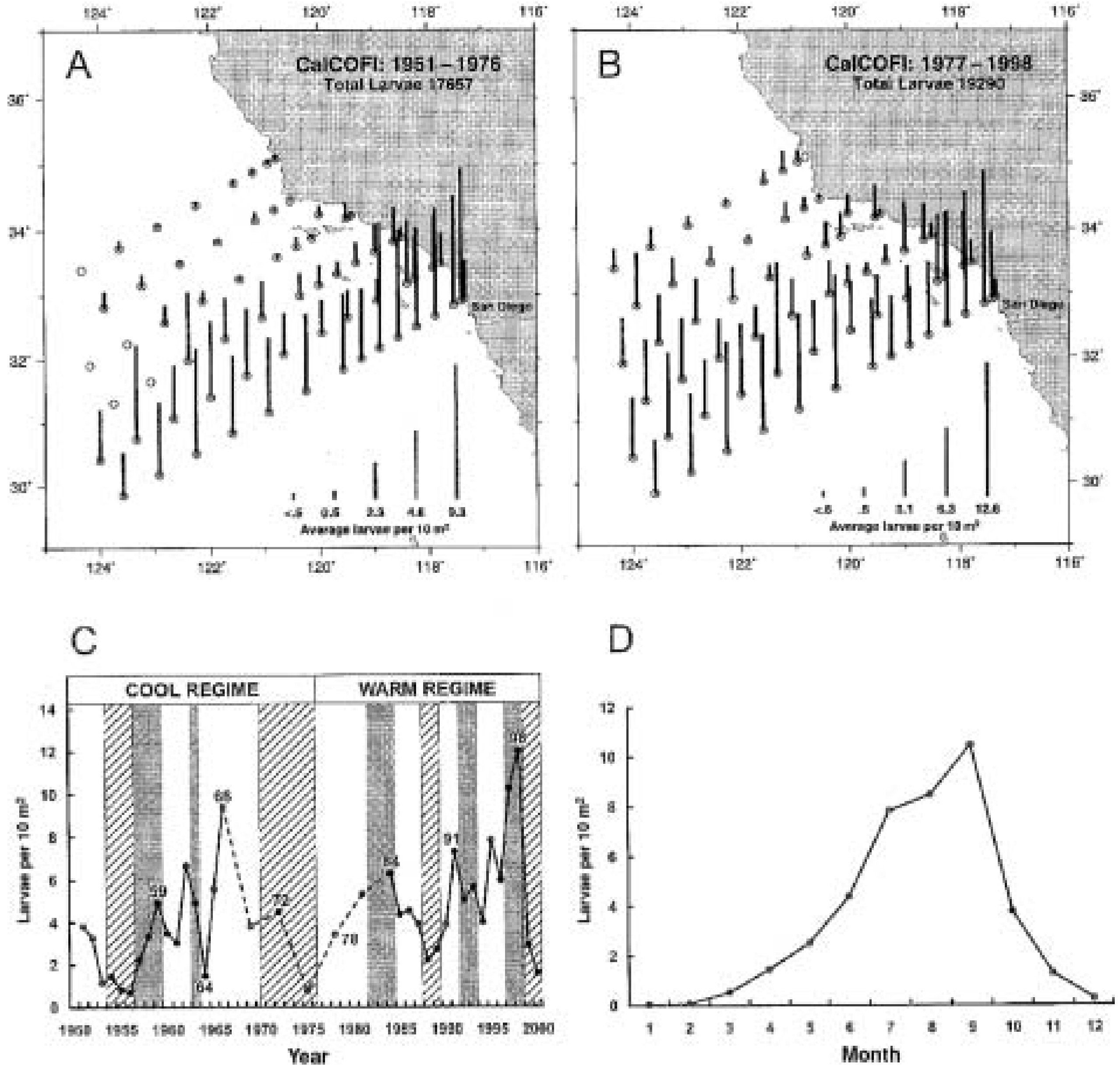

FIGURE 11-21 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Triphoturus mexicanus* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

widely spaced transects in the Bight, McGowen (1993) identified six assemblages of fish eggs and larvae (fig. 11-24, 11-25). Abundance patterns in the cross-shelf direction clearly were present, but indications of alongshore patterns within the SCB were weak or absent. The Genyonemus assemblage, consisting of white croaker (*Genyonemus lineatus*) larvae, northern anchovy eggs, and eggs and/or larvae of four flatfishes, sanddabs, California halibut (*Paralichthys californicus*), diamond turbot (*Hypsopsetta guttulata*), and hornyhead turbot (*Pleuronichthys verticalis*) (fig. 11-24A), was characterized as most abundant between about the 15–36 m isobaths throughout the Bight. Eggs of white croaker and California halibut were not included in McGowen's analysis, but Watson et al. (1999), working in the northern SCB, showed that both occurred primarily shoreward of about the 60-m isobath, with peak abundance between about the 20–30 m isobaths for white croaker and the 40–60 m isobaths for California halibut. Gruber et al. (1982), working in the southern Bight, used recurrent group analysis (Fager, 1957) to identify a small, nearshore (<54 m bottom depth) group containing the larvae of white croaker and California halibut, with one affiliate, hornyhead turbot. Larval sanddabs were classified as affiliates of a cosmopolitan group, and diamond turbot was identified as an inshore taxon but was not included as a member or affiliate of a recurrent group. Sanddab larvae also are members and associates of a broadly distributed coastal recurrent group in the California Current system (fig. 11-7; Moser et al., 1987). Most of the members of Genyonemus do occur in small numbers seaward of the inner shelf region, and they are collected during CalCOFI ichthyoplankton surveys, where their abundances

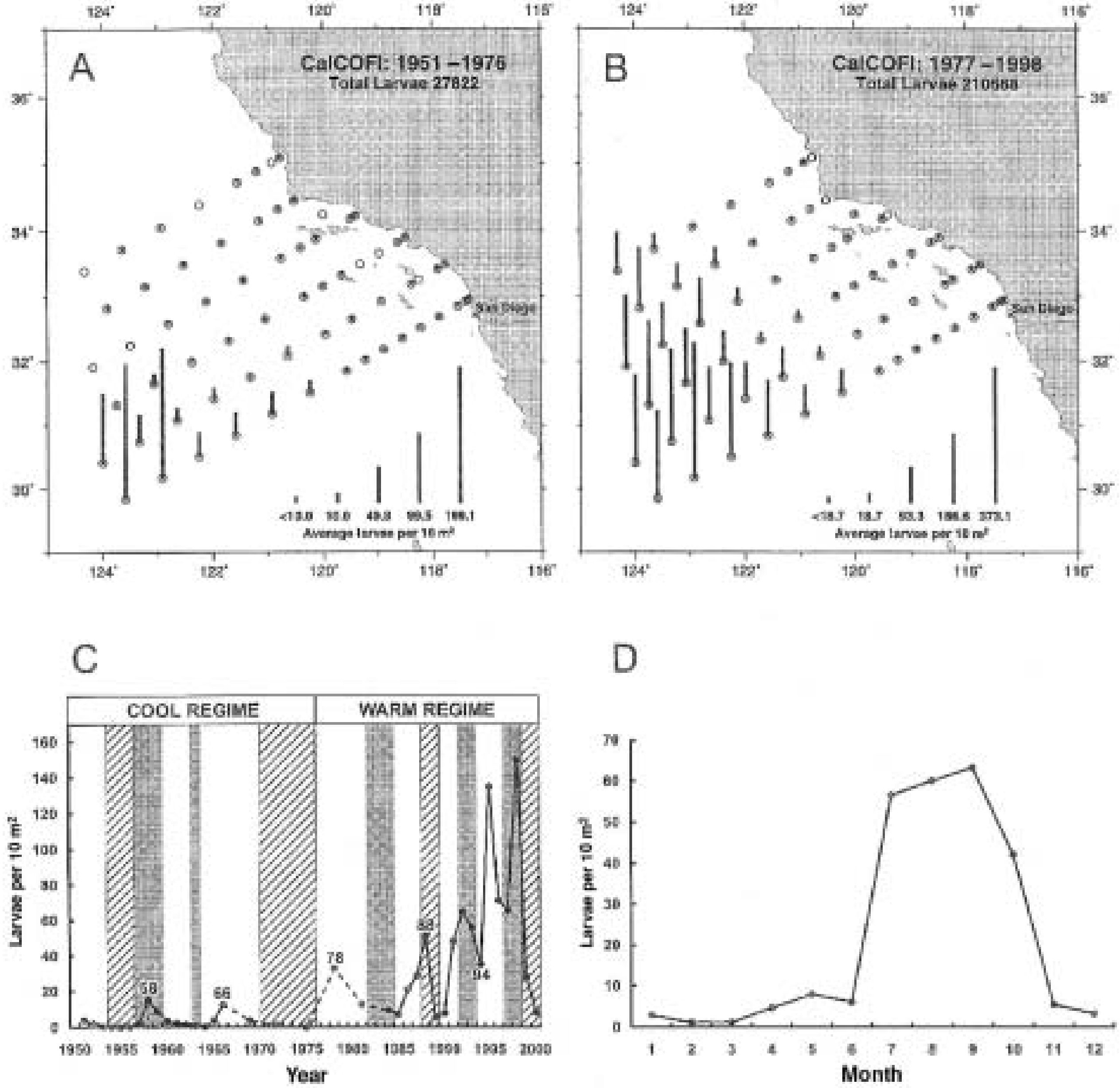

FIGURE 11-22 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Vinciguerria lucetia* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

seem to track trends in the nearshore zone reasonably well (e.g., Moser and Watson, 1990; Moser et al., 2001b).

McGowen's (1993) coastal Stenobrachius assemblage included larval northern anchovy, northern lampfish, rockfishes, and bay goby (*Lepidogobius lepidus*), together with the eggs of California smoothtongue (fig. 11-24B). Members of this assemblage were characterized as most abundant seaward from the 36-m isobath, with no apparent alongshore pattern in the Bight. Gruber et al. (1982) placed northern anchovy, northern lampfish, and rockfish larvae in an offshore/cosmopolitan recurrent group, and larval northern lampfish and rockfish (as well as larval California smoothtongue) also are members of a California Current recurrent group of subarctic-transitional species more likely to be found nearer the shore south of Point Conception than farther north (fig. 11-7; Moser et al., 1987). Larval northern anchovy also are members of a different California Current group (Citharichthys) but have reasonably strong affinities with the subarctic-transitional group (Moser et al., 1987).

McGowen's Sardinops egg assemblage contained Pacific sardine eggs and spotted turbot (*Pleuronichthys ritteri*) larvae (fig. 11-24C), and the Sardinops larvae assemblage contained Pacific sardine larvae and spotted turbot eggs (fig. 11-24E). Both assemblages were most abundant between the 22–36 m isobaths in the central Bight (McGowen's study was conducted during the period when sardine spawning was largely restricted to the nearshore zone) and both extended farther seaward where they were collected during CalCOFI surveys. Larval Pacific sardine also are members of a broadly distributed coastal recurrent group in the California Current system

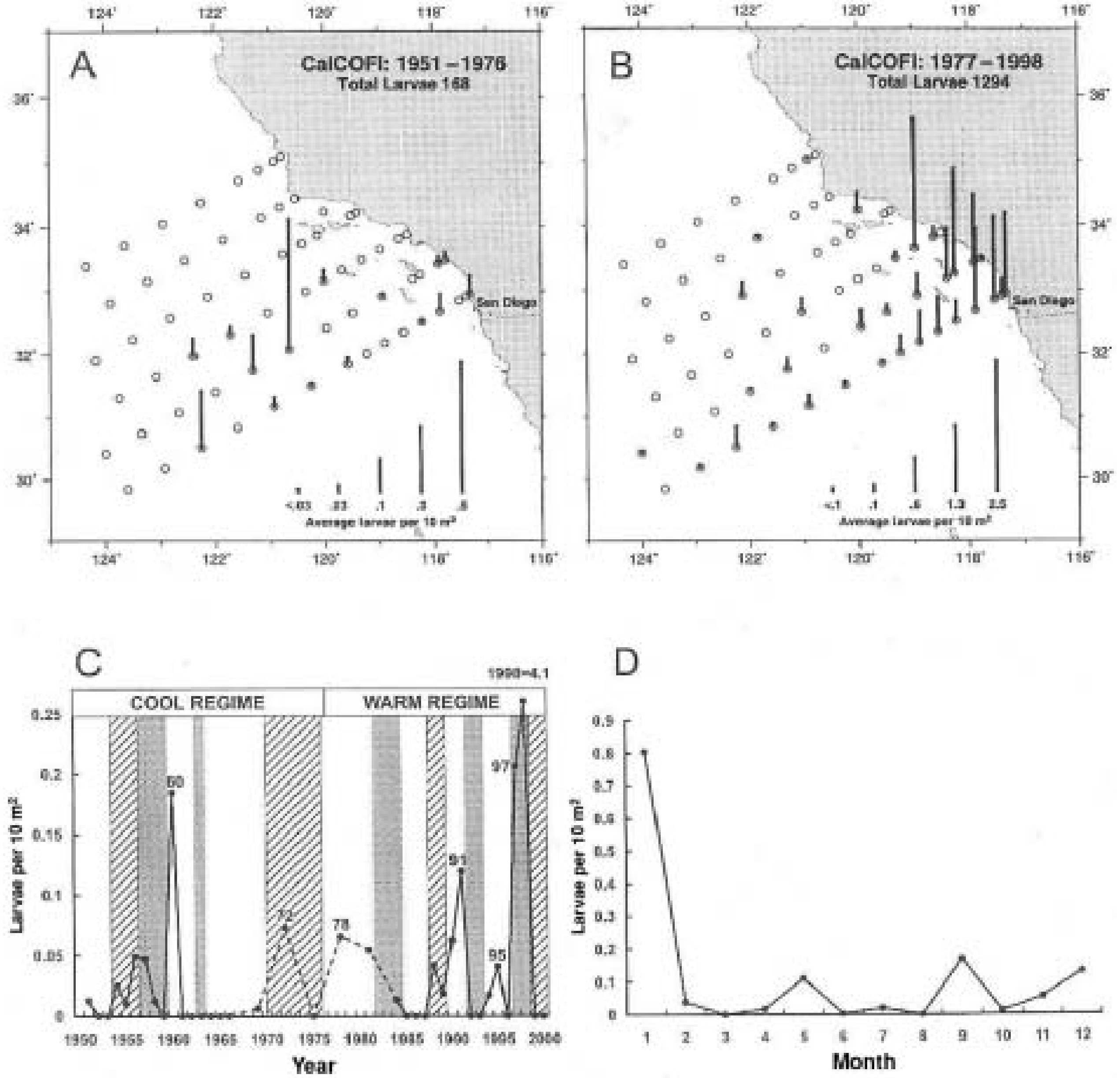

FIGURE 11-23 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Diogenichthys laternatus* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

(Moser et al., 1987). Gruber et al. (1982) classified the larvae of both Pacific sardine and spotted turbot as nearshore but included neither as a member or associate of a recurrent group.

Paralabrax included the eggs and larvae of 14 taxa (fig. 11-25) of temperate–subtropical affinity, five subsets of two to six taxa each reflected primarily cross-shelf, and in one case alongshore, location. The largest subset, including larvae of kelp and sand basses (*Paralabrax*), blennies of the genus *Hypsoblennius*, California barracuda (*Sphyraena argentea*) eggs, bigmouth sole (*Hippoglossina stomata*) eggs and larvae, fantail sole (*Xystreurys liolepis*) larvae, and California tonguefish eggs, was most abundant between the 22–36 m isobaths; an alongshore pattern was not apparent in the Bight. California corbina (*Menticirrhus undulatus*) and California barracuda larvae were most abundant in the same depth zone, primarily in the central Bight. Five species in two of the subsets, California lizardfish eggs, and basketweave cusk-eel, señorita (*Oxyjulis californica*), California sheephead, and California tonguefish larvae, were most abundant over a broad depth range between the 22–75 m isobaths. Larval blacksmith (*Chromis punctipinnis*) and Mexican lampfish were most abundant at the most seaward stations (75 m depth); there was no alongshore pattern in the Bight. Watson et al. (1999) found similar cross-shelf spawning locations for señorita and California sheephead but suggested a broader depth range, perhaps extending seaward to the vicinity of the 100-m isobath, for California barracuda. Gruber et al. (1982) included kelp and sand bass and *Hypsoblennius* larvae in a nearshore (shoreward of the 54-m isobath) recurrent group; Mexican lampfish was considered an offshore taxon but not

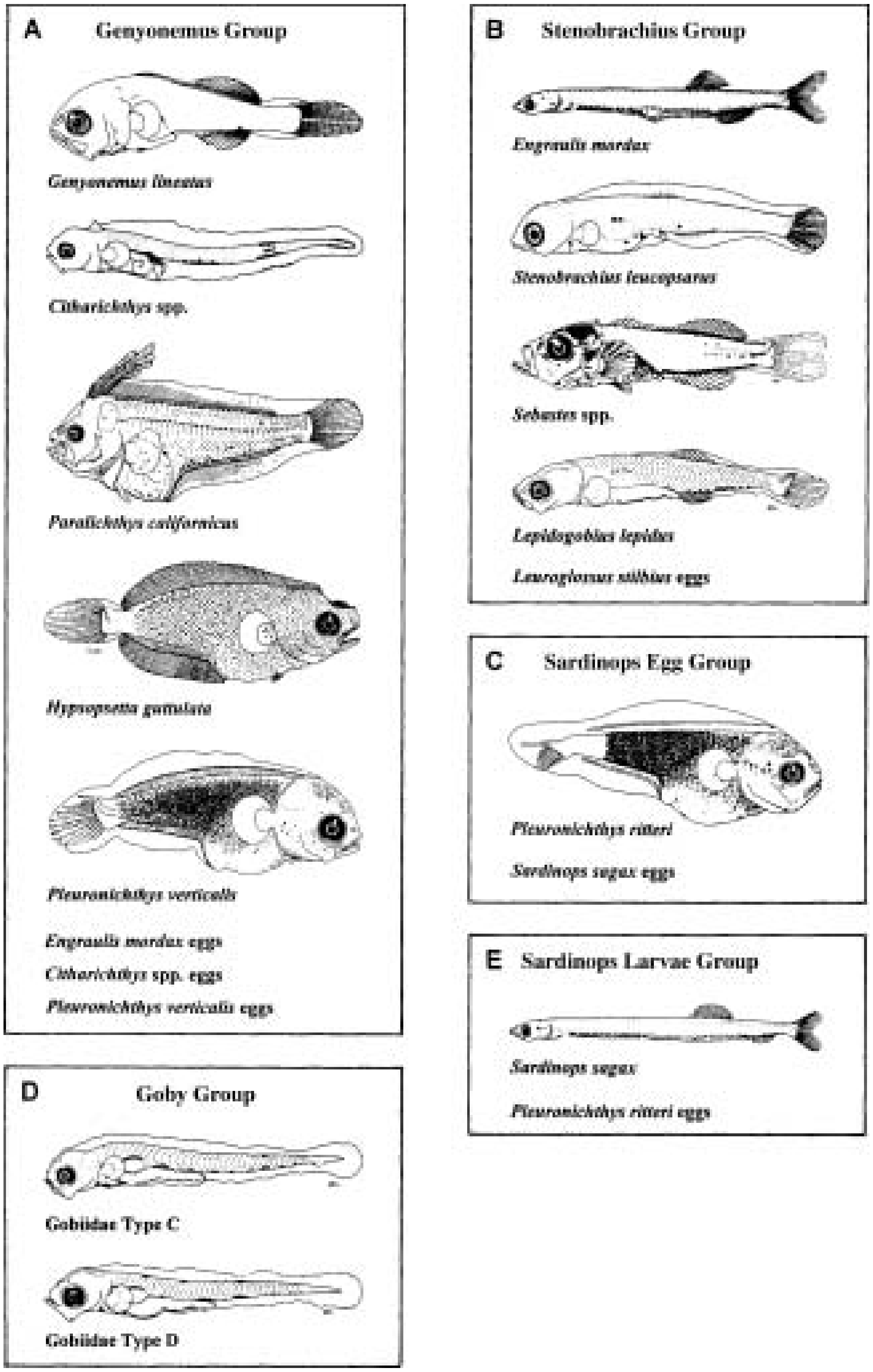

FIGURE 11-24 Members of the Genyonemus (A), Stenobrachius (B), Sardinops Egg (C), Goby (D), and Sardinops larvae (E) coastal ichthyoplankton assemblages of the Southern California Bight (McGowen, 1993). All illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained.

included as an associate or member of a recurrent group. Larval Mexican lampfish do belong to a broadly distributed temperate–subtropical recurrent group in the California Current. McGowen's *Synodus* subset of Paralabrax was nearly the same as the California Current recurrent group Synodus, a group of temperate–tropical coastal taxa (Moser et al., 1987).

The sixth SCB coastal assemblage (Goby) contained two types of undentified goby larvae (fig. 11-24D), probably mostly arrow goby and early stages of bay goby. Both were abundant shoreward of the 36-m isobath, primarily shoreward of the 22-m isobath. In the SCB, larval bay goby occur in small numbers at the most shoreward CalCOFI stations (e.g., Moser et al., 2001a), but larval arrow goby rarely occur as far seaward as the most inshore CalCOFI stations.

Icanberry et al. (1978) conducted a 15-month ichthyoplankton survey at two stations (20-m and 60-m isobaths) off Diablo Canyon, central California. With one exception, the coastal ichthyoplankton assemblages described by McGowen (1993) from the SCB were not present off Diablo Canyon. Major elements of McGowen's coastal Stenobrachius assemblage were present off Diablo Canyon, including larval northern lampfish, northern anchovy, and rockfish. Larval bay goby, another Stenobrachius member, were not identified in the Icanberry et al. study, but the species is present in the area and an unidentified gobiid larval type had a seasonal pattern similar to that of other members of the group. In addition, croakers (probably white croaker) and cabezon also had similar seasonal occurrence. Larval northern lampfish were most abundant at the offshore

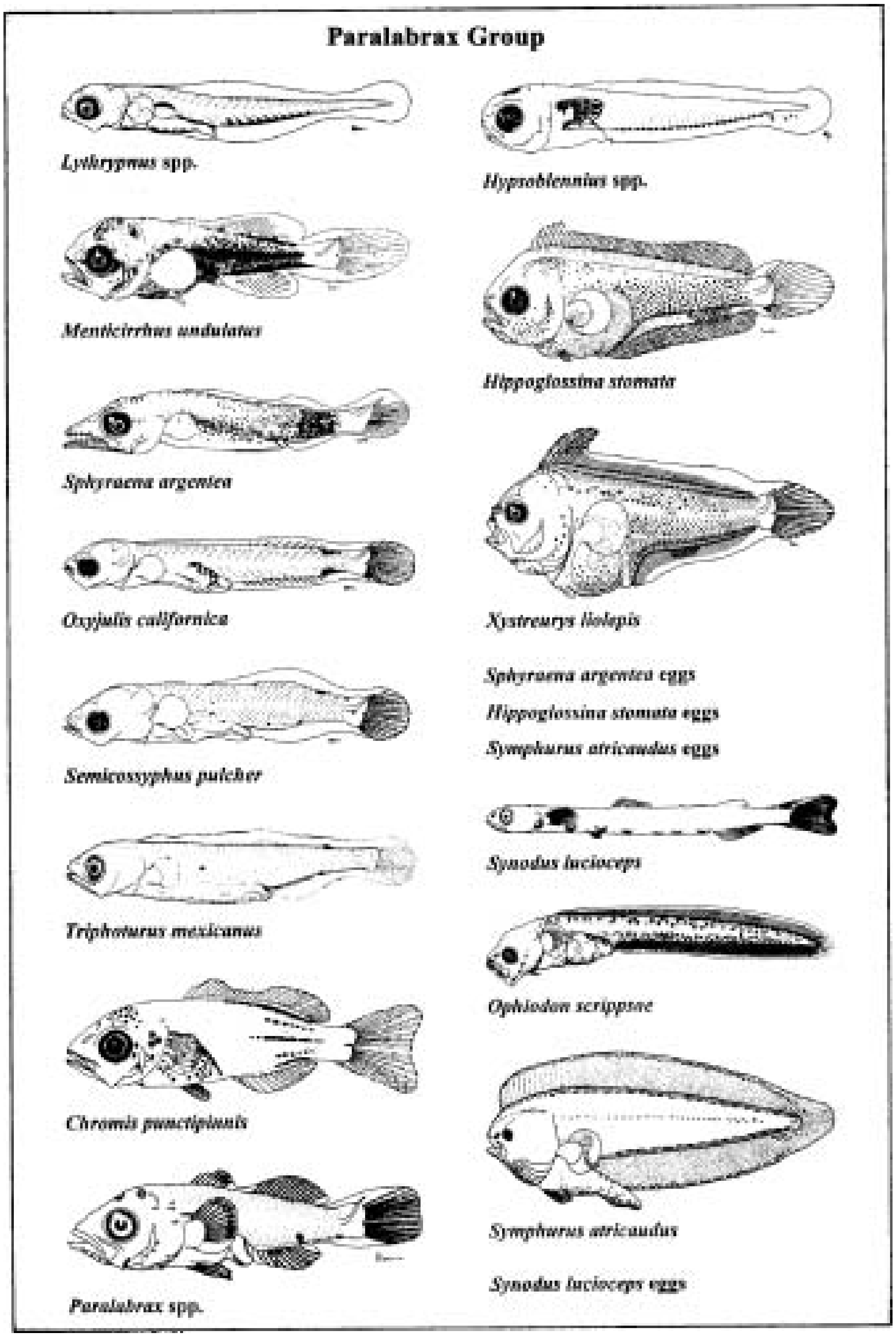

FIGURE 11-25 Members of the Paralabrax coastal ichthyoplankton assemblage of the Southern California Bight (McGowen, 1993). All illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained.

station; abundances of northern anchovy, rockfishes, and croakers did not differ between the two stations.

A group of larvae more or less analogous to McGowen's Genyonemus assemblage included the hexagrammids, painted greenling (*Oxylebius pictus*), lingcod, and kelp/rock greenlings (*Hexagrammos* spp.), and three unidentified "Blennioidei" types (the category "Blennioidei" of Icanberry et al. probably included Zoarcoidei). This group had seasonal occurrence similar to Genyonemus, but unlike Genyonemus, its members may not have been concentrated at shallow depths in the coastal zone: the abundance of "Blennioidei" did not differ between the 20-m and 60-m stations. There were no obvious analogs to McGowen's Sardinops or Paralabrax assemblages, and the Goby analog consisted of two sculpin taxa (*Artedius* spp. and an unidentified type). *Artedius* larvae were most abundant at the inshore station.

Little information is available concerning open coastal ichthyoplankton assemblages of northern California, but a study by Richardson and Pearcy (1977) off central Oregon that included coastal stations may serve as a proxy. They identified a coastal assemblage of 53 taxa that occurred over the shelf at stations 2–28 km from shore (primarily 2–18 km from shore, 20–85 m bottom depth). Thirteen taxa (fig. 11-26) accounted for 92% of the total larvae in the coastal assemblage; these tended to be most abundant 6–9 km from shore (46–59 m bottom depth). Richardson and Stephenson (1978) used cluster analysis of a summer subset of the same data to identify a smaller coastal assemblage that contained the larvae of nine

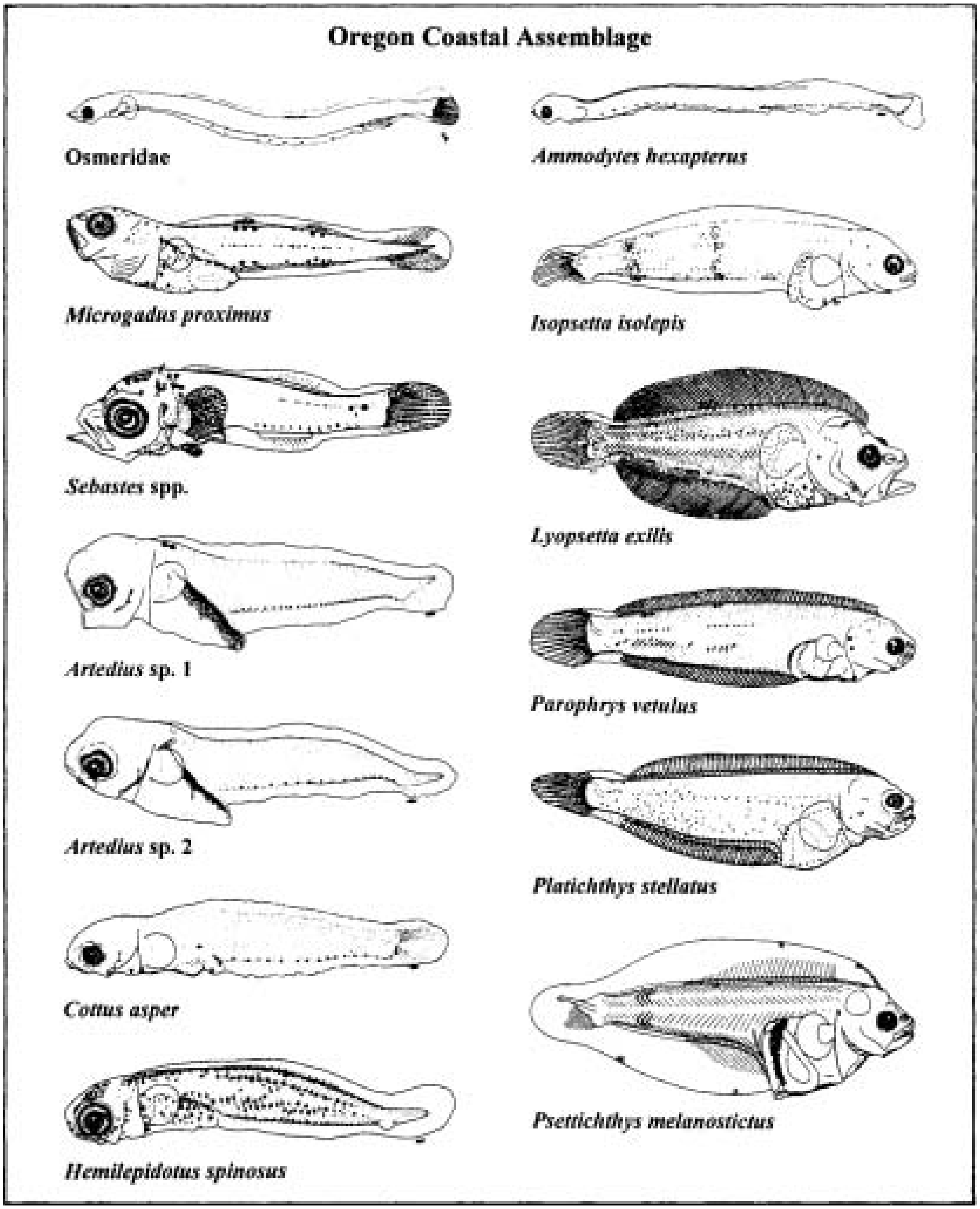

FIGURE 11-26 The 13 most abundant members of the central Oregon coastal ichthyoplankton assemblage (Richardson and Pearcy, 1977). *Microgadus proximus* from Matarese et al. (1981); *Sebastes* from Kendall (1989); *Artedius* sp. 1 (= *A. harringtoni*) and sp. 2 (= *A. fenestralis*), *Cottus asper* and *Hemilepidotus spinosus* from Richardson and Washington (1980); *Isopsetta isolepis* from Richardson et al. (1980a); *Platichthys stellatus* from Matarese et al. (1989); other illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained.

taxa including smelts (Osmeridae), Pacific tomcod (*Microgadus proximus)*, butter sole (*Isopsetta isolepis*), sand sole (*Psettichthys melanostictus*), three unidentified sculpins (two *Artedius* and one *Icelinus* species), pricklebreast poacher (*Stellerina xyosterna*), and unidentified snailfish (Cyclopteridae) larvae. A separate analysis (Richardson and Stephenson, 1978) of a larger subset of coastal stations (2–18 km from shore) in all seasons, that included most of Richardson and Pearcy's (1977) coastal assemblage, yielded two seasonal assemblages, one of 16 primarily (94%) coastal, spring–summer taxa that included all nine taxa of Richardson and Stephenson's coastal assemblage, and a mixed coastal and offshore group (66% coastal) of 12 taxa that were most abundant in winter and spring. The remaining 20 taxa were not classified.

Coastal Assemblages—Geographic and Seasonal Distribution

Seasonal spawning patterns are at least as important as cross-shelf location in structuring coastal ichthyoplankton

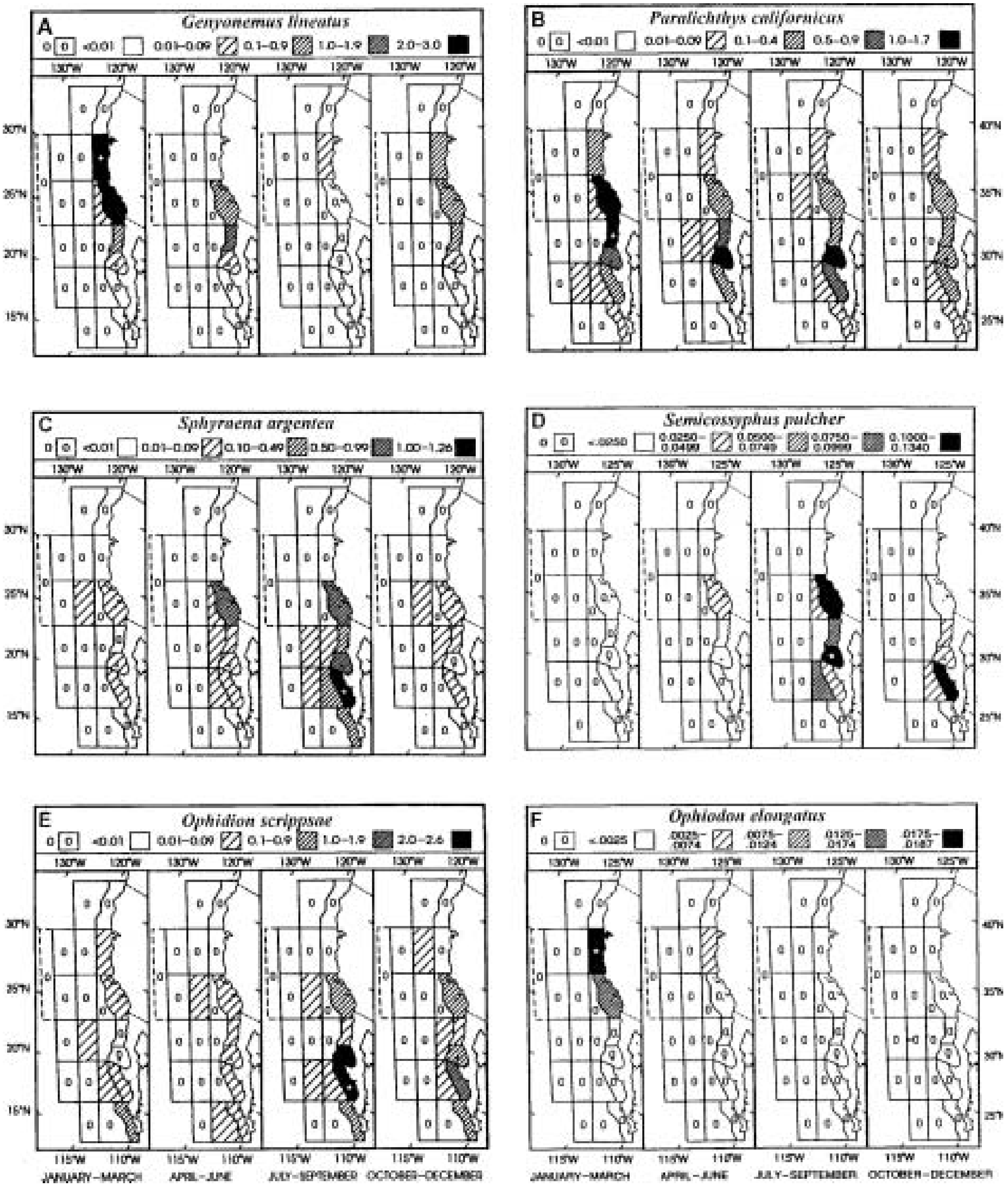

FIGURE 11-27 Quarterly maps showing mean larval abundance (number per 10 m^2) from 1951 to 1984 in each of 22 CalCOFI regions (Moser et al., 1993) for *Genyonemus lineatus* (Genyonemus assemblage of the coastal Southern California Bight; McGowen, 1993), *Paralichthys californicus* (Genyonemus), *Sphyraena argentea* (Paralabrax), *Semicossyphus pulcher* (Paralabrax), *Ophidion scrippsae* (Paralabrax), and *Ophiodon elongatus* (central California analog to Genyonemus assemblage of the coastal Southern California Bight).

assemblages. McGowen's (1993) Southern California Bight Genyonemus assemblage was characterized as a winter–spring group. Based on a study near McGowen's southernmost transect, Walker et al. (1987) also identified a winter–spring group that included larval white croaker (fig. 11-27A) but placed the other Genyonemus taxa in another group characterized as being present year-round with highest abundance in winter and spring. The nearshore group of Gruber et al. (1982), which contained larval white croaker and California halibut, was identified as an autumn through spring group, and another Genyonemus member, larval sanddabs, was classified as an affiliate of a winter through summer group. Watson et al.

(1999) collected white croaker eggs during late winter/spring and reported highest abundance during that period for eggs of three Genyonemus group flatfish species (speckled sanddab, California halibut, and diamond turbot) but noted that speckled sanddab and California halibut continued to spawn at lower levels during summer. Moser and Watson (1990) showed that California halibut spawns year-round, with a peak in late winter/spring and smaller increases in midsummer and autumn (fig. 11-27B). A principal spawning peak during late winter/spring in the northern part of its range is somewhat unexpected, given the warm-water affinity of California halibut; it may reflect an adaptation to the microzooplankton production cycle along the California coast (Moser and Watson, 1990). The members of Genyonemus are coastal, warm-water taxa broadly distributed from central California to the central or southern Baja California Peninsula, essentially the San Diegan faunal Province (e.g., Hubbs, 1960), but extending into the Oregonian Province to the north. In most cases, abundance is centered in the warmer waters south of Point Conception (figs. 11-27A,B; also see CalCOFI Atlas 31, pp. 6, 118, and Moser et al., 1994a: CalCOFI Atlas 32, p. 80).

Like Genyonemus, the Stenobrachius coastal assemblage was characterized as a primarily winter–spring group but with broader seasonal occurrence. Walker et al. (1987) placed larval northern lampfish in a winter–spring group, but classified the remaining Stenobrachius larvae (together with most of the Genyonemus larvae) in a separate group described as present year-round with highest abundance in winter and spring. Gruber et al. (1982) placed larval northern anchovy, northern lampfish, and rockfishes in a winter through summer recurrent group, and Moser et al. (1987) described the last two as primarily autumn through spring taxa. Geographic distributions of most of the Stenobrachius larvae are described above under CalCOFI Assemblages.

The Sardinops egg and larvae assemblages were present throughout the year in the coastal zone with highest abundance in spring and autumn, suggesting a bimodal spawning season. Walker et al. (1987) described the larvae of both species as belonging to a group of year-round spawners with winter–spring peak abundance, and Gruber et al. (1982) characterized the larvae of both as most abundant in autumn. Seasonal and geographic distributions of larval Pacific sardine in the larger CalCOFI study area are described above under CalCOFI assemblages; sardine eggs, not surprisingly, are distributed seasonally and geographically much like the larvae (CalCOFI Atlas 31, p. 22; fig. 11-12B), except that the eggs are relatively more abundant in spring. Larval spotted turbot in CalCOFI collections typically are most abundant from midsummer to autumn along the central Baja California Peninsula, especially in the vicinity of Sebastian Viscaino Bay, reflecting the extensive adult habitat available there (CalCOFI Atlas 31, p. 226).

McGowen (1993) characterized the Paralabrax assemblage taxa as summer–autumn spawners; larval kelp/sand bass, *Hypsoblennius* spp., and bigmouth sole were most abundant in summer, and the others were abundant in both summer and autumn. Walker et al. (1987) included larvae of eight of the Paralabrax taxa in their analysis, classifying six as summer spawners and two, *Hypsoblennius* spp. and Mexican lampfish, as spring–summer spawners. On the other hand, Gruber et al. (1982) described larval Mexican lampfish, kelp/sand bass, and *Hypsoblennius* spp. as most abundant in summer and autumn. Seasonal and geographic distributions of some Paralabrax group taxa are described above under CalCOFI Assemblages: Mexican lampfish (CalCOFI Atlas 31, p.16), lizardfishes (CalCOFI Atlas 31, p. 54), basketweave cusk-eel (fig. 11-27E), and tonguefishes (CalCOFI Atlas 31, p. 72). Larvae of several of the Paralabrax shorefish taxa occur in small numbers farther offshore into the CalCOFI sampling area; all of these occurred primarily from Point Conception southward to central or southern Baja California Sur with peak abundance in summer or autumn, usually off the Baja California Peninsula (figs. 11-27C, D; CalCOFI Atlas 31, pp. 66, 102, 110, 124, 140, 210).

The Goby coastal assemblage of two undentified larval types occurred year-round with no dominant seasonal pattern, although it did display some tendency toward higher larval abundance in winter and spring (McGowen, 1993). Walker et al. (1987) included both arrow and bay gobies, the species most likely represented by the Goby assemblage, in a group of year-round spawners with peak larval abundance in winter and spring, and in the SCB, larval bay gobies are collected year-round with highest abundance from autumn through spring, at inshore CalCOFI stations (Moser et al., 2001a).

In central California, the group of larvae analogous to McGowen's Stenobrachius assemblage (northern anchovy, northern lampfish, rockfishes, unidentified croaker, and goby larvae that may have been white croaker and bay goby) were collected through much or all of the year with highest abundances in winter and spring (Icanberry et al., 1978). Larvae more or less analogous to McGowen's Genyonemus assemblage (painted greenling, lingcod, kelp/rock greenlings, "Blennioidei") were collected mostly or entirely during winter in central California (Icanberry et al., 1978). Small numbers of larvae of all four taxa have been collected during CalCOFI surveys; within the larger survey area, all were most abundant in the coastal zone off central or northern California in winter (fig. 11-27F; CalCOFI Atlas 32, pp. 46, 48, 84), reflecting their subarctic–warm temperate affinities.

The central California Goby analog consisted of two sculpin taxa that were collected year-round with no clear seasonal pattern. Larvae of most sculpin species occur relatively infrequently and in low abundance in CalCOFI collections; larvae of the family as a whole occur year-round in the CalCOFI survey area but are most abundant from late winter through late spring with highest abundance in the coastal zone of northern California (Moser et al., 1993), reflecting their cool-water (Oregonian) affinity.

Larvae of nine of Richardson and Pearcy's 13 most abundant central Oregon coastal taxa have been identified from CalCOFI surveys in sufficient numbers to map their larger scale distributions (CalCOFI Atlas 31, pp. 12, 84, 86; CalCOFI Atlas 32, pp. 6, 20, 42, 70, 118, 128). Within the CalCOFI area, all nine were most abundant in the coastal zone off central or northern California, with winter or spring abundance peaks.

Coastal Assemblages—Interannual and Decadal Changes

Responses to ENSO events and the 1976 to 1977 regime shift varied among taxa of the Genyonemus assemblage of SCB coastal taxa. California halibut showed no change in distribution, relatively little difference in abundance between the cool and warm regimes, and no consistent response to ENSO episodes (fig. 11-28A–C). The somewhat higher overall average larval abundance apparent during the warm regime was largely attributable to very high abundance in 1981; apart

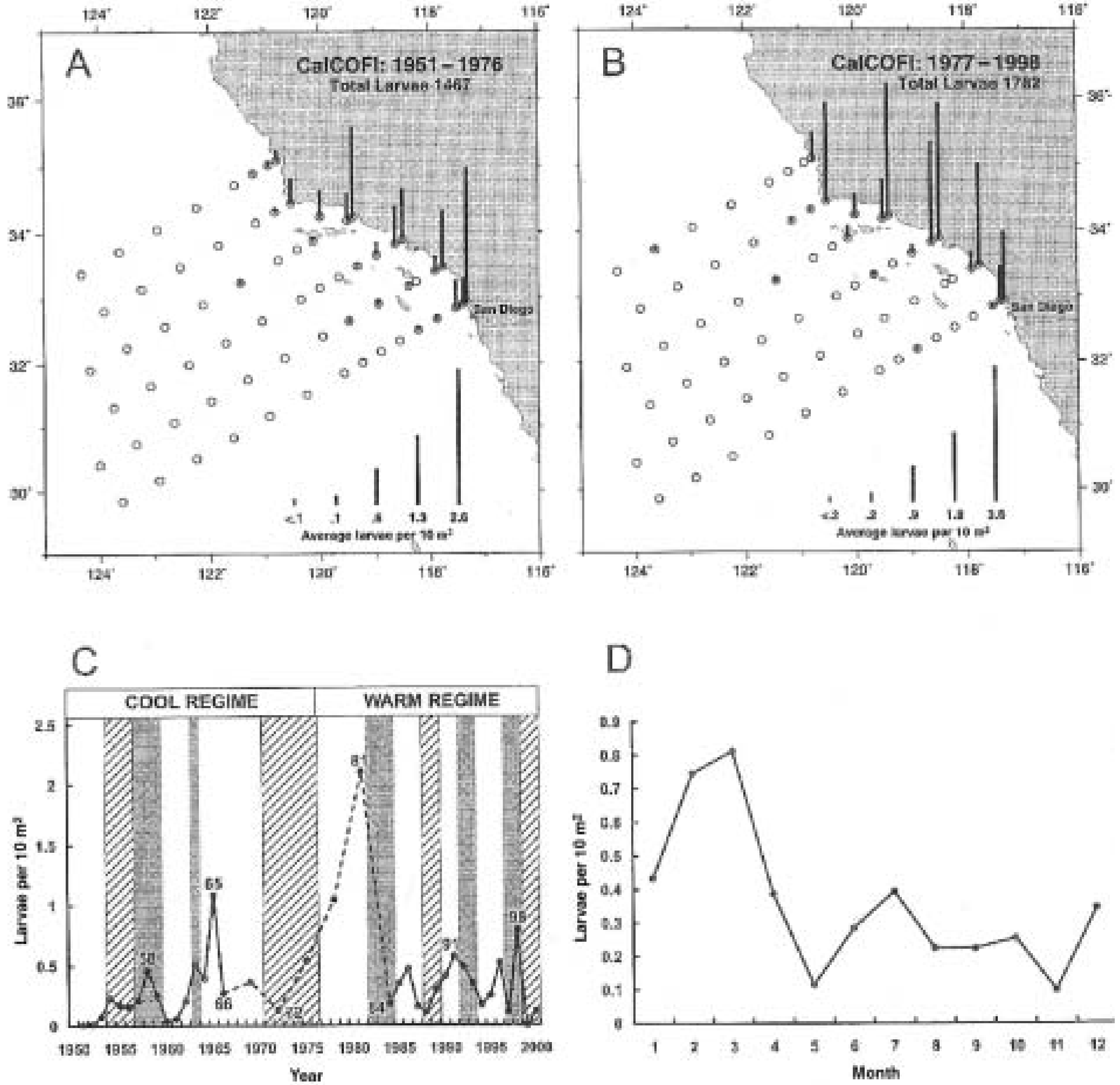

FIGURE 11-28 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Paralichthys californicus* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

from that year, annual mean abundances differed little between the cool and warm regimes (fig. 11-28C). The interannual differences in larval abundance are well correlated with commercial landings of California halibut through most of the CalCOFI time series, suggesting that larval abundance reflects adult abundance and that larval surveys could be used as a fishery-independent tool in managing the California halibut fishery (Moser and Watson, 1990). Among the other Genyonemus members, white croaker displayed fluctuating larval abundance with a general declining trend since at least the late 1980s and a tendency for larval abundance to decline more during El Niño events. Larval Pacific and speckled sanddabs, and hornyhead turbot were more abundant, on average, during the warm regime than during the cool regime. Both sanddab species tended to decline in larval abundance during El Niño events and, from the late 1980s to the late 1990s, larval speckled sanddab and hornyhead turbot declined to abundance levels comparable to those of the cool regime. Abundance increased rapidly after 1999 for both sanddab species but changed little for hornyhead turbot. Larval diamond turbot, like California halibut, showed little evidence of ENSO- or PDO-related change in abundance or distribution (Moser et al., 2001a) but gradually declined in abundance in CalCOFI collections and reached zero by 1998.

Among the Stenobrachius group of coastal SCB larvae, interannual and decadal-scale changes are described under CalCOFI assemblages for northern anchovy (figs. 11-13, 11-14), northern lampfish (fig. 11-15), and two of the rockfish species

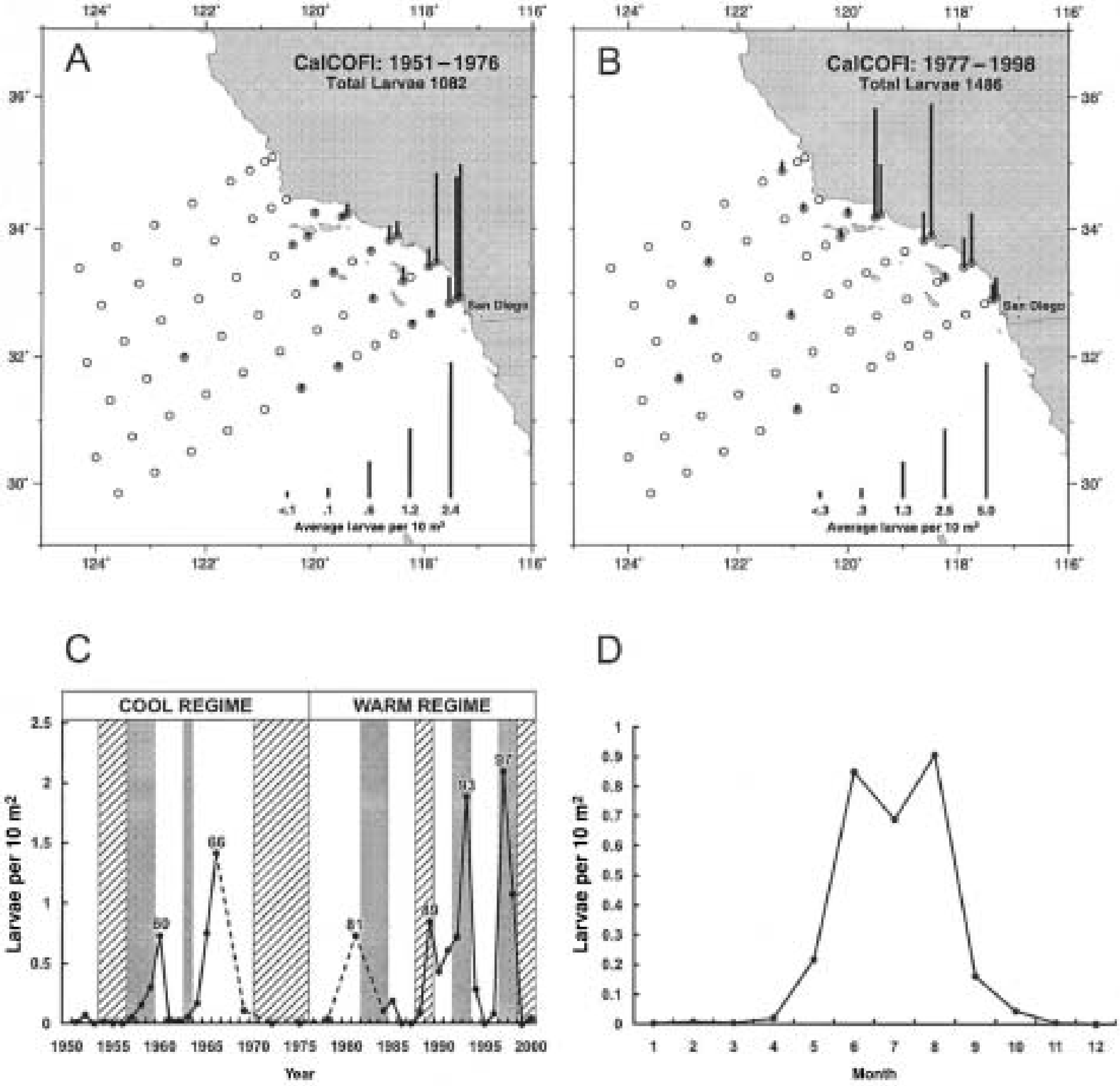

FIGURE 11-29 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Sphyraena argentea* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

(figs. 11-17, 11-18); the remaining species, bay goby, showed variable but generally declining larval abundance in CalCOFI collections since 1985 but no relationship between ENSO events and abundance. Larval spotted turbot of the coastal Sardinops egg assemblage were more abundant, on average, and were more or less evenly distributed inshore throughout the entire SCB during the warm regime, in contrast to the cool regime when they were largely concentrated in the southern part of the Bight (Moser et al., 2001a). This is consistent with their summer–autumn abundance peak and the warm-water affinity of the adults. However, larval abundance trends within the SCB apparently are unrelated to ENSO events.

Larval California barracuda of the Paralabrax assemblage provide an example of ENSO and PDO effects on warm-water, summer spawners of coastal SCB. Larval California barracuda increased in abundance through the warm regime, and their distribution along the coast shifted northward, from highest abundance in the south with no occurrences from Point Conception northward during the cool regime, to highest abundance in the central and northern Bight with some occurrences north of the Bight in the warm regime (fig. 11-29A,B). Larvae tended to be more abundant during El Niño events, although a direct relationship is far from clear, and at least during the warm regime, abundance tended to peak at about 4-year intervals (fig. 11-29C). Fantail sole showed essentially the same trends (fig. 11-30), increased abundance and larval distribution spreading northward during the warm regime (fig. 11-30A,B), increased abundance during El Niño

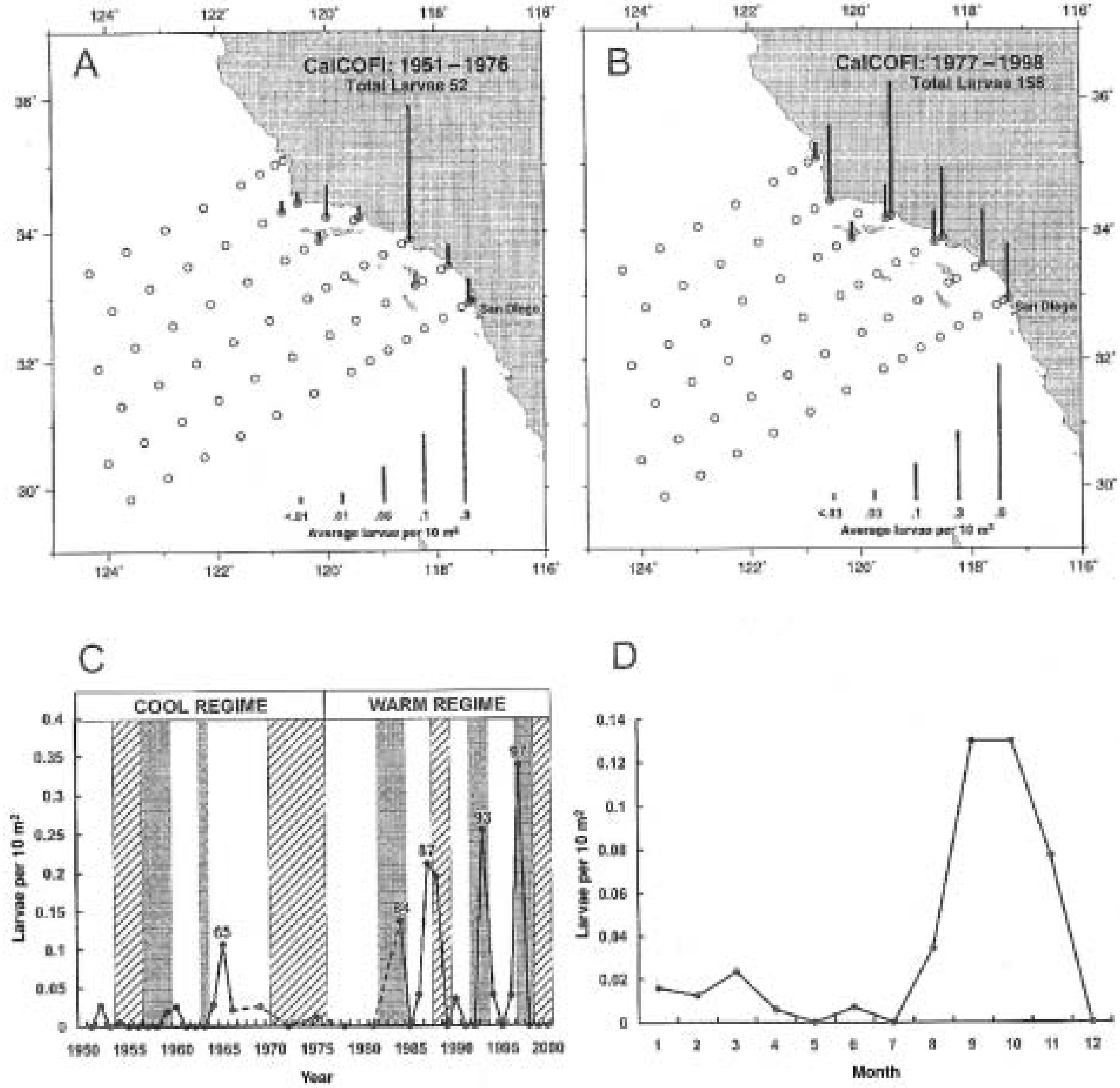

FIGURE 11-30 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Xystreurys liolepis* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

events, and decreased abundance during La Niña events (fig. 11-30C). Spawning is primarily in late summer and autumn (fig. 11-30D), when the water is warmest. This pattern contrasts sharply with that of California halibut (fig. 11-28), another paralichthyid flatfish, and reflects the more tropical affinity of fantail sole. A final example of PDO and ENSO effects on larval abundance and distribution of a shorefish species with tropical–subtropical affinity is provided by California lizardfish. Again, larval abundance increased, and the alongshore distribution extended northward during the warm regime (fig. 11-31A,B), but in this case, larval abundance and ENSO events were not closely coupled (fig. 11-31C). Larval abundance peaked in the early 1990s and subsequently declined to levels not much higher than those of the cool regime. The remaining coastal Paralabrax taxa also increased in larval abundance during the warm regime, except for blacksmith and California tonguefish which changed little. In contrast to the examples above, most of the other Paralabrax taxa displayed only small changes in alongshore distributions, with slight increases in abundance in the northern SCB and/or to the north of the SCB during the warm regime (Moser et al., 2001a). The California tonguefish was unusual in that its larval distribution contracted southward during the warm regime—opposite what one would expect based on its warm-water affinity. Four Paralabrax taxa in addition to California lizardfish, (kelp/sand bass, blacksmith, señorita, bigmouth sole) declined in abundance beginning in the mid-1980s to early 1990s and reached levels comparable to those

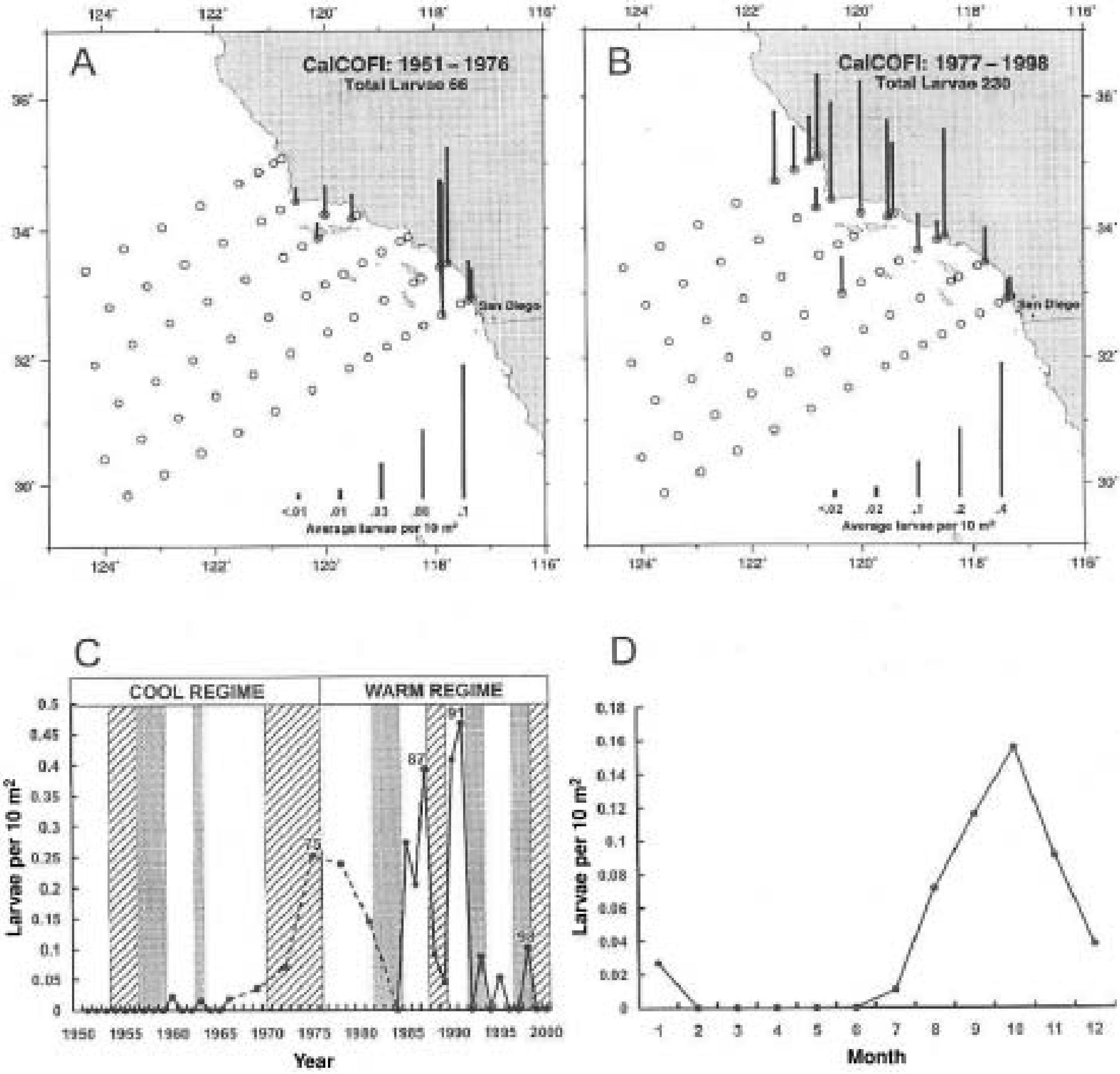

FIGURE 11-31 Interannual and decadal scale changes in larval abundance (number per 10 m^2) of *Synodus lucioceps* in the Southern California Bight (Moser et al., 2001a). A: map of mean abundance at CalCOFI stations during the cool regime; B: map of mean abundance at CalCOFI stations during the warm regime; C: mean annual abundance relative to PDO and ENSO events (El Niño: shaded; La Niña: hatched; the wide, hatched bar from 1970 to 1976 represents three closely spaced La Niña events); D: mean monthly abundance.

of the cool regime by the late 1990s (Moser et al., 2001a). In addition to California barracuda and fantail sole, three other Paralabrax species (blacksmith, California sheephead, bigmouth sole) displayed some tendency for larval abundance to peak during or just after El Niño events, although in all three cases there also were mismatches between abundance peaks and warming events (Moser et al., 2001a).

Coastal Assemblages—Summary

The results of the various coastal ichthyoplankton studies in the SCB agreed generally with regard to patterns of seasonal and spatial distributions of the ichthyoplankters but differed to some degree in the details of the temporal and spatial patterns of individual taxa. They also differed in the allocation of some taxa to the various coastal ichthyoplankton assemblages. These interstudy differences resulted primarily from differences in sampling and analytical methodologies. In general, seasonal abundance patterns that have been recognized in all SCB studies reflect spawning primarily during winter–spring (cool water), summer–fall (warm water), or more or less evenly throughout the year with interannual variation of up to a few weeks in initiation and termination of spawning. About two-thirds of the coastal fishes in the SCB are planktonic spawners and most have distinct seasonal patterns of highest larval abundance; evidence for more even year-round spawning among the coastal taxa appears to be largely limited to some of the inner shelf demersal spawners. Horizontal spatial patterns within the Bight are primarily cross-shelf rather than alongshore, probably reflecting the relative magnitudes of cross-shelf and alongshore flow in the SCB: coastal currents are primarily alongshore and cross-shelf transport is relatively weak.

The central California coastal larval fish assemblage reflects a higher proportion of demersally spawning taxa (about 60% of the oviparous species) but as in the SCB, more or less even spawning throughout the year may be largely limited to some of the inshore demersal spawners. Larvae that hatch from demersal eggs typically are larger, more developed, and more competent in the first days after hatching than larvae that hatch from small planktonic eggs. The much higher proportion of demersally spawning coastal taxa may reflect more vigorous coastal circulation off central California, especially stronger upwelling (Parrish et al., 1981), compared with the SCB. The majority of central Californian coastal fishes apparently spawn principally during winter and spring, before or during the principal upwelling period. The majority of coastal larvae appear to be broadly distributed across the shelf, perhaps reflecting upwelling during some part of their period of high abundance.

Off Oregon, 87% of the coastal assemblage fish larvae are of demersal spawners. Here, most coastal fish larvae occur between late winter and early summer, typically primarily before and/or after the spring upwelling period. The majority apparently tend to be most abundant in the inner to midshelf zones.

Larval abundances and distributions of coastal taxa in the SCB, where the most complete time series is available, tended to respond to ENSO and PDO events as would be predicted based on adult zoogeographic affinities. Larvae of warm-water taxa tended to be more abundant, higher abundance extended farther north during the warm regime, and they tended to become more abundant during ENSO warm events and/or less abundant during cool events. Cool-water taxa tended to display the opposite patterns. These were most apparent for taxa with the strongest warm- and cool-water affinities; taxa whose ranges are centered in or near the SCB had less apparent responses (or none at all) to ENSO and PDO events.

Bay and Estuarine Assemblages

Bay and estuarine habitats are quite limited on the Pacific coast. They account for only about one-fifth of the total coastline (Emery, 1967), and their ichthyoplankton assemblages typically are small compared with those of the more extensive bay and estuarine systems of the Atlantic and Gulf coasts. Larval fish assemblages of Californian bays and estuaries typically are composed predominantly of resident species (fig. 11-32), often with relatively small contributions from open coastal species. In southern California, the larval fish assemblages (fig. 11-32A) typically are dominated by gobies (Leithiser, 1981; Snyder, 1965; McGowen, 1977; White, 1977; Nordby, 1982; and Edmands, 1983, all cited in McGowen, 1993); ~60–90% of the total larvae is some combination of longjaw mudsucker (*Gillichthys mirabilis*), arrow goby, cheekspot goby (*Ilypnus gilberti*), and shadow goby (*Quietula y-cauda*) (reliable diagnostic characters were unavailable during most of the studies cited above and thus larvae of the last three species commonly were incompletely distinguished or were not distinguished in those studies). Silversides typically contribute another ~5–10% of the total larvae, topsmelt (*Atherinops affinis*) is probably the most common species. Anchovies commonly account for ~1–5% of the total larvae but can be the dominant taxon, contributing more than half the total (e.g., Allen et al., 1983). Any or all of the nonresident northern anchovy and two resident *Anchoa* species may be present. Blenniids (*Hypsoblennius* spp.) typically contribute another 1–3% of the total. These four families typically account for ≥85% (often >95%) of the fish larvae collected in the bays and estuaries of southern California. All except the anchovies are demersal spawners. The blennies and gobies spawn year-round, usually with higher larval abundance in the spring to autumn period. Topsmelt spawns from spring through early autumn (larvae of the spring–summer spawning California grunion, *Leuresthes tenuis*, and especially the winter–spring spawning jacksmelt, *Atherinopsis californiensis,* also may occur in bays and estuaries), and the *Anchoa* species are summer spawners. Apart from northern anchovy and *Hypsoblennius* spp., these taxa are uncommon to rare as far from shore as the inshore CalCOFI stations (e.g., Moser et al., 1993, 1994a).

As in southern California, goby larvae are an important component of the central and northern Californian bay and estuarine ichthyoplankton (fig. 11-32B,C). They occur year-round with higher abundance in summer and autumn and contribute somewhat less than half to more than 90% of the total larvae (Eldridge and Bryan, 1972; Eldridge, 1977; Yoklavich et al., 1992; G. M. Cailliet and E. Grannis, pers. commun., October 2002). Longjaw mudsucker and arrow goby are important components of the central California larval goby assemblage, and bay goby becomes an important member of the assemblage in northern California and Oregon (Eldridge and Bryan, 1972; Pearcy and Myers, 1974) where cheekspot and shadow gobies drop out. Pacific herring (*Clupea harengus*) is an important seasonal component of the central and northern Californian and Oregonian bay/estuarine larval fish assemblages, where it can account for half or more of the total larvae in winter and spring. In central California, northern anchovy may contribute up to about a quarter of the total bay/estuarine fish larvae, but in northern California and Oregon, it becomes only a very minor component of the bay/estuarine ichthyoplankton (Pearcy and Myers, 1974; Eldridge, 1977; Misitano, 1977; Yoklavich et al., 1992). Sculpins usually are minor components of southern Californian bay and estuarine ichthyoplankton but can contribute on the order of 5% of the total in central California during winter and spring and can become important contributors to total larval abundance during winter and spring in northern California and Oregon. Osmerid smelts may account for up to ~5–10% of total fish larvae during winter and spring in central and northern California. Both families spawn demersally.

In the estuaries and bays generally, ichthyoplankton species richness typically is highest and the proportion of the eggs and larvae that are of coastal species typically is greatest toward the mouth. In the interiors of the bays and estuaries, ichthyoplankton typically is composed predominantly of resident species. Some coastal fishes, primarily flatfishes, use estuaries as nursery areas (e.g., Pearcy and Myers, 1974; Misitano, 1976, 1977; Krygier and Pearcy, 1986; Boehlert and Mundy, 1987, 1988; Gunderson et al., 1990; Kramer, 1991; Yoklavich et al., 1992), and juveniles may be found far into the interior, although spawning and most or all of larval development is in open coastal waters.

Bay and Estuarine Assemblages—Summary

The most abundant bay and estuarine fish larvae are predominantly of demersally spawning species. Because typically they are larger and more competent early in larval life than

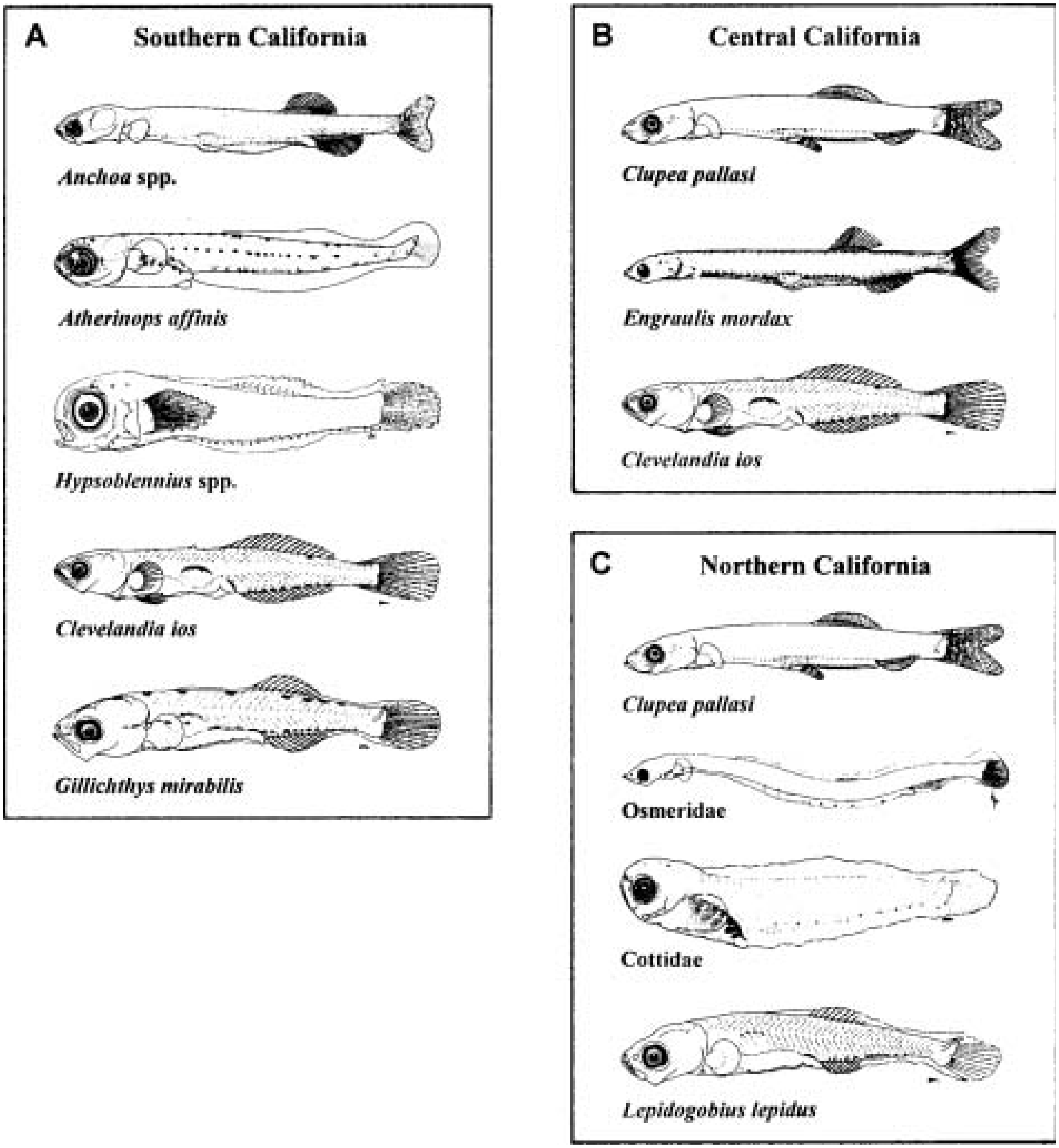

FIGURE 11-32 Characteristic taxa of bay and estuarine larval fish assemblages of (A) southern California, (B) central California, and (C) northern California. Most illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained; *Anchoa* spp. from Caddell (1988), *Atherinops affinis* and *Clupea pallasi* from Matarese et al. (1989), and Cottidae from Richardson and Washington (1980).

the larvae of planktonic spawners, they may be better able to resist or avoid transport out of the bay/estuarine environment during the early larval period than larvae hatched from planktonic eggs. In addition, the larvae of resident demersal spawners especially tend to be dominant in the bay and estuarine interiors, where less dynamic tidal water exchange may further facilitate larval retention. In southern California the most abundant larvae are gobies, anchovies, silversides, and blennies. To the north, goby larvae may be somewhat reduced in relative abundance, but they remain an important component of the ichthyoplankton and may be dominant in some cases. Anchovies also may be reduced in relative abundance in central California, and they are a minor component of the northern ichthyoplankton. Silversides and blennies become minor components of the bay/estuarine ichthyoplankton in central California and are absent to the north. Clupeids are added as a seasonally important component of both the central and northern assemblages, sculpins increase in relative abundance in central and northern California, and smelts are an important winter–spring taxon in central and northern

California. Resident species typically contribute the largest fraction of total ichthyoplankton in the interiors of bays and estuaries; coastal taxa typically occur primarily nearer the estuary and bay mouths.

Vertical Distribution

Ahlstrom (1959) analyzed 22 discrete depth samples taken on nine cruises during a 14-year period off southern California and Baja California and found that most planktonic fish eggs and larvae occurred in the upper part of the water column that includes the upper mixed layer and thermocline. Further, he determined that species occupied different strata within the upper water column and that the limits of these strata varied in relation to the upper mixed layer depth. The highly productive coastal pelagic species have shallow distributions generally limited to the upper 50 m of the water column. Ahlstrom (1959) found that ~80% of Pacific sardine larvae occurred in the upper 48 m, and in an earlier study (Ahlstrom, 1954) he found 93% of their larvae in the 0–42 m stratum. Sardine eggs were similarly distributed. Vertical distributions of eggs and larvae of northern anchovy and associated species were analyzed from 104 discrete depth tows taken at two sites off southern California in March 1980 (Moser and Pommeranz, 1999). Northern anchovy eggs were slightly shallower than larvae (~95% vs. 90% in the upper 30 m); peak egg concentration occurred at the surface and peak larval occurrence was in the 10–20 m stratum. Boehlert et al. (1985) found northern anchovy larvae at even shallower depths at a midshelf site off Newport, Oregon. Larvae were restricted to the upper 10 m with about equal concentrations in the 0–5 and 5–10 m strata. Hunter and Sanchez (1976), examining Ahlstrom's (1959) data on northern anchovy distribution, found that larvae > ~ 12 mm occurred at the surface only at night and proposed that postflexion larvae migrate to the surface at night to fill their air bladders and float with little energy expenditure during nonfeeding hours. This hypothesis was supported by Brewer and Kleppel (1986) who found anchovy larvae > 12 mm at the surface exclusively at night in Santa Monica Bay, California. Two other coastal pelagic species, chub and jack mackerel, also have shallow distributions. Ahlstrom (1959) found 80% of jack mackerel larvae above 80 m and 80% of chub mackerel larvae above 23 m; eggs of the two species have similar distributions. Moser and Smith (1993) found somewhat broader depth distributions for these species in a series of MOCNESS samples taken at the Ensenada Front at the southwest corner of the SCB, although peak concentrations of both species were in the 25–50 m stratum.

Shallow distributions typically are found for shorefish eggs and larvae. For example, Ahlstrom (1959) found that ~80% of labrid larvae and all of the California barracuda and blacksmith larvae occurred in the upper 10 m. At CalCOFI station 90.26, over the continental slope, Moser and Pommeranz (1999) found that larvae of white croaker, California pompano (*Peprilus simillimus*), queenfish (*Seriphus politus*), and California halibut occurred primarily in the upper 30 m with peak concentrations for the first two species in the 10–20 m stratum and in the 0-10 m stratum for the last two. On the shelf, white croaker, queenfish, and other croakers become epibenthic soon after hatching, some while still in the yolk-sac stage (Schlotterbeck and Connally, 1982; Barnett et al., 1984; Brewer and Kleppel, 1986; Jahn and Lavenberg, 1986). Late-stage and transforming California halibut larvae migrate to the neuston where they may be carried shoreward for settlement by onshore winds and by surface slicks generated by tidally forced internal waves (Shanks, 1983, 1986; Moser and Watson, 1990).

Larvae of other abundant demersal fishes such as >60 species of rockfishes are found somewhat deeper in the water column, although still within the zone that includes the mixed layer and thermocline. In Ahlstrom's (1959) samples, 97% of the rockfish larvae occurred at depths shallower than 80 m and 75% of the larvae were between 25 and 80 m (Moser and Boehlert, 1991). In the Moser and Pommeranz (1999) study, 90% of the rockfish larvae were in strata shallower than 80 m; however, at their slope station, highest densities were in the 20–30 m stratum and in the neuston, whereas their offshore station had no larvae in neuston samples and the highest larval concentrations were in the 40–80 m stratum. Boehlert et al. (1985) found an even shallower distribution over the shelf at Newport, Oregon, apparently related to a shallow thermocline (<30 m); 95% of the rockfish larvae occurred above 40 m and 70% were within the 5–30 m depth range (Moser and Boehlert, 1991). Off central California, Sakuma et al. (1999) found highest catches of postflexion rockfish larvae in the 0–40 m stratum during the day and in the 20–60 m stratum at night, with peak catches in the 20–40 m stratum. Larvae of postflexion shortbelly rockfish, *S. jordani*, were more evenly distributed with slightly elevated catches in the 20–40 m and 60–90 m strata during the day and fairly uniformly elevated catches in strata from 20–90 m during the night. Sakuma et al. provided evidence of vertical diel movement and confirmed the finding of previous investigators that the rockfish larvae do not occur below the thermocline.

Pacific hake is an abundant demersal species whose larvae occur within or below the thermocline. Ahlstrom (1959) found that only 5% of hake larvae occurred between the surface and 48 m and that the average center of abundance was at 72 m. Similarly, Mullin and Cass-Calay (1997) found the largest fraction of hake larvae at 50–75 m, with slightly lower concentrations in the 75–100 m stratum; Moser and Pommeranz (1999) found highest concentrations in the 40–80 m stratum. Hake eggs occurred in relatively high concentrations in strata from 50–150 m, with peak concentrations at 75–100 m (Moser et al., 1997). Larvae of four species of sanddabs occur commonly in the California Current region and have wide vertical distributions that can extend below the thermocline (Ahlstrom, 1959; Moser and Pommeranz, 1999). Sakuma et al. (1999) found that postflexion larvae of Pacific sanddab were most abundant at 60–90 m during the day and 40–60 m during the night, whereas larval speckled sanddab were most abundant at 60–90 m during the day but at 20–40 m at night, providing evidence for diel migration through the pycnocline.

Larvae of midwater fishes occupy a wide range of vertical habitats in the California Current region. Larvae of Pacific lightfish are found at relatively shallow depths, primarily from the surface to ~125 m, with a maximum concentration at 50–75 m depth (Moser and Smith, 1993). Larvae of species in the two major subfamilies of myctophids have contrasting vertical distributions; lampanyctine larvae occupy relatively shallower strata than larvae of myctophines (Moser and Smith, 1993). Within the lampanyctines, northern lampfish larvae range from near surface to 200 m with peak abundance in the 20–40 m stratum (Ahlstrom, 1959; Moser and Pommeranz, 1999). Dogtooth, broadfin, and Mexican lampfish, and California headlightfish (*Diaphus theta*) have similar overall distributions with peak concentrations at 25–50 m, 25–50 m, 50–75 m, and 50–75 m, respectively (Moser and

Smith, 1993). Among the myctophines, larvae of California, longfin, and blue lanternfish were captured as deep as ~300 m, with upper ranges of 25 m, 50 m, and 75 m and peak concentrations at 100–125 m, 75–100 m, and 125–150 m, respectively. California flashlightfish larvae were deeper in the water column, ranging from 175–500 m with a peak at 200–225 m. The vertical distributions of the larvae of the two myctophid subfamilies are in sharp contrast to the distributions of the adults: adult myctophines generally have shallower distributions compared to adult lampanyctines and are stronger vertical migrators, often coming to the surface at night. The fact that the larvae and adults of each subfamily are effectively separated vertically may be an adaptation that results in reduced mortality from cannibalism (Moser and Smith, 1993).

The deepest known larval vertical distributions in the California Current region are found in argentinoids and sternoptychids. Larvae of the bathylagids, California smoothtongue and popeye and snubnose blacksmelt, are found mainly within and below the thermocline, to ≥300 m, with highest abundance in strata between 50 m and 200 m (Ahlstrom, 1959; Moser and Smith, 1993; Moser and Pommerz, 1999). Eggs of California smoothtongue have a somewhat wider vertical distribution than larvae, from the surface to ~300 m, with highest concentrations in the same depth zone or slightly shallower, between 50–100 m (Ahlstrom, 1959). Larvae of an argentinoid, dusky pencilfish (*Microstoma* spp.), range from 150–850 m with highest concentrations from 200–400 m, below depths sampled quantitatively by CalCOFI bongo tows (Moser and Smith, 1993). Larvae of the hatchetfish genus *Argyropelecus* occur even deeper in the water column. They were the dominant taxon in closing net tows taken at 131–262 m on the NORPAC Expedition (Ahlstrom, 1959). Moser and Smith (1993) found *Argyropelecus* larvae in strata from 300–1000 m, at the Ensenada Front in July; another sternoptychid, bottlelight (*Danaphos oculatus*), had a similar distribution in those samples.

The surface zone, or neuston, is inhabited by the early life stages and adults of a large array of fish species; eggs and larvae of some occur throughout the upper water column, whereas those of others are found exclusively in surface waters and have evolved special adaptations for life in that zone (Moser, 1981; Moser et al., 2001b,c). Use of the term "neuston" for surface-living marine organisms is controversial because it was applied originally by Naumann (1917) to organisms associated with the surface film in freshwater habitats. Banse (1975) reviewed the evolution of the term, which is now used by most workers in referring to the uppermost (upper ~10–20 cm) layer of the sea and to the assemblage of organisms that lives in that zone, either permanently or facultatively (Moser et al., 2001b,c, 2002). Obligate neustonic larvae have evolved independently in a variety of phylogenetic lineages of marine fishes. Most prominent are the beloniforms (flyingfishes, halfbeaks, needlefishes, sauries) where juveniles and adults also occupy the surface zone. In the California Current region, neustonic larvae have evolved within the atheriniforms (e.g., topsmelt, grunion), scorpaeniforms (e.g., sablefish, lingcod, greenlings, cabezon and some other sculpins), within a variety of perciform families, such as the carangids (e.g., yellowtail, pompanos), coryphaenids (dolphinfish), and istiophorids (billfishes), and the pleuronectiforms (turbots of the genus *Pleuronichthys*). Sablefish (*Anoplopoma fimbria*), a demersal species of the continental slope, has a complex ontogeny that includes neustonic larvae and deeply distributed planktonic eggs. Off central California, egg distributions ranged from 160–800 m depth with highest concentration between 240–400 m (Moser et al., 1994b). McFarlane and Beamish (1992) hypothesized from laboratory experiments that newly hatched yolk-sac larvae sink to ~1000 m and then ascend gradually to the surface during about a 40-day period. Larvae are 8–9 mm when they reach the surface and rapidly accrue the heavy melanistic pigment characteristic of the neustonic stage (Kobayashi, 1957; Ahlstrom and Stevens, 1976; Kendall and Matarese, 1987; Doyle, 1992b; Moser et al., 1994b). Growth is rapid, up to 2 mm/day (Boehlert and Yoklavich, 1985), supporting the general notion that the neuston is a favorable habitat for growth and survival for species that have adapted to its special requirements.

Life History

Ichthyoplankton Specializations

Marine ichthyoplankters have evolved a large array of specializations in morphology, pigmentation, behavior, and physiology that contribute to their survival in the demanding epipelagic environment. Fascination with these life stages began when the early researchers first observed them under the microscope and continues today as our knowledge of their remarkable characteristics grows. For some of these (e.g., general transparency of eggs and larvae, heavy melanistic pigmentation and firm body structure in neustonic larvae, superficial neuromasts present in newly hatched marine larvae) their adaptive value is obvious; for others, adaptive significance is suggested by their frequency of appearance in disparate phylogenetic lineages (Moser, 1981; Govoni et al., 1984; Webb, 1999). Knowledge of the possible functions of these morphological specializations has been limited to the realm of speculation, owing to the difficulty in culturing marine fish larvae, particularly highly specialized ones, and the lack of opportunities to study them in experimental aquaria. Nonetheless, the specialized features of fish eggs and larvae provide a useful suite of taxonomic characters for workers in the growing fields of ichthyoplankton ecology and population monitoring, who have established a large fund of basic knowledge for the investigators who eventually will observe these larvae in laboratory cultures or directly in the sea. In this section, we discuss a few of the more interesting examples of morphological specialization in ichthyoplankton. For detailed information on ichthyoplankton taxonomy of the California Current region, see Matarese et al. (1989) and CalCOFI Atlas 33 (Moser, 1996). The Ahlstrom Symposium (Moser et al., 1984) summarized worldwide knowledge of teleost ontogeny and focused on its potential contribution to systematic investigations. Kendall and Matarese (1994) summarized the status of the descriptions of marine teleost life histories, including the many identification guides that had been published up to that time. An identification guide to ichthyoplankton of the western central North Atlantic is being prepared (Richards, in press). Recent guides to the fish larvae of the Indo-Pacific regions also are available (Neira et al., 1998; Leis and Carson-Ewart, 2000). Relevant information is presented in Webb's (1999) chapter on developmental and evolutionary aspects of fish larvae and in other chapters in Hall and Wake (1999).

The maximum size of most marine fish larvae ranges from ~10–20 mm; however, larvae of some species attain considerably larger sizes and, in some species, transformation occurs at sizes <10 mm. The largest larvae are found in eels; the notacanthiform *Leptocephalus giganteus* attains a length of almost 2 m (Nielsen and Larsen, 1970), and the larva of the anguilliform *Thalassenchelys coheni* attains a length of 30 cm (Smith, 1979) and a weight of >20 gm (Moser, 1981). Large size in marine fish larvae is associated with extended planktonic life, best illustrated by the European eel (*Anguilla anguilla*). The work of Schmidt (1932) showed that adult eels migrate from European rivers to the Sargasso Sea where they reproduce; then, the developing larvae are carried back to Europe by the North Atlantic Current, a journey that lasts 2–3 years, and the larvae attain a length of ~75 mm. The range of sizes among flatfishes is greater than in any other group of marine teleosts (Moser, 1981). Larvae of Mazatlan sole (*Achirus mazatlanus*) hatch at 1.3–1.6 mm and transform within a size range of 2.8–4.7 mm (Ortiz-Galindo et al., 1990). California halibut transform at 7.5–9.4 mm (Oda, 1991). In contrast, larvae of some flatfishes attain large sizes; for example, Dover sole (*Microstomus pacificus*) may reach ~60 mm and remain planktonic for 1–3 years (Toole et al., 1993; Butler et al., 1996), and rex sole (*Glyptocephalus zachirus*) larvae up to ~70 mm long have been reported (Pearcy et al., 1977). Small size and short larval life in shallow-living shelf species such as California halibut or the estuarine Mazatlan sole reduce the dispersal of their planktonic larvae away from bottom habitat appropriate for settlement (Moser, 1981). Extension of the planktonic phase through sustained growth in deep-living species such as Dover sole permits maximum dispersal of the population and increases the probability of successful settlement following shoreward and bottomward drift or migration (Moser, 1981). Also, the existence of overlapping multiple year-classes of pelagic larvae may be a causal factor in the relatively small interannual recruitment variability characteristic of this species.

A recurring theme in larval fish morphology is the enlargement or elongation and proliferation of anatomical structures (e.g., finfold, gut, eyes, head spines, fin spines, and soft tissue) (figs. 11-33–11-36). Enlarged or voluminous finfolds are characteristic of several groups (e.g., anglerfishes, snailfishes, tetraodontiforms) (e.g., figs. 11-33D, 11-34B). Moderate extension of the gut, where it is trailing free from the body, occurs, for example, in some congrid leptocephali (Castle, 1984), in some stomiiforms (e.g., *Ichthyococcus*), and in the golden lanternfish (*Myctophum aurolaternatum*) (fig. 11-35D; Moser, 1981). In other stomiiforms (e.g., *Eustomias*, some astronesthines and malacosteines), the trailing gut may exceed the body length and develop a prominent pigment pattern and/or elaborate ornamentation (fig. 11-35A, E, G; Moser, 1981, 1996; Kawaguchi and Moser, 1984). Usually, the trailing gut is broken off in net-caught specimens but in a hand-caught, unidentified malacosteine larva, the intact gut was five times the length of the body (fig. 11-35G; Moser, 1981). In some neobythitine ophidiiform "exterilium" larvae, the gut is extended as a loop and may be ornamented with pigmented finger-like extensions and an arborescent appendage, reminiscent of siphonophore structures (fig. 11-35J; Fraser and Smith, 1974; Moser, 1981). A looped gut extension occurs also in some cynoglossid flatfishes (fig. 11-35I; Ahlstrom et al., 1984). Elongate fin rays are found commonly in marine fish larvae. In some taxa, most of the soft or spinous rays in the median or paired fins are elongate (e.g., *Bathysaurus*, *Physiculus*, *Nannobrachium hawaiiensis*, *Sebastes paucispinis*, gempylids; fig. 11-34). In other taxa, one or more rays of the median or paired fins are elongate and, in the case of spinous rays, may bear secondary spinules (e.g., epinephalines, acanthurids, balistids) or, where the elongations are composed of soft tissue, have ornamentation usually in the form of serial pigmented spatulate swellings (e.g., in the myctophid genera *Loweina* and *Tarletonbeania*, among carapids, lophiiforms, lampridiforms, liopropomine serranids, the carangid genera *Alectis* and *Selene*, many paralichthyid genera, and the bothid flatfish genus *Arnoglossus*; fig. 11-33). In notacanthiforms (e.g., *Leptocephalus giganteus*), an elaborate appendage emerges from the caudal region and exceeds the body in length (fig. 11-35F). The potential for strong, elongate fin spines to deter predators is obvious (Moser, 1981; Govoni et al., 1984; Baldwin et al., 1991; Webb, 1999); however, a role for the trailing ornamented extensions found in many phylogenetic lineages is enigmatic. Their resemblance to structures on siphonophores suggests their potential for predator deterrence through siphonophore mimicry (Kendall et al., 1984; Govoni et al., 1984). Baldwin et al. (1991) suggested an even more fascinating possibility, ". . . siphonophore mimicry may be an adaptation to attract food items. Tim Targett (pers. commun.) observed behavior of a living larva of *Liopropoma* in a bucket aboard a research vessel and noted that zooplankton appeared to be attracted to the elongate filaments, which the larva kept suspended above its head. Harbison et al. (1977) found that species of five families of hyperiid amphipods associate with gelatinous zooplankton in relationships ranging from commensalism to obligate parasitism. Attracting prey by luring this fauna away from siphonophores could be a primary function of elongate filaments. . . ."

Head spination is rare in larvae of "primitive" teleosts but becomes highly developed in many acanthopterygiian orders (e.g., in beryciforms, zeiforms, scorpaeniforms, perciforms, pleuronectiforms; fig. 11-36). Among these groups, larval head spines have developed on almost every superficial head bone; however, they are most often encountered in association with bones of the opercular-preopercular series, and with the posttemporal, supracleithral, parietal, frontal, and circumorbital bones. Like the elongate spinous fin rays, their role in predator deterrence seems obvious, although alternative possibilities have been suggested (Moser, 1981; Webb, 1999).

Vision is the most important sensory modality for larval fish feeding, and it is not surprising that marine teleosts have evolved a variety of specializations in eye morphology. A recurrent theme is the presence of elliptical eyes in larvae of many lineages. For example, in myctophids, larvae of the two major subfamilies differ in eye shape, with narrow elliptical eyes in myctophines and round, or nearly round, eyes in lampanyctines (Moser and Ahlstrom, 1970). In some groups, the eyes protrude from the head to various degrees or are distinctly stalked (e.g., notacanthiforms, bathylagids, myctophids, stomiiforms; fig. 11-35A–D). Elliptical eyes can be more fully rotated compared to round eyes, and the subsequent enlargement of the visual field could be advantageous for feeding and predator avoidance (Weihs and Moser, 1981). The visual field would be further enlarged in larvae with stalked eyes; in blackdragon (*Idiacanthus*) larvae, the stalks reach 30% of the body length and may increase the visual field by an order of magnitude (Weihs and Moser, 1981).

Trophic Relationships

In an attempt to explain large interannual abundance changes observed in cod and herring stocks, Hjort (1914) hypothesized that the number of recruits each year is determined during a

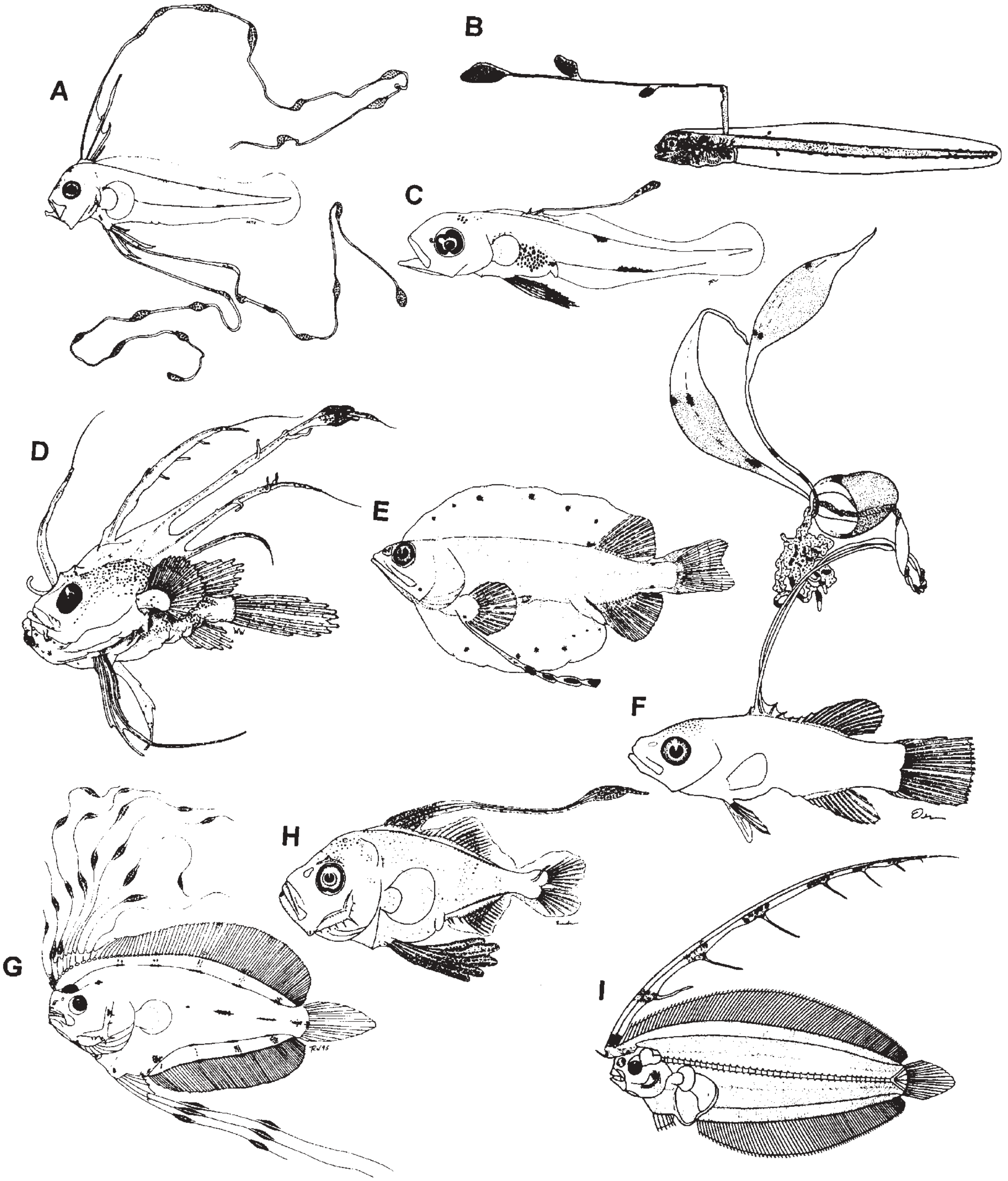

FIGURE 11-33 Examples of fish larvae with elongate, ornamented spinous, or segmented fin-rays. Except where noted, illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained. A: Trachipteridae, *Zu cristatus*, 5.8 mm; B: Carapidae, *Carapus acus*, 3.8 mm (Padoa, 1956); C: Melamphaidae, *Melamphaes lugubris*, 4.8 mm; D: Lophiidae, *Lophiodes spilurus*, 8.1 mm; E: Myctophidae, *Loweina rara*, 17.6 mm; F: Serranidae, *Liopropoma* sp., 11.0 mm (Kendall et al., 1984); G: Paralichthyidae, *Cyclopsetta panamensis*, 17.8 mm; H: Carangidae, *Selene brevoortii*, 6.4 mm; I: Bothidae, *Arnoglossus japonicus*, 30.5 mm (Amaoka, 1973).

critical period early in larval life. His critical period concept was that the strength of a year class is determined primarily by the availability of suitable food to the first-feeding larvae, although survival could be reduced if currents were to transport the larvae to an area unsuitable for continued development. Cushing (1974, 1975, 1982) extended Hjort's concept in the match/mismatch hypothesis, based on the observations that fish in temperate North Atlantic waters tend to spawn at a relatively fixed time each year corresponding more or less with the spring and/or autumn plankton production peaks, and that plankton production tends to be more variable in time than fish spawning. Cushing suggested that the match or mismatch of fish spawning and plankton production is crucial in determining larval survival and explains, at least in part, the variability in year-class strength. Later, Cushing (1990) added a second part to the hypothesis, suggesting that at

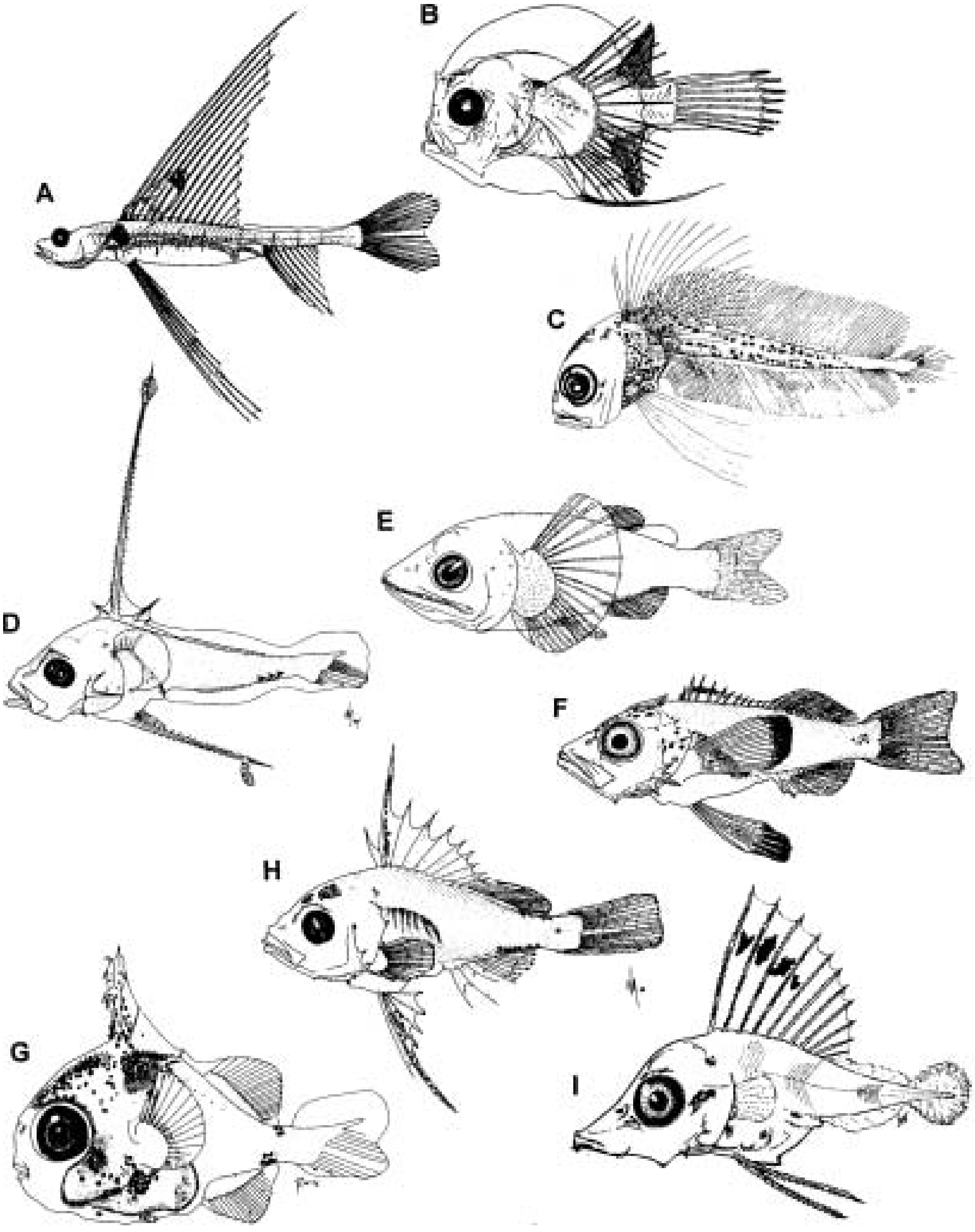

FIGURE 11-34 Examples of fish larvae with enlarged or elaborate fins. Except where noted, illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained. A: Bathysauridae, unidentified, 33 mm (Marshall, 1961); B: Caulophrynidae, *Caulophryne* sp., 9.5 mm (Bertelsen, 1951); C: Moridae, *Physiculus rastrelliger*, 12.7 mm; D: Serranidae, *Paranthias colonus*, 5.9 mm; E: Myctophidae, *Nannobrachium hawaiiensis*, 9.4 mm; F: Scorpaenidae, *Sebastes paucispinis*, 14.0 mm; G: Balistidae, *Balistes polylepis*, 4.0 mm; H: Lutjanidae, *Lutjanus peru*, 10.7 mm; I: Gempylidae, *Diplospinus multistriatus*, 5.3 mm (Voss, 1954).

lower latitudes, fish spawning may be more closely attuned to local plankton production in oceanic upwelling and divergence zones through the mechanisms of adult feeding and multiple batch spawning, thus minimizing the mismatch between larval fish and plankton production cycles. Lasker (1975, 1978, 1981) also extended Hjort's hypothesis, as the stable ocean concept, based on work with the northern anchovy off the California coast; he suggested that a stable environment facilitates the development and maintenance of patches of suitable organisms at densities that promote larval survival and growth and conversely, that strong turbulence results in poor feeding conditions with attendant reduced larval growth and survival, leading to poor recruitment. However, "stable" does not necessarily mean "static," and low level turbulence may be beneficial (e.g., Cushing, 1990). Rothschild and Osborn (1988) demonstrated that contact rates between planktonic predators and their prey depend on the concentrations of both and also on their velocities and

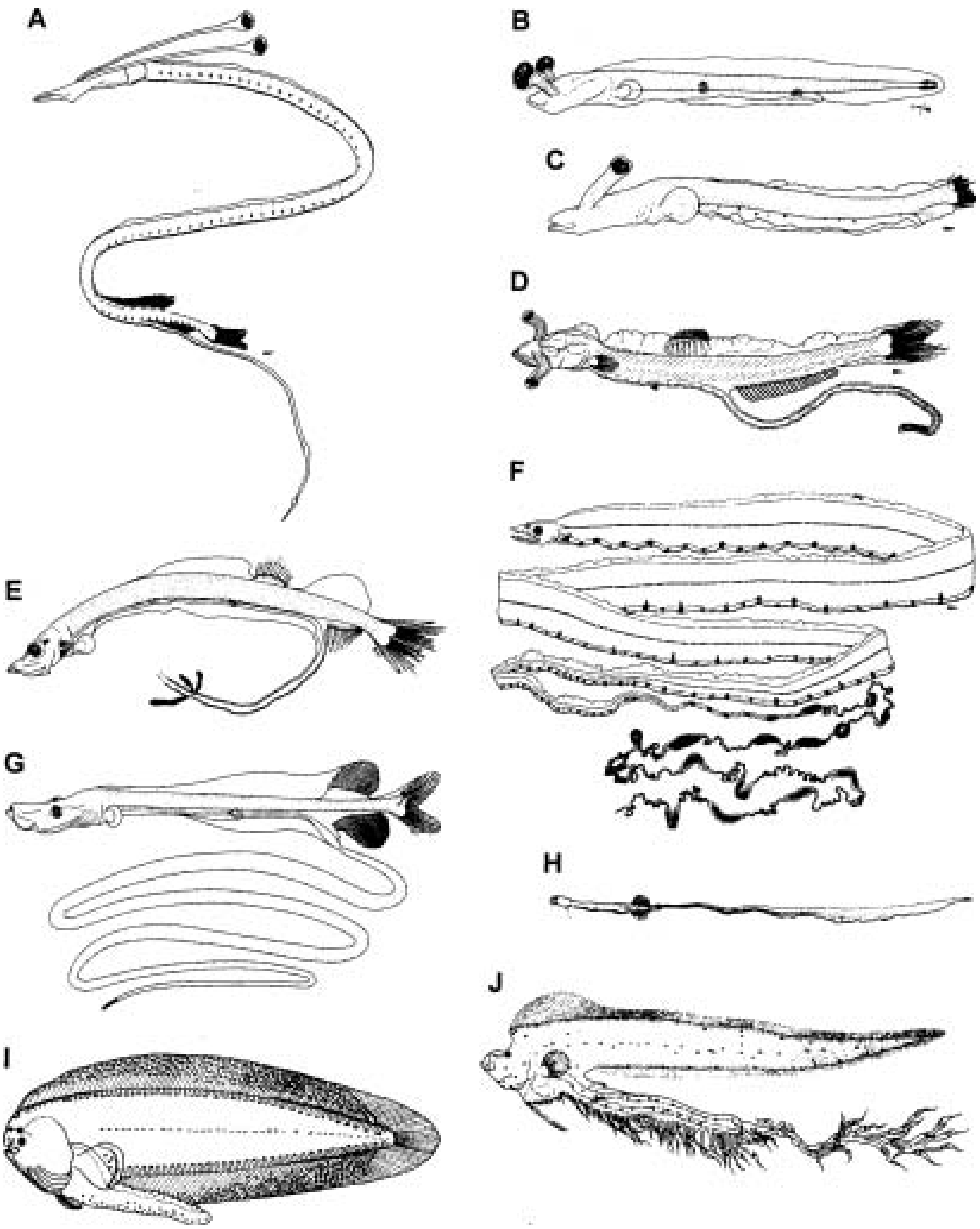

FIGURE 11-35 Examples of fish larvae with elongate soft tissue structures. Except where noted, illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained.A: Idiacanthidae, *Idiacanthus antrostomus*, 55.0 mm; B: Bathylagidae, *Bathylagus pacificus*, 7.1 mm; C: Bathylagidae, *Bathylagus bericoides*, 17.7 mm; D: Myctophidae, *Myctophum aurolaternatum*, 25.8 mm; E: Astronesthidae, unidentified, 33.0 mm (Kawaguchi and Moser, 1984); F: Notocanthidae, *Leptocephalus giganteus*, 314.0 mm; G: Malacosteidae, unidentified, 34.5 mm (Moser, 1981); H: Mirapinnidae, *Eutaeniophorus festivus*, 35 mm (105 mm TL) (Bertelsen and Marshall, 1956); I: Cynoglossidae, *Symphurus atricaudus*, 23.0 mm; J: Neobythitinae, unidentified, 64.0 mm (Moser, 1981).

that small-scale turbulence can increase the predator–prey encounter rate. Lasker (1975) provided direct observational evidence that strong turbulence can reduce larval feeding, and several studies have provided indirect evidence in the form of correlations of food availability and/or turbulence with larval survival or recruitment (e.g., Arthur, 1976; Smith and Lasker, 1978; O'Connell, 1980; Bailey, 1981; Methot, 1983; Grover and Olla, 1986; Peterman and Bradford, 1987; Cass-Calay, 1997) that could be interpreted as showing that larval feeding conditions are important in determining larval survival and subsequent recruitment. However, correlations do not demonstrate causality and other interpretations are possible. Some studies have shown that other factors (e.g., temperature, currents) strongly influence larval survival and/or recruitment

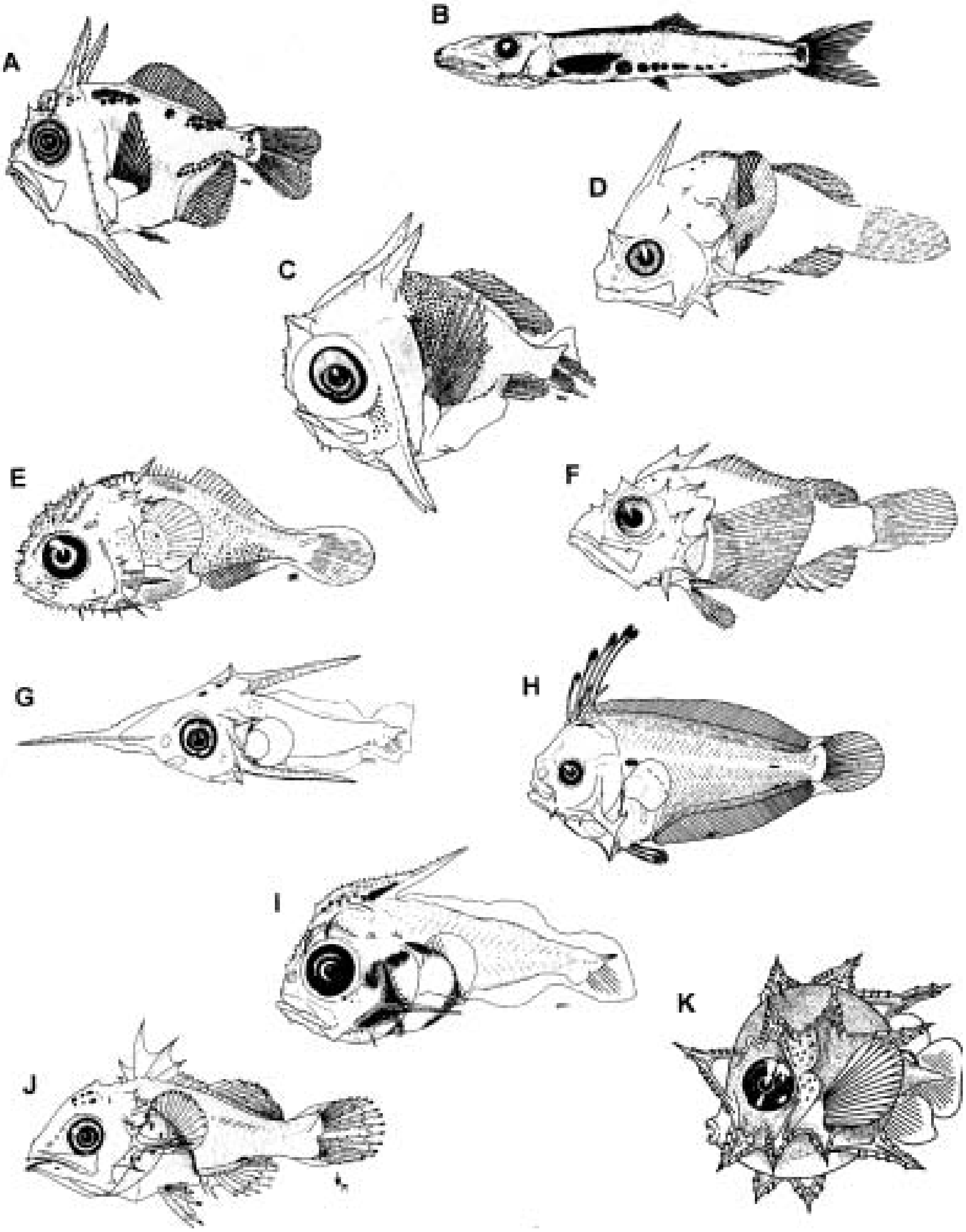

FIGURE 11-36 Examples of fish larvae with enlarged spines on the head and/or pectoral girdle. Except where noted, illustrations are from publications by personnel at SWFSC and are reproduced from Moser (1996), where original attributions can be obtained. A: Diretmidae, *Diretmus argenteus*, 6.2 mm; B: Paralepididae, *Sudis atrox*, 21.5 mm; C: Anoplogastridae, *Anoplogaster cornuta*, 4.3 mm; D: Scorpaenidae, *Pontinus sierra*, 5.0 mm; E: Malacanthidae, *Caulolatilus princeps*, 6.0 mm; F: Scorpaenidae, *Sebastolobus altivelis*, 11.2 mm; G: Holocentridae, *Sargocentron suborbitalis*, 4.2 mm; H: Paralichthyidae, *Syacium ovale*, 6.5 mm; I: Priacanthidae, *Pristigenys serrula*, 4.0 mm; J: Serranidae, *Hemanthias signifer*, 6.6 mm; K: Molidae, *Ranzania laevis*, 2.8 mm (Tortonese, 1956).

(e.g., Cowen, 1985; Houde, 1989; Houde and Zastrow, 1993), and some have shown poor correlations, at least in some years, between food availability or larval abundance and recruitment (e.g., Anderson, 1988; Peterman et al., 1988; Butler, 1989; Kendall et al., 1996; Bradford and Cabana, 1997; Kendall, 2000). This suggests that larval survival may not always be the critical factor in determining recruitment success. Nevertheless, since Hjort's (1914) work, feeding has been a major focus in studies of larval survival and recruitment in marine fishes, although in recent years, the emphasis has begun to shift to other areas of investigation (e.g., physical processes, predation, dynamics of the juvenile stage).

The majority of marine fishes in California waters are oviparous, and have planktonic eggs. The larvae that hatch from these eggs typically are relatively poorly developed at hatching, but by the end of the yolk-sac stage, little yolk remains and the larvae have developed to the point that feeding can commence. Larvae that hatch from demersal eggs and larger planktonic eggs typically are larger and more vagile and have greater internal nutrient reserves that may confer greater initial resistance to starvation, compared with larvae from small planktonic eggs (e.g., Chambers, 1997). Most planktonic fish eggs in the California Current region fall within the range of about 0.5–3.0 mm in diameter; "typical" planktonic eggs are about 1 mm. Larvae that hatch from those eggs complete yolk absorption in about 3–7 days and reach the point of irreversible starvation if they are unsuccessful in obtaining a sufficient number of prey of sufficient quality within another 1–8 days (e.g., Lasker et al., 1970; Hunter and Kimbrell, 1980a; Bailey, 1982). Resistance to starvation subsequently increases (e.g., Hunter, 1976a; Theilacker, 1986).

Larval fish consume a wide variety of plankters; copepods, especially their naupliar and copepodite stages, typically are a major component of larval fish diets in the California Current region (e.g., Arthur, 1976, 1977; Hunter and Kimbrell, 1980a; Sumida and Moser, 1980, 1984; Mullin et al., 1985; Brewer and Kleppel, 1986; Grover and Olla, 1987; Watson and Davis, 1989). Other common prey taxa include diatoms, dinoflagellates, tintinnids, rotifers, appendicularians, mollusk veliger larvae, and cladocerans (e.g., Gadomski and Boehlert, 1984; Sumida and Moser, 1984; Mullin et al., 1985; Brewer and Kleppel, 1986; Jahn et al., 1988; Watson and Davis, 1989). Fish larvae may become important in the diets of older larvae of some species such as California barracuda and chub mackerel (Hunter, 1981). The largest size prey that can be eaten is determined by larval fish mouth size and the critical prey dimension is width rather than length. Small larvae consume small prey, typically in about the 30–100 μm width range. The maximum prey size selected increases more or less rapidly as the larvae grow, but the minimum size consumed increases much more slowly; thus larger larvae can select from among a larger range of prey sizes, presumably subsisting on smaller prey when the larger, more energetically valuable, but rarer (e.g., Vlymen, 1977) prey are unavailable (e.g., Sumida and Moser, 1980, 1984; Hunter, 1981; Watson and Davis, 1989).

Marine fish larvae are visual predators that feed during daylight hours (e.g., Arthur, 1976; Hunter, 1981; Sumida and Moser, 1984; Watson and Davis, 1989; Margulies, 1997), although some feeding at lower light levels also has been suggested for some species (e.g., Watson and Davis, 1989; Mullin and Cass-Calay, 1997). First-feeding larvae have limited visual range. Prey is perceived only within distances less than about 0.5–1.0 body lengths; perceptual range increases with larval growth (e.g., Hunter, 1972, 1981; Margulies, 1997). Water viscosity is an important factor in determining swimming behavior and speed in small fish larvae. The lack of fin rays and supporting structures and the relatively poorly developed musculature of typical first-feeding marine teleosts results in swimming speeds somewhat less than about a body length per second. As larvae grow, viscosity becomes relatively unimportant, leading to a change in swimming behavior from intermittent burst swimming to a beat and glide mode (e.g., Weihs, 1980), and average swimming speed increases as a function of larval length (e.g., Hunter, 1981). Owing to their limited swimming ability and small visual range, first-feeding larvae are capable of searching only a small volume of water for prey, probably not much more than about 100 mL, per hour, but they have the ability to remain in a patch of food if one is encountered (e.g., Hunter and Thomas, 1974). Searchable volume increases rapidly as swimming speed and perceptual range increase with larval growth (e.g., Hunter, 1972, 1981).

Laboratory rearing studies have shown that to survive, first-feeding larvae must find enough food to grow on the order of 15–20% per day (e.g., Houde and Schekter, 1980); high food densities on the order of 1000 or more microcopepods per liter are required for high survival rates (e.g., O'Connell and Raymond, 1970; May, 1974; Hunter, 1981). However, these high food concentration requirements generally were based on larval rearing in static systems and did not take into account possible increased encounter rates in the sea resulting from microscale turbulence (Rothschild and Osborn, 1988). Average densities of copepod nauplii and microcopepods in the sea are two or three orders of magnitude lower (e.g., Beers and Stewart, 1969; Arthur, 1977) than those indicated as necessary by the laboratory studies. Even given the potential benefit of microscale turbulence, it seems likely that fish larvae must depend on plankton patches, where concentrations of prey are higher than average. Plankton patchiness on scales of kilometers to centimeters has been demonstrated in the California Current region (Lasker, 1975; Haury, 1976; Mullin, 1979; Owen, 1981, 1989), although the highest concentrations of fish larvae and their potential prey do not always coincide (e.g., Jahn et al., 1988; Frank, 1988; Watson and Davis, 1989). O'Connell (1980) found patches of starving and well-fed northern anchovy larvae off southern California, and Lasker (1978) demonstrated that northern anchovy larvae fed successfully at high natural prey densities in water collected from the chlorophyll maximum zone, but not at the low densities available in surface water or in water from either stratum after a storm dispersed the chlorophyll maximum. On the other hand, Butler (1989) and Owen et al. (1989) found little difference in survival and the condition of larval northern anchovy under eutrophic and relatively oligotrophic conditions off southern California.

Predation may have as large an effect on recruitment as larval feeding, but it has been the subject of far fewer directed studies than feeding. Predation probably is the major source of mortality during the egg and yolk-sac larval stages (e.g., Hunter and Kimbrell, 1980b; Hunter, 1981; Hewitt et al., 1985). Many kinds of invertebrates, such as cnidarian medusae, ctenophores, chaetognaths, copepods, amphipods, and euphausids, are known larval fish predators (e.g., Lillilund and Lasker, 1971; Theilacker and Lasker, 1974; Alvariño, 1980; Brewer et al., 1984). Most of these are effective predators only on the nonmotile and weakly swimming early stages through yolk absorption (e.g., Feigenbaum and Reeve, 1977; Landry, 1978; Hunter, 1981); predation may become a less important source of mortality than starvation during early feeding-stage larval life (e.g., Hewitt et al., 1985), although starving larvae probably are more vulnerable to predation (e.g., Hunter, 1976b; Cushing, 1990), so that predation may be the immediate cause of death of a starving larva. As the larvae grow and increase in competence, their susceptibility to starvation and to most planktonic predators diminishes, although they may actually become more vulnerable to some (e.g., Houde, 1997) and they remain very susceptible to mobile predators such as juvenile and adult planktivorous fishes (e.g., Hunter and Kimbrell, 1980b; Hunter, 1981; Pepin et al., 1987) through at least mid- to late larval life when escape responses improve or schooling behavior begins (e.g., Hunter, 1981; Webb, 1981; Margulies, 1989). Predators, as well as food, are patchily distributed in the sea, and as has been suggested in larval fish feeding studies, patchiness may be critical in determining larval mortality due to predation (Hunter, 1981). Whatever the cause(s) of mortality may be, it seems probable that the growth rate during early life (through larval or juvenile stage) is a critical determinant in survival and subsequent recruitment (e.g., Anderson, 1988; Lo et al., 1995).

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