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Ecology of pelagic larvae and juveniles of the genus *Sebastes*

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Synopsis

Pelagic larvae and juveniles of the genus *Sebastes* are widely distributed in the continental shelf and slope waters of subarctic to temperate oceans, with greatest abundance in the Northern Hemisphere. We review the ecology and distribution of these planktonic and micronektonic life stages in relation to oceanographic conditions. Special attention is paid to the west coast of North America, where abundance of larvae from samples collected during 1951–1981 is described. After transformation, the pelagic juveniles are widely distributed, often at great distances from benthic adult habitats. These stages are most frequently distributed in either midwater or near-surface habitats; this dichotomy may require different strategies for successful recruitment.

Introduction

After parturition, larvae of the genus *Sebastes* lead a pelagic existence of varying duration and are one of the most abundant kinds of fish larvae in the temperate and subarctic North Atlantic and North Pacific Oceans (Ahlstrom 1961, Bainbridge & Cooper 1971). Relatively little is known about their ecology or that of the older micronektonic juveniles. One of the major stumbling blocks to research on these age groups is the difficulty in identifying them to species (Moser et al. 1977). Published studies, however, reveal interspecific variation in parturition seasons, vertical and horizontal distributions of larvae, habitats occupied between the larval period and settlement and duration of the planktonic phase. In this paper, we review the literature on the pelagic, early life history stages of *Sebastes* and describe the distribution and ecology of larvae in the California Current region.

Spawning periodicity

The timing of spawning is critical to the survival of fish larvae. In *Sebastes*, insemination may precede fertilization by 6 months (Sorokin 1961), and parturition is equivalent to spawning in oviparous fishes. Timing of spawning in marine fishes is often related to feeding seasonality of adults, allowing needed energy reserves (Guillemot et al. 1985). Alternatively, features in the pelagic environment where the larvae reside, particularly physical factors and prey concentrations, may be of critical importance (Iles & Sinclair 1982). Parrish et al. (1981) suggested that fish species off the west coast of North

America have evolved to spawn in winter when upwelling and the attendant offshore Ekman transport are minimal. Their hypothesis is only partially supported by an examination of the spawning seasonality of *Sebastes* species off this coast (Wyllie Echeverria 1987); many species also spawn in summer months, and the extended larval periods may subject their larvae to offshore dispersal. Further, certain species may spawn more than a single brood (Moser 1967, MacGregor 1970). Within species, spawning seasonality may be distinct with a clear peak (Anderson 1984) or extended with a minor peak. For example, the year-round presence of small, pelagic, juvenile *S. diploproa* suggests that at least limited spawning occurs in all months of the year (Boehlert 1977).

Distribution patterns of larvae

Atlantic

In the North Atlantic, ichthyoplankton surveys reveal that larvae of *Sebastes* are seasonally abundant and widespread; Tåning (1949) showed that larval *Sebastes* were abundant in the Atlantic north of 50° latitude where boreal mixed water of 3–8.5° C was at depths of 200–500 m (see also Templeman 1959). Subsequent surveys in the Norwegian and Barents seas (Baranenkova & Khokhlina 1961), central Atlantic (Einarsson 1961, Henderson 1961, Bainbridge & Cooper 1971) and western Atlantic (Templeman 1959) generally confirmed Tåning's (1949) observations, and the central Atlantic surveys revealed a vast concentration of *Sebastes* larvae in the Irminger Sea southwest of Iceland. Because of the difficulty in distinguishing the larvae of *S. marinus, S. mentella* and *S. fasciatus*, some conclusions of these studies apply to the genus as a composite, and definitive information on individual North Atlantic species awaits improvement in the taxonomy of larvae (Kendall 1991).

Southern oceans

The genus may be represented by only a single species, *S. capensis*, in the Southern Hemisphere, present in both Atlantic and Pacific oceans (Chen 1971). Very little information is available on distributions of larvae of this species, partly due to its relative scarcity in plankton collections. For example, *S. capensis* represented only 0.05% of all larvae collected off northern Chile (Loeb & Rojas 1988). Sanchez & Acha (1988) reported catches of *S. oculatus (S. capensis*?) larvae and pelagic juveniles over the Patagonian shelf between 39° and 55° latitude. Although overall occurrences were low (5.5% of positive tows), abundance (number per 10 m^2) reached a peak of 55% of the total catch of larvae in December. This suggests that populations of *Sebastes* off Chile and Argentina may be fundamentally different. More research will be necessary to describe the species composition, distribution and abundance of *Sebastes* larvae in the Southern Hemisphere.

North Pacific

Wide-ranging ichthyoplankton surveys have not been made in the western Pacific. A number of localized surveys showed that larvae of several *Sebastes* species are seasonally abundant and generally confined to the coastal shelf: *S. inermis* (Harada 1962, Okiyama 1965, Kim et al. 1985), *S. pachycephalus* and *S. hubbsi* (Senta 1962), *S. pachycephalus, S. oblongus* and *S. marmoratus* (Kuwahara & Suzuki 1983).

Numerous ichthyoplankton surveys have been conducted in the Bering Sea and Gulf of Alaska. Waldron (1981) summarized ichthyoplankton data available for the former and found that larvae of *Sebastes* occurred in spring and summer samples from two regions. Most larvae occurred from the Aleutian Islands north to about 60° N over the continental slope and adjoining regions. A second area of concentration was near Bowers Ridge in the southwestern Bering Sea. Lisovenko (1967) described the distribution and abundance of *S. alutus* larvae from an ichthyoplankton survey in the Gulf of Alaska. His description of diagnostic taxonomic features of the larvae, however, is not convincing, and his conclusions probably apply to a mixture of species. He reported much higher densities of *Sebastes* larvae in the northern region of the Gulf of Alaska than in areas to the west and east and postulated that larvae were entrained in the anticyclonic gyre of the Alaska Current. This was not corroborated by LeBrasseur's (1970) surveys, which covered much of the Gulf of Alaska. *Sebastes* had the highest incidence of all types of larvae; they were concentrated over the continental shelf and slope west of the Queen Charlotte Islands, with some encountered seaward to 300 nmi.

Kendall & Dunn (1985) presented data on the distribution of *Sebastes* larvae from 11 ichthyoplankton surveys conducted over the continental shelf off Kodiak Island, Alaska. Larvae first appeared along the edge of the shelf in spring, were abundant and widely distributed over the shelf in summer and were generally restricted to midshelf in fall cruises. The authors suggested that this apparent shift in distribution resulted from differential timing of extrusion among species. Kendall & Ferraro (1988) also found high densities of *Sebastes* larvae along the continental slope in a more wide-ranging survey between the Kenai Peninsula and Umnak Island, March-June 1985. As in Kendall & Dunn (1985), their sampling pattern was restricted to the slope region and did not demonstrate the full seaward extent of *Sebastes*. A comprehensive view of the areal and temporal distribution of *Sebastes* larvae in the Gulf of Alaska and Bering Sea in relation to major oceanographic features will require annual, wide-ranging surveys.

Sebastes spp. was the most abundant taxon of fish larvae taken on a survey during April-May 1967 from Vancouver Island, Canada, to the Oregon-California border, accounting for 29% of the total fish larvae (Waldron 1972). Larvae were concentrated over the continental shelf and slope, but were found seaward to > 250 nmi and were unusually abundant near Cobb Seamount. Larvae of *Sebastes* occurred prominently in several surveys along the Oregon coast (Richardson & Pearcy 1977, Richardson et al. 1980). Highest mean abundances occurred over the outer continental shelf, or beyond it, where *Sebastes* spp. were dominant components of the offshore ichthyoplankton assemblage. Richardson et al. (1980) proposed that longshore coastal currents help maintain the distinct inshore and offshore assemblages and that a cellular circulation pattern near the continental slope works in concert with seasonal onshore-offshore surface drift to transport *Sebastes* larvae seaward in summer and shoreward in winter.

In a series of ichthyoplankton surveys off the Washington, Oregon and northern California coasts, larvae of *Sebastes* spp. were abundant and widespread both latitudinally and offshore during spring months (Kendall & Clark 1982). Larvae became more restricted to coastal waters in summer and latitudinally patchy along the coast during fall and early winter. Larvae from oblique bongo net samples were consistently smaller (peak length frequency at 3–5 mm) than those caught in neuston (surface) tows (modal peak in the 10–30 mm range). This is consistent with the relatively high densities of rockfish larvae and juveniles captured by Shenker (1988) in a large neuston trawl. These data suggest that larvae of some *Sebastes* species utilize the surface waters as a prerecruitment habitat.

California Cooperative Oceanic Fisheries Investigations

Since 1939 the California Cooperative Oceanic Fisheries Investigations (CalCOFI) has carried out joint biological and oceanographic surveys off the west coast of the United States and Mexico, primarily off California and Baja California (Hewitt 1988). These surveys have produced the most extensive ichthyoplankton time series available, both temporally and spatially. The distribution and abundance of *Sebastes* spp. larvae have been described for segments of the time series (Ahlstrom 1961, Ahlstrom et al. 1978), and some progress has been made on the identification of individual species. Complete life history series of eight species have been established, and five of these (*S. aurora, S. jordani, S. levis, S. macdonaldi, S. paucispinis*) are sufficiently distinct to warrant their identification in recent CalCOFI survey samples (Moser et al. 1977, 1985). Complete early life history series of *S. melanostomus* (Moser & Ahlstrom 1978) and *S.*

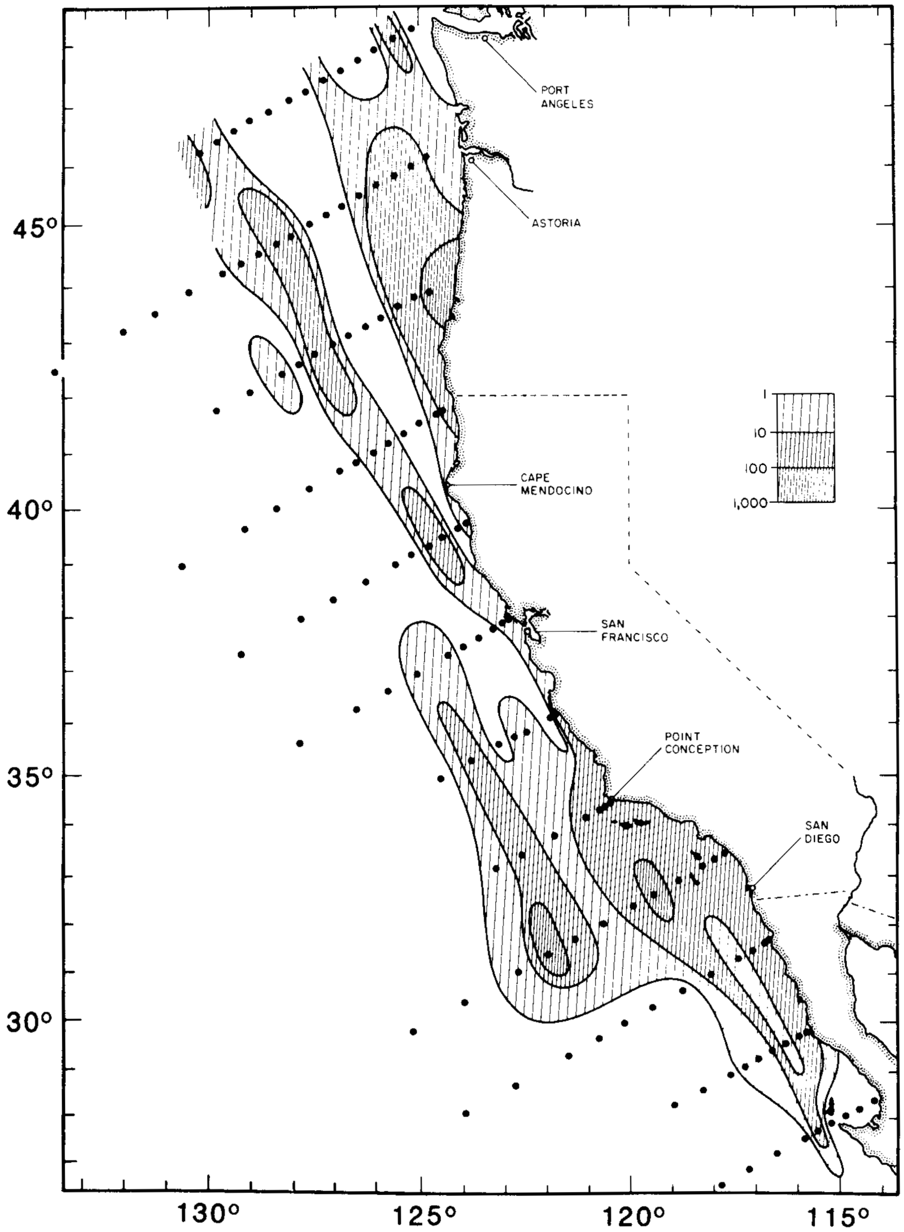

Fig. 1. Relative abundance of *Sebastes* spp. larvae (number under 10 m^2) taken off Washington, Oregon, California and Baja California during CalCOFI cruise 7205 (modified from Ahlstrom et al. 1978).

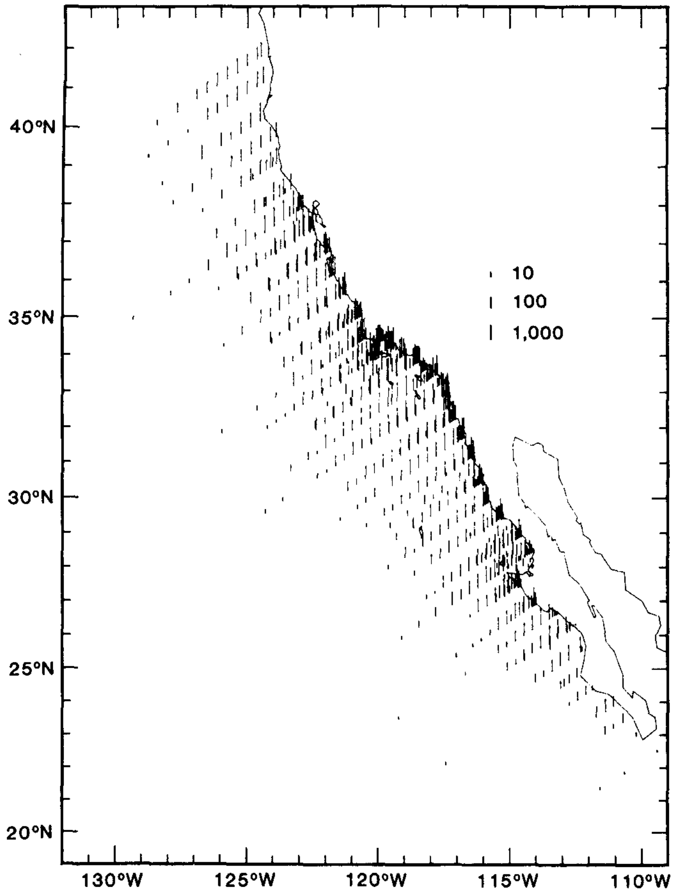

Fig. 2. Summed abundance (number under $10\,m^2$) of *Sebastes* spp. larvae collected on CalCOFI surveys during 1951–1981; numbers indicated by exponentially scaled bars.

dallii (Moser & Butler 1981) have been described, but their larvae have not been routinely identified in CalCOFI samples because of the possibility of confusion with closely related species. Larvae of *S. cortezi* were identified only in CalCOFI samples taken in the Gulf of California during 1957 and 1958. In this paper, we utilize the recently established CalCOFI ichthyoplankton data base (Ambrose et al. 1987) to describe the distribution and abundance patterns of *Sebastes* spp. from 1951 to 1981.

Off California and Baja California, as reported for other regions, *Sebastes* larvae are concentrated over the continental shelf and slope and are found as far as 300 nmi beyond the shelf (Fig. 1, 2). Distributions of larvae are patchy along the coast and certain regions (e.g. Cape Mendocino, San Francisco, Pt. Conception, Southern California Bight, and Pt. Eugenia) consistently have higher concentrations of larvae (for additional examples, see distribution maps in Ahlstrom et al. 1978). *Sebastes* larvae ranked fourth overall in abundance in the 1951–1981 CalCOFI time series, comprising 6.2% of all larvae collected (Smith & Moser 1988). Mean incidence (65%) and abundance (71 larvae per $10\,m^2$) were highest off central California, were slightly lower off northern California and declined gradually toward the southern end of the survey

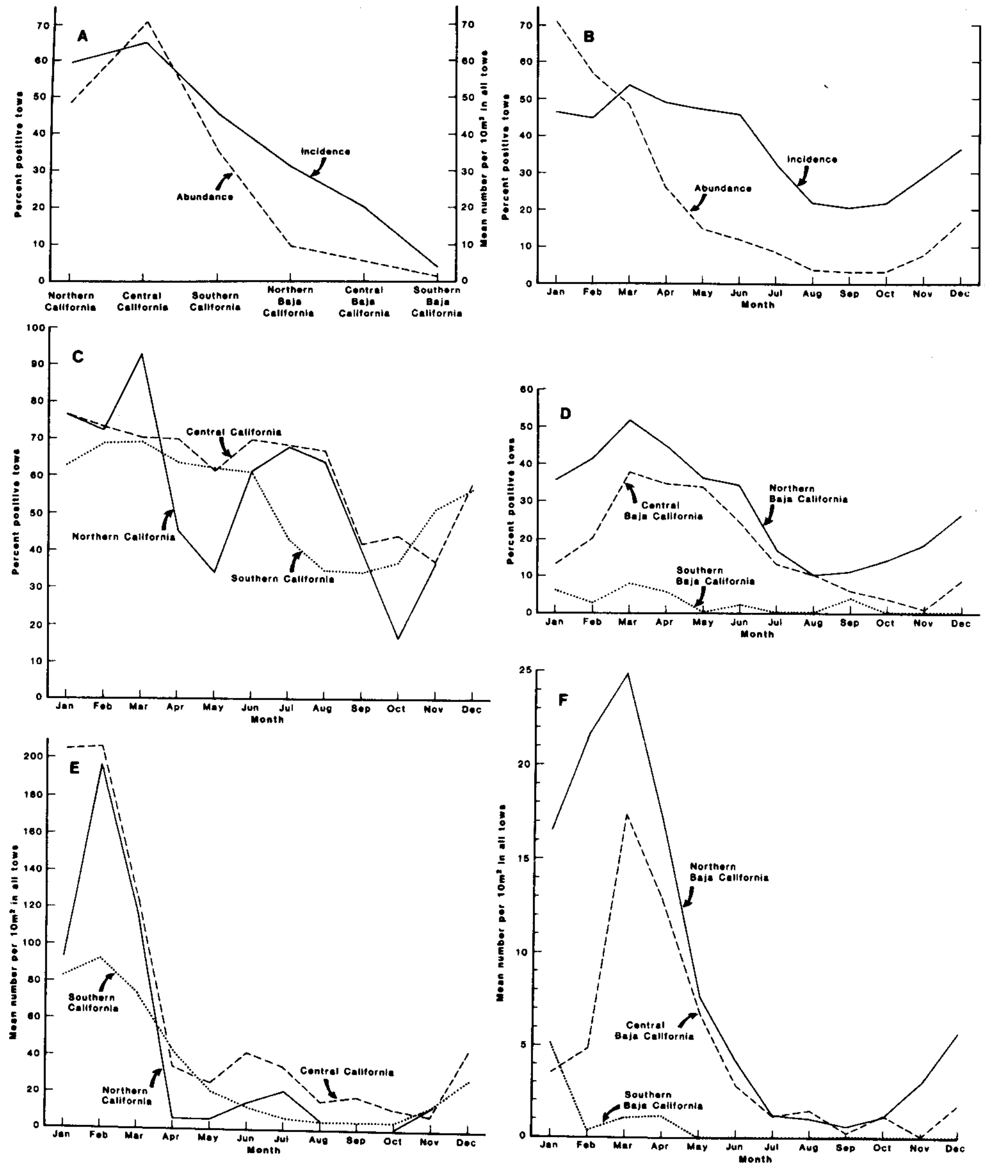

Fig. 3. Mean incidence (percent positive tows) and abundance (number under 10 m^2) of *Sebastes* spp. larvae sampled on CalCOFI surveys off California and Baja California during 1951–1981. (A) overall incidence and abundance in six coastal zones; (B) seasonal incidence and abundance for entire CalCOFI survey area; (C) seasonal incidence for California; (D) seasonal incidence for Baja California; (E) seasonal abundance for California; (F) seasonal abundance for Baja California.

pattern (Fig. 3A). For all regions combined, mean incidence was high (> 40%) from January through June with a peak of 54% in March (Fig. 3B). A July-September decline was followed by a gradual increase in October-December. Overall mean abundance was highest in January (71 larvae per 10 m^2), declined to one-tenth that value in August-September and then increased in October-December. The seasonal incidence of larvae captured off southern California was similar to that for all regions combined, but incidence off northern California was distinctly bimodal with peaks in March and June-August (Fig. 3C). Incidence for central California was intermediate between these two patterns. The north to south trend in seasonal incidence continued through Baja California (Fig. 3D). In the northern portion, a broad dome of relatively high incidence existed from January to June, followed by a gradual summer decline. Onset of peak incidence was later off central Baja California, and several small incidence peaks characterized southern Baja California.

Seasonal abundance was bimodal for northern and central California (Fig. 3E), but the summer peaks were much less pronounced than the corresponding peaks in incidence (Fig. 3C). The summer peak could be caused by either the release of a second brood of larvae by the same species that produced the January-March peak or release from a different group of species with a later parturition season. Alternatively, the summer peak could represent larvae that were produced north of the sampling area by summer-spawning species and then transported to northern and central California waters by the California Current. The summer peak was not evident in southern California (Fig. 3E). Abundance curves for Baja California clearly indicate a later onset of parturition and a broader spring peak compared with California, even though absolute values were one-tenth the former (Fig. 3F).

Regional maps of incidence and abundance of *Sebastes* larvae show seasonal onshore-offshore as well as latitudinal trends (Fig. 4). The late winter-early spring maxima for all coastal regions are clearly shown, with a sharp reduction off Baja California. The extent of offshore distribution of larvae is much greater off California than Baja California, where it is progressively more coastal towards the southern region of the peninsula. The seasonal bimodality off northern California appears in July-September as a gradient with highest values in the coastal zone. Because *Sebastes* spp. larvae are not abundant north of California in these months (Richardson & Pearcy 1977, Kendall & Clark 1982), they probably represent a late reproductive peak of northern California species. The offshore distribution of larvae is greatest off central California and is sustained throughout the year. Relatively high incidence and abundance are maintained along the coast through spring and summer. Off southern California, coastal incidence and abundance decrease after the January-March peak but increase in October-December, in advance of other coastal regions. The broad winter-spring peak in incidence and abundance off Baja California is evident in the regional maps, with offshore extent and relative values decreasing to the south.

Peak production of *Sebastes* larvae off California and Baja California coincides with low ocean temperatures in those regions and declines as seasonal warming progresses northward (Fig. 4; Reid et al. 1958). Mean zooplankton abundance is inversely related to temperature and is generally higher in coastal regions because of upwelling. Our data (not illustrated) indicate a close areal and seasonal match between zooplankton concentration and abundance of *Sebastes* larvae; peak abundance of larvae slightly precedes peak zooplankton abundance. The zooplankters retained by CalCOFI nets are generally larger than those eaten by fish larvae, however, and peak abundance of smaller copepods at younger stages may coincide more closely with abundance of *Sebastes* larvae.

Abundance of *Sebastes* larvae is characterized by large interannual variation off California and Baja California (Fig. 5A, B). Values for central and southern California were comparatively low during the 1950's, with a minimum in 1959 when a major period of ocean warming (El Niño) had reached its full effect. This was followed by a general trend of increasing abundance in the 1960's and 1970's, with peaks in 1963 and 1969 in central California and a peak in 1972 in southern California. Mean abun-

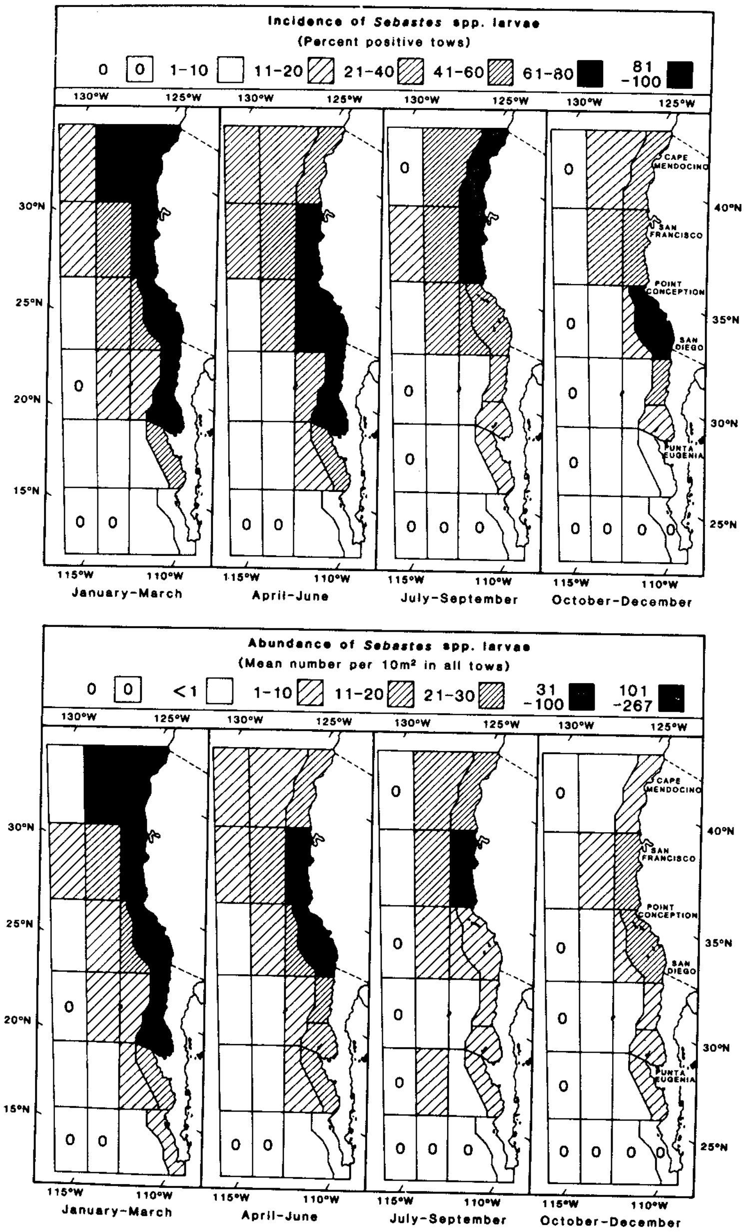

Fig. 4. Mean incidence (above) and abundance (below) of *Sebastes* spp. larvae in 23 CalCOFI regions sampled during 1951–1981.
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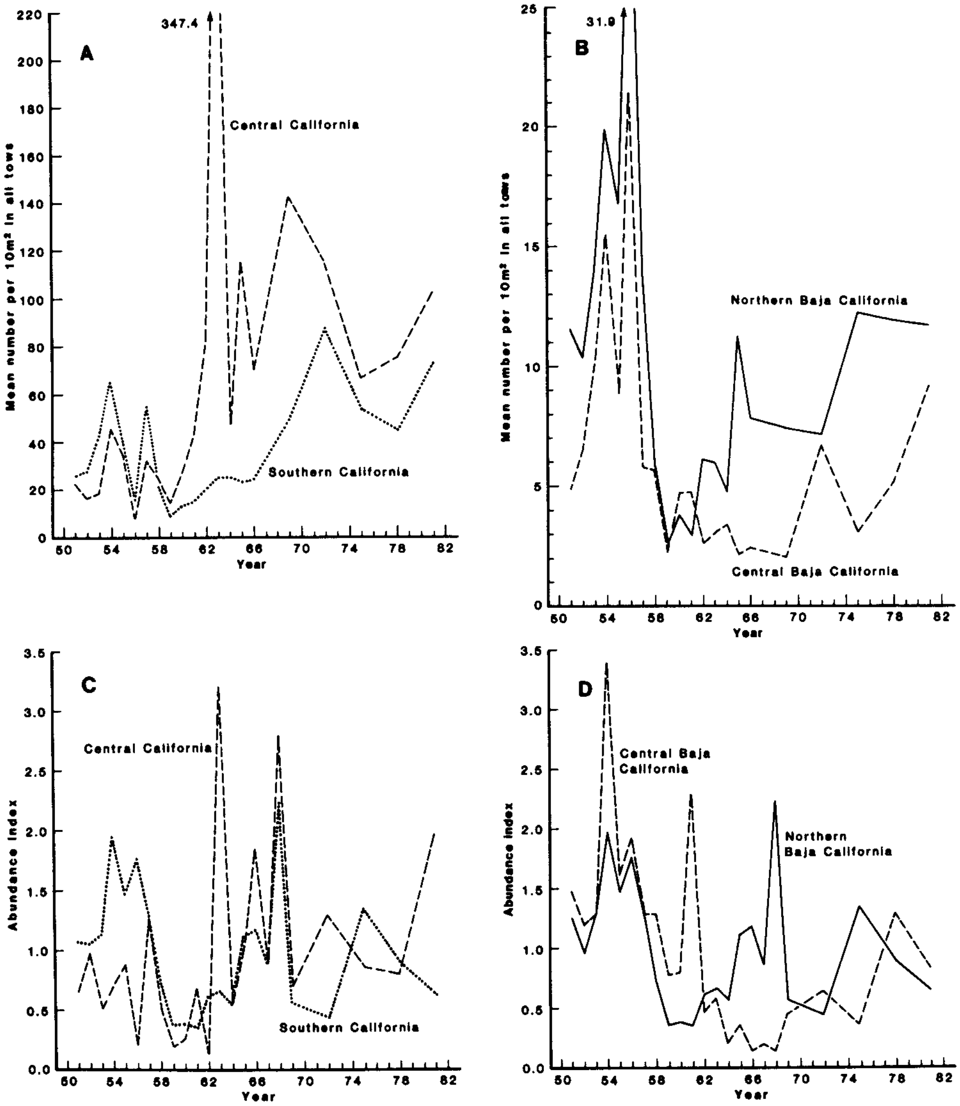

Fig. 5. Interannual variation in abundance of *Sebastes* spp. larvae in four coastal zones sampled on CalCOFI surveys off California and Baja California during 1951–1981. (A and B) mean annual abundances; (C and D) annual indices estimated by ANOVA techniques described by MacCall & Prager (1988).

dance was generally tenfold lower in Baja California (Fig. 5B) and contrasted sharply with that to the north. Values were relatively high in the 1950's until the 1958–1959 El Niño when there was a sharp decline. Abundance increased gradually in northern Baja California but remained low throughout the 1960's in central Baja California.

To compensate for uneven seasonal and areal coverage on annual CalCOFI surveys, an ANOVA method developed by MacCall & Prager (1988) was used to predict missing data and normalize interannual abundance values. Trends in ANOVA abundance indices (Fig. 5C, D) were similar to those derived from mean values (Fig. 5A, B). Depressed values during the 1957–1959 El Niño were evident for California and Baja California as was the strong peak in 1963 in central California (Fig. 5C, D). Indices for both central and southern California peaked in 1968 and then declined to near average values through most of the 1970's. In Baja California, indices declined sharply during the 1957–1959 El Niño and then showed opposite trends in northern and central Baja California. In 1961, a strong peak in central Baja California contrasted with a low index for northern Baja California; in 1968, a strong peak in northern Baja California coincided with an extremely low index for central Baja California.

Except for the depressed abundance during the 1958–1959 El Niño, when temperatures were high and zooplankton abundance was low, a relationship between interannual variation in environmental conditions (Chelton et al. 1982, Roesler & Chelton 1987) and abundance of *Sebastes* larvae is not evident. Trends and short-term shifts in abundance of larvae reflect fluctuations in biomass of dominant species and also variability in survival of early larvae. These result from vastly different interactions with physical and biotic environmental parameters and can only be understood by integrated studies of adult population processes and survival of larvae.

Study of abundance patterns of larvae for individual species has been impeded by the difficulty in identifying larvae (see Kendall 1991). Overall distribution patterns (Fig. 6) for species identified in CalCOFI plankton surveys are markedly different (Moser et al. 1977, 1985). Larvae of *S. aurora* and *S. paucispinis* have broad distributions from central Baja California to well north of the sampling region. *Sebastes jordani* larvae are more coastally and latitudinally confined, while *S. levis* larvae are restricted largely off the outer coast of southern California. *Sebastes macdonaldi* occurs primarily off Baja California. It is the only species of *Sebastes* whose adults and juveniles have been found there and in the Gulf of California; however, its larvae have not been reported from the latter (Moser 1972). *Sebastes cortezi* is an endemic species found along the chain of islands on the western side of the Gulf of California where strong tidal currents produce relatively low surface temperatures. The distributional differences among species contribute to the observed differences in seasonality of different geographic regions. Because different species probably respond to environmental features in different ways, it may be difficult to assess the role of environmental factors in interannual variation in abundance at the generic level (Fig. 5). MacGregor (1986) described seasonal and interannual abundance for larvae of four species (*S. paucispinis, S. jordani, S. levis* and *S. macdonaldi*) taken on several CalCOFI surveys. A complete description of any single species for the entire time series, however, awaits a comprehensive reexamination of CalCOFI samples containing *Sebastes* larvae.

Vertical distribution

The vertical distribution of *Sebastes* spp. larvae was described by Ahlstrom (1959) from 22 series of opening/closing nets taken at 15 stations off southern California and Baja California. Larvae were mainly in the upper mixed layer and within the thermocline but not below it; 97% were at depths shallower than 80 m, and 75% occurred between about 25 and 80 m depth. Boehlert et al. (1985) found a relatively shallower distribution for *Sebastes* spp. larvae off Oregon where the thermocline also was shallower (< 30 m); 95% of the larvae were at less than 40 m, and 70% occurred within the 5–30 m range. Similarly, Sanchez & Acha (1988) found preflexion larvae of *S. oculatus* (*S. capensis*?)

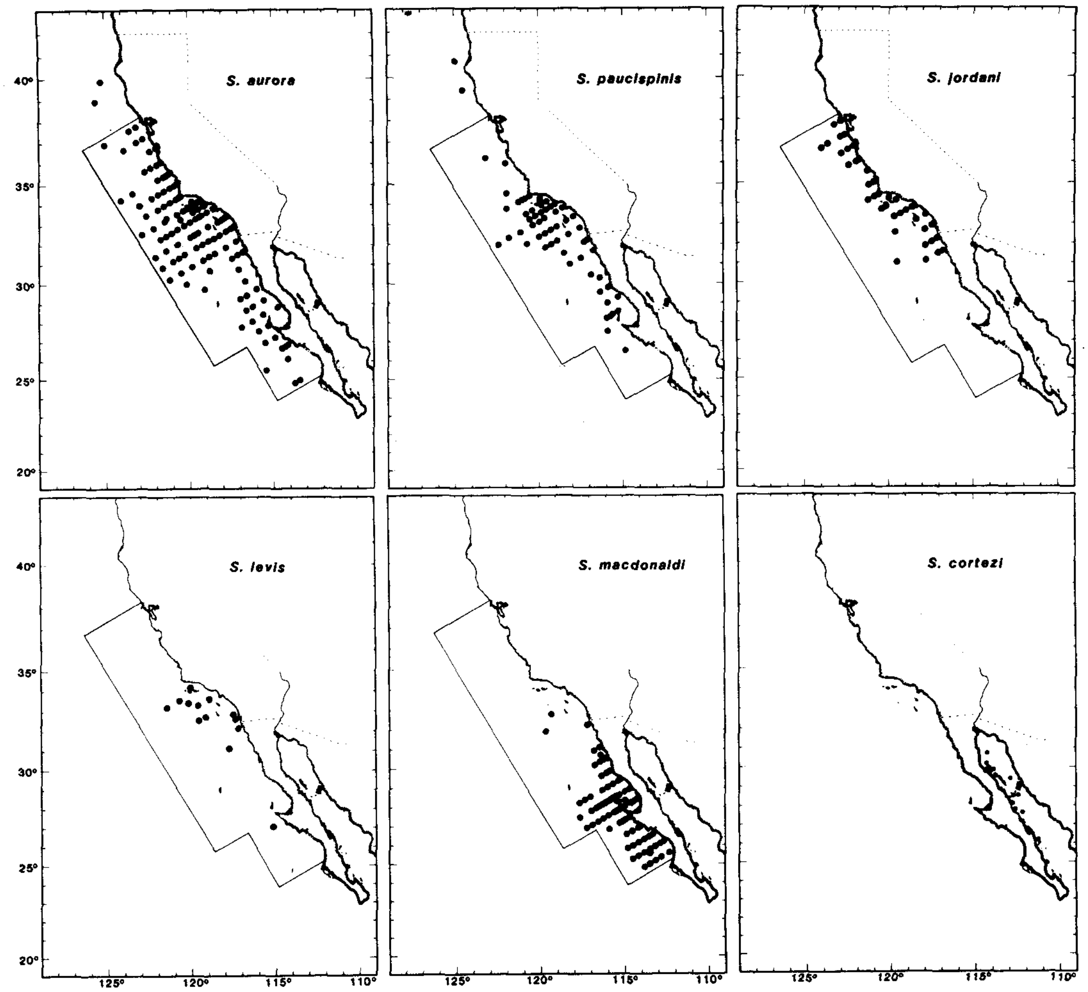

Fig. 6. Occurrences of larvae of six species of *Sebastes* on annual CalCOFI surveys (*S. aurora*, 1951–1981; *S. paucispinis*, 1953 and 1956; *S. jordani*, 1966; *S. levis*, 1951, 1955, 1968, 1969; *S. macdonaldi*, 1953, 1960, 1965, 1966; *S. cortezi*, 1956, 1957; area of frequent station occupancy is outlined; modified from Moser et al. 1977, 1985).

limited to the 10–30 m stratum over the Patagonian shelf. Kuwahara & Suzuki (1983) found an even shallower distribution of three species of *Sebastes* larvae in Wakasa Bay, Japan. More than 90% of the larvae of *S. marmoratus* and *S. pachycephalus*, and all *S. oblongus* larvae, occurred in the 0–25 m stratum. Approximately 63% of *S. marmoratus*, 87% of *S. pachycephalus* and 95% of *S. oblongus* were caught in surface tows.

Pommeranz & Moser (1987) reported on the distribution of eggs, embryos and larvae of northern anchovy, *Engraulis mordax*, taken in a series of 63 discrete depth tows at two stations off southern California in March-April 1980. Their shelf station was 2.4 nmi offshore over a bottom depth of about 350 m, and their offshore station (38.4 nmi offshore) was over a basin of about 1200 m depth. We analyzed catches of *Sebastes* larvae in these tows for the present paper. About 90% of the larvae of *Sebastes* spp. occurred at depths shallower than 80 m at both sta-

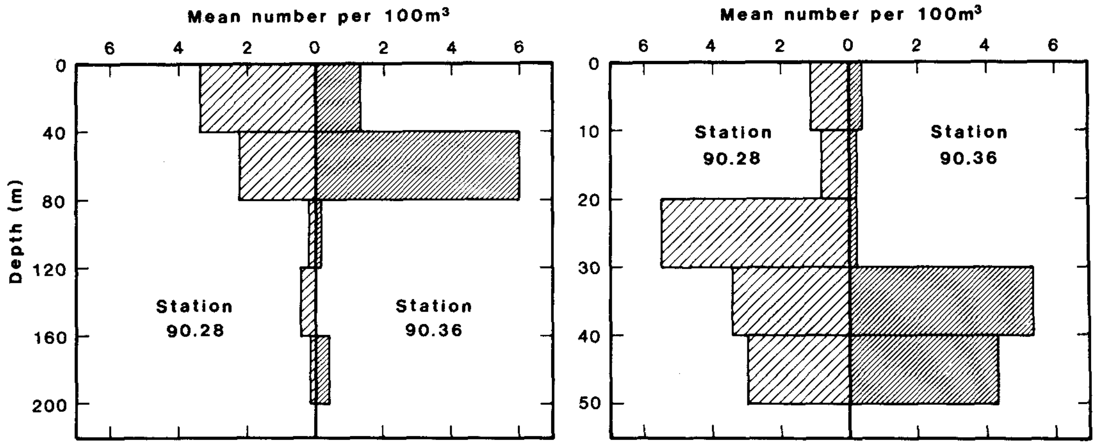

Fig. 7. Vertical distribution of *Sebastes* spp. larvae at two CalCOFI stations off southern California. Broad cross-hatching indicates the shelf station (Sta. 90.28) over a bottom depth of 350 m; narrow cross-hatching indicates the offshore station (Sta. 90.36) over a bottom depth of 1200 m.

tions (Fig. 7). The two stations differed markedly at the 20–30 m stratum; this stratum contained a large proportion of the total larvae at the shelf and virtually no larvae offshore. This difference corresponded with thermocline depth (about 20–40 m at the shelf station and 30–50 m at the offshore station). Interestingly, no larvae were taken at the surface at the offshore station, whereas the shelf station had a mean of 1.47 larvae per 100 m^3 in the neuston, 97% of these in the day hauls. About two-thirds of the mean volume of zooplankton in the upper 200 m was in the 0–80 m stratum, and the mean volume at the shelf station was about twice that at the offshore station. There was no clear relationship between mean zooplankton volume and mean densities of larvae; however, pump samples taken concurrently at the shelf station had peak concentrations of copepod nauplii in the 20–30 m stratum (Mullin et al. 1985).

Nearshore distribution

Information on the nearshore distribution of *Sebastes* spp. larvae is available from a 7-year ichthyoplankton survey off the San Onofre Nuclear Generating Station (SONGS) in California (W. Watson personal communication). This survey measured abundance patterns of fish larvae along a transect covering 6–75 m depth (Barnett et al. 1984, Walker et al. 1987). Based on these studies, the abundance of *Sebastes* spp. larvae has a strong seasonal pattern, with a winter-spring peak and a marked increase with increasing depth. The strong seasonal peak in abundance (Fig. 8) was restricted to a single month in 1978 (March) and 1979 (January). Such a narrow spawning peak in a restricted nearshore region could result from a smaller species complement compared with deeper, more speciose habitats. The two subsequent, small peaks could represent production of larvae from less abundant species or extrusion of multiple broods from an abundant species. Interestingly, three major kinds of *Sebastes* larvae were found in the samples.

In the onshore-offshore dimension, abundance increases abruptly at the shelf break to a mean of 32 larvae per 10 m^2 of sea surface (4.5 per 100 m^3; Fig. 9A). This agrees closely with the long-term mean (36 per 10 m^2) for CalCOFI samples off southern California (see Fig. 3C). Small numbers of larvae were found in the neuston and epibenthos (Fig. 9B), but highest densities were usually in midwater. This may change with growth, however, because all juveniles and most late-stage larvae occurred in surface samples (W. Watson personal communication).

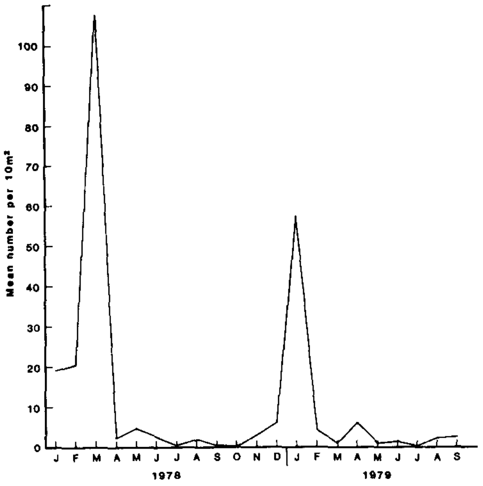

Fig. 8. Mean monthly abundance (number per 10 m^2) of *Sebastes* spp. larvae off San Onofre, California, during January 1978 to September 1979.

Ichthyoplankton assemblages

The relationship between *Sebastes* larvae and other ichthyoplankton has been examined in a number of analyses employing the recurrent group technique, a method that groups taxa based on their coincidence in time and space. When the CalCOFI time series from 1954 to 1960 was analyzed as a whole, *Sebastes* larvae were grouped with those of three abundant mesopelagic species and the Pacific hake, *Merluccius productus*, a demersal shelf and slope species (Moser et al. 1987). Analysis of individual years showed that *Sebastes* was also strongly associated with the northern anchovy, *Engraulis mordax*. A similar grouping was shown by Gruber et al. (1982) for a coastal survey in the Southern California Bight. In a survey off Washington, Oregon and northern California, Clark & Kendall (1985) showed that *Sebastes* larvae formed a group with the larvae of three deep-living flatfishes (*Glyptocephalus zachirus, Microstomus pacificus, Lyopsetta exilis*). *Sebastes* also had strong affinities with larvae of a group of mesopelagic species that contained two of the same species that were grouped with *Sebastes* larvae in the CalCOFI study. In bongo net collections from the northern Gulf of Alaska, *Sebastes* larvae were grouped with *G. zachirus* larvae and larvae of a genus of deep-living ronquils, *Bathymaster* spp.; the group formed by these species had strong affinities with two other flatfishes, the deep-living *Hippoglossoides elassodon* and the shallow-living *Psettichthys melanostictus* (Kendall & Dunn 1985). These studies generally support the contention of Richardson & Pearcy (1977) that *Sebastes* spp. larvae are distributed predominantly offshore.

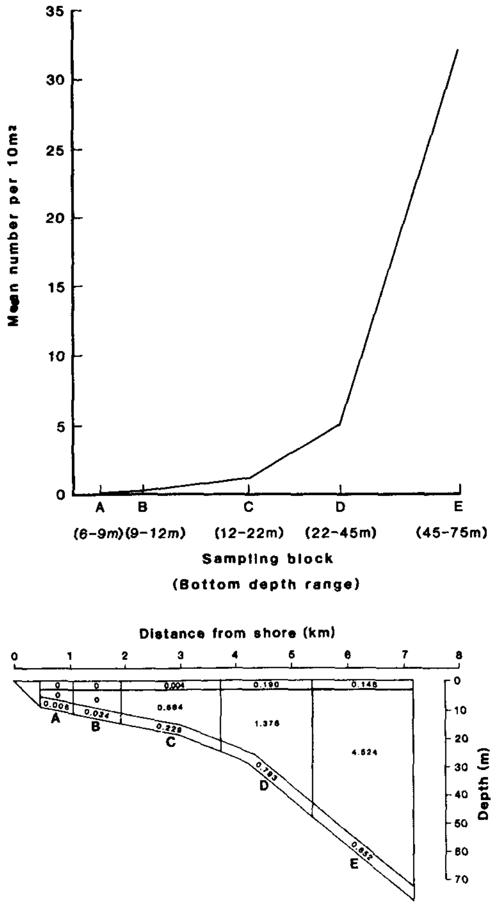

Fig. 9. Mean abundance and density of *Sebastes* spp. larvae on a transect off San Onofre, California, 1978–1983; (above) mean abundance (number per 10 m^2) for each sampling block and (below) mean density (number per 100 m^3) at surface, water column and epibenthos in each sampling block (shading highlights the stratum with the highest densities of larvae).

Growth of larvae and juveniles

Growth rates of adult *Sebastes* are variable from species to species (Chen 1971), so it would not be surprising to find significant interspecific differences in the growth of larvae and juveniles. Boehlert & Yoklavich (1983) summarized data on growth of juvenile *Sebastes* species and noted greater than sixfold differences in laboratory experiments and nearly fourfold differences in field observations of growth. In the laboratory, growth is highly dependent upon temperature; average growth of newly settled *S. melanops* at 18° C was 3.4 times that at 7° C, although individual growth was a complex function of temperature, fish size and ration (Boehlert & Yoklavich 1983). The optimum temperature for growth for both *S. melanops* and *S. diploproa* (Boehlert 1981) shifts ontogenetically. Smaller fish grow fastest at higher temperatures, with a declining thermal optimum for growth with increasing size through the juvenile period. This is in keeping with the thermal ecology of many species, because younger juvenile fishes often select higher temperatures (Norris 1963).

Growth rates in the field integrate a range of environmental features and thus may be quite different from those in the laboratory. Several studies have measured growth in the field by counting otolith growth increments, which have been confirmed as daily in *S. melanops* by Yoklavich & Boehlert (1987). Studies using these techniques on larvae and pelagic juveniles of *Sebastes* demonstrated growth rates to be linear over the sizes measured (Fig. 10). The range of growth rates among species was as great as that measured in the laboratory, with the slowest measured for *Sebastes* spp. from the Atlantic (0.109 mm per day, Penney & Evans 1985) and the fastest for *S. paucispinis* (approximately 0.666 mm per day; D. Woodbury personal communication). *Sebastes jordani* has the second fastest growth observed (0.568 mm per day), despite having one of the smallest adult sizes in the genus.

Although juvenile growth rates measured in the laboratory have been comparable to those in the field, growth rates of larvae in laboratory rearing trials have not been as fast, especially with eastern North Pacific species. Kendall & Lenarz (1987) summarized rearing trials for seven species through 30–40 days and noted growth rates of 0.08–0.14 mm per day. These experiments cannot be considered characteristic of field growth, however, because mortality rates were typically very high and feeding conditions of larvae often less than optimum. This contrasts with the success of rearing *S. schlegeli* in Japan. Hoshiai (1977) noted growth rates of 0.385 mm per day in rearing trials of this species through 50–70 days of age. This species has a larger egg and larger size at parturition (6.89 mm) and thus rearing may be facilitated by the ability to use larger foods.

Feeding of larvae

Feeding has been examined for the planktonic larvae of several species of *Sebastes*. They appear to be diurnal feeders, and the percentage of larvae feeding decreases with increasing depth (Marak 1974). Sumida & Moser (1984) noted feeding during 0800–1600 Pacific standard time for *S. paucispinis*. They interpreted the decreasing stomach contents after this time to characterize a rapid evacuation rate (compared to gadoid larvae). Diurnal incidence of feeding in three species of *Sebastes* larvae from the nearshore waters of Japan was nearly 100% (Kuwahara & Suzuki 1983).

Generally, *Sebastes* larvae have been characterized as opportunistic feeders. Earliest larvae typically feed on copepod nauplii and to a lesser extent on invertebrate eggs, as confirmed in the North Atlantic (*Sebastes* spp., redfish complex; Bainbridge & McKay 1968, Marak 1974), in the western Pacific (*S. pachycephalus*, *S. marmoratus* and *S. oblongus*; Kuwahara & Suzuki 1983) and in the eastern Pacific (*S. paucispinis*; Sumida & Moser 1984). Larger larvae continue to feed on nauplii but also begin to take copepodites, adult copepods, euphausiids and limited numbers of other larger prey. Although most of the studies cited above observed an increase in the largest size of prey consumed with increasing growth, smaller prey items remain important in larger larvae, suggesting prey encounter rather than selectivity as the important feature of larval feeding in the genus (Kuwahara & Suzuki 1983). Bainbridge & McKay (1968) described the feeding of redfish and cod larvae; at equivalent sizes, the cod larvae took larger

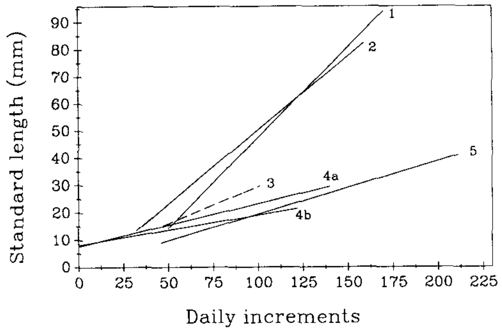

Fig. 10. Growth of field-collected pelagic *Sebastes* larvae and juveniles from studies using daily growth increments. In all cases, lines represent regressions within the bounds of length and age actually measured: 1 – *S. paucispinis* (D. Woodbury personal communication, N = 260); 2 – *S. jordani* (D. Woodbury personal communication, N = 302); 3 – *S. melanostomus* (Moser & Ahlstrom 1978, N = 4); 4a, b – Atlantic *Sebastes* spp. from 1980 and 1981, respectively (Penney & Evans 1985, N = 609, 539); 5 – *S. diploproa* (Boehlert 1981, N = 21).

prey items. Sumida & Moser (1984) compared feeding in *S. paucispinis* with that of another gadoid, *Merluccius productus*, and noted a similar phenomenon. At small sizes, *M. productus* larvae had larger mouths but continued to consume larger mean prey sizes than larvae of *S. paucispinis*, even after relative mouth size in the latter became greater than in *M. productus*. Although studies of feeding in pelagic juveniles have not been published, current research in central California suggests that pelagic juveniles remain opportunistic feeders, with significant dietary overlap between species (C. Reilly personal communication).

Pelagic juvenile habitats and transition to the benthic habitat

At transformation to pelagic juveniles, different strategies become apparent for different species; much of our information is inferential, however, for these larger sizes are typically more difficult to sample. Midwater trawls take a variety of species over a range of depths, including *S. saxicola, S. diploproa, S. proriger, S. jordani, S. goodei* (Berry & Perkins 1965), *S. macdonaldi* (Moser 1972), *S. melanostomus, S. aurora,* the subgenus *Sebastomus* (Moser & Ahlstrom 1978), *Sebastes crameri, S. helvomaculatus, S. pinniger* (Richardson & Laroche 1979), *S. auriculatus, S. caurinus, S. entomelas, S. flavidus, S. hopkinsi, S. levis, S. melanops, S. miniatus, S. mystinus, S. nigrocinctus, S. paucispinis, S. rastrelliger, S. semicinctus, S. serranoides, S. serriceps* and *S. wilsoni* (Kendall & Lenarz 1987). Other gear types sample in shallower waters; dip nets and purse seines have taken other species in association with drifting kelp. In the eastern Pacific, these have included *S. diploproa, S. paucispinis, S. rubrivinctus, S. serriceps, S. dallii* (Mitchell & Hunter 1970, Boehlert 1977) and, in the western Pacific, *S. thompsoni, S. vulpes* and *S. schlegeli* (Ikehara 1977). Brodeur & Pearcy (1986), using larger purse seines off Oregon and Washington, took 15 species of *Sebastes*. Species most frequently caught were *S. melanops, S. flavidus, S. mystinus, S. jordani* and *S. entomelas*.

Shallow-water residence

Residence in surface waters is known for pelagic juveniles of many species of *Sebastes*; those aggregating around drifting objects, however, typically occur within the upper meter of the ocean. Off southern California, Mitchell & Hunter (1970) sampled *S. diploproa* juveniles around drifting kelp, *Macrocystis pyrifera*, with a small purse seine, and Boehlert (1977) sampled them with small-mesh dip nets. Pelagic juveniles are present year-round, with the smallest sizes near 12 mm standard length (SL) but reaching sizes as great as 58.7 mm SL. Length frequencies suggest that the majority of recruitment of small individuals to the surface kelp habitat occurs from August to the following March (Boehlert 1977). Daily growth increment analysis suggests that the new recruits are approximately 60–70 days of age (Fig. 10); growth during the pelagic juvenile phase, at least to a length of 42 mm and ages of about 225 days, was nearly linear (Boehlert 1981).

The transition from pelagic to benthic juveniles in *S. diploproa* generally occurs at a size threshold of about 40 mm SL based upon the presence of benthic juveniles at depths down to 200 m. Although juveniles near the size threshold are present in surface waters nearly year-round, the surface-to-benthic migration occurs seasonally, generally from late spring to early summer (Boehlert 1977). Length-frequency analysis of surface and benthic specimens, however, suggests a 2-month hiatus between the disappearance of migratory surface fish and appearance of new, small benthic juveniles. This may involve a transitory midwater residence, although relatively few specimens have been taken there (Boehlert 1977). Surface specimens of *S. diploproa,* like many other species of *Sebastes*, are distributed far offshore from appropriate benthic habitat. Animals migrating to deep water in this offshore area would not reach bottom; instead, we propose that they reside in intermediate depths (Fig. 11). Recruitment to the nearshore is problematic in this case. In summer months off southern California, the general pattern of geostrophic flow at 250 m is to the northeast (Reid 1962); residence in this layer could facilitate coastward advection.

The surface living behavior of *S. diploproa* is a specialization of shallow-water residence. Recent studies indicate that pelagic juveniles of most species of *Sebastes* occupy the upper 100 m of the water column (Brodeur & Pearcy 1986, W. Lenarz personal communication). Preliminary evidence indicates that species occupy different depth strata within this zone; for example, *S. paucispinis* occurs in the 0–30 m stratum, *S. entomelas, S. flavidus* and *S. mystinus* occur in the 30–100 m stratum, while *S. goodei* and *S. hopkinsi* occupy the entire upper 100 m (W. Lenarz personal communication). Apparently depth stratification does not reflect specialized feeding habits and may be related to different mechanisms of settlement. Submergence to the 200 m zone of shoreward geostrophic flow could provide a mechanism for some species. Species occupying strata between 30 and 200 m could be carried in the shoreward subsurface flow that compensates for offshore Ekman transport during spring and summer (Sverdrup & Fleming 1941). Species that remain in the upper 30 m may be carried shoreward by flow reversals associated with the relaxation of upwelling or by compensating onshore flows related to upwelling filaments.

Midwater residence

Midwater residence following transformation has been shown for *S. melanostomus* (Moser & Ahlstrom 1978). Analysis of *Sebastes* juveniles captured in 217 midwater trawl samples taken over deep basins off southern California and Baja California revealed a recurring group of a few common types. Of these, *S. melanostomus* accounted for 16% and was distinguished by a remarkable pattern of melanistic bars, which alternated with transparent zones on the body and fins. Length-frequency distributions showed a size progression from April to October, and daily growth rings on otoliths of specimens taken from albacore, *Thunnus alalunga*, stomachs indicated that juveniles > 30 mm SL are 3–4 months old. Although most of the samples came from oblique integrated tows to various depths (maximum 1350 m), a series of 17 discrete depth tows showed *S. melanostomus* juveniles occupying the 200–250 m depth stratum. Thus, midwater residence, primarily at 200–250 m, would subject them to shoreward geostrophic flow similar to that hypothesized for the midwater juveniles of *S. diploproa.* The barred pigment pattern possibly serves to break up the body outline and camouflage the pelagic juveniles from predators. Disruptive pigmentation is characteristic of pelagic juveniles of *S. aurora*, the subgenus *Sebastomus* and *Sebastolobus altivelis*, which all co-occurred with *Sebastes melanostomus* (Moser & Ahlstrom 1978). *Sebastolobus altivelis* may recruit directly to the deep slope and basin habitats of the adults by descending vertically (Moser 1974). Further indirect evidence of a distinct midwater residence for some species of *Sebastes* is afforded by the results of a 6-year midwater trawl survey off central California (W. Lenarz personal communication). Pelagic juveniles of *S. melanostomus, S. aurora* and the subgenus *Sebastomus* were virtually absent from a series of > 500 midwater trawl samples taken during April-June 1983–1989. Sampling was restricted to the upper 100 m (mostly at 30 m depth), well above the depth occurrence of *Sebastes* species exhibiting midwater pelagic juvenile residence.

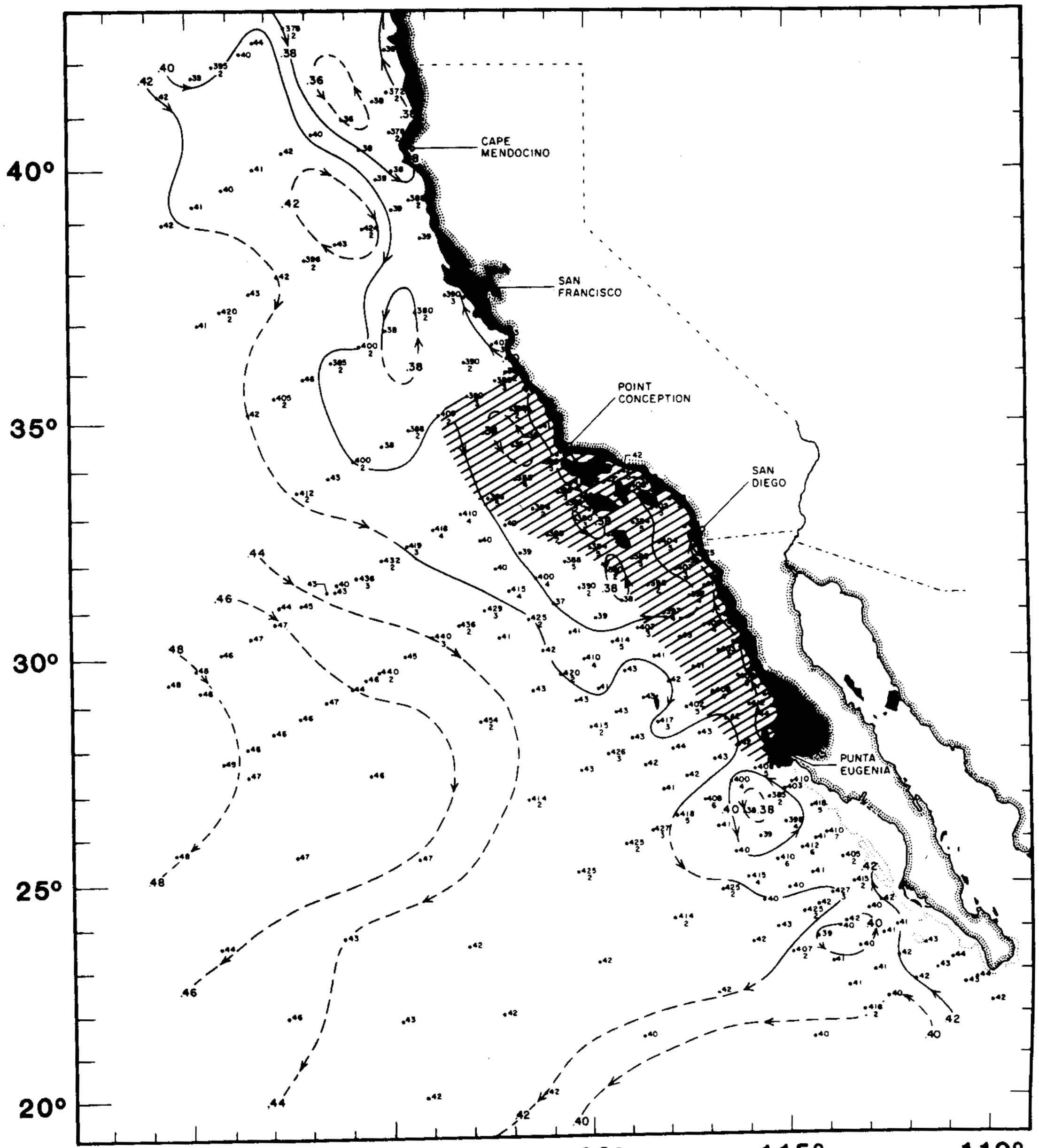

Fig. 11. Distribution of pelagic juvenile *S. diploproa* in central and southern California taken in surface collections (cross-hatched areas) in relation to mean geostrophic flow at 200 m depth during August 1950–1964; numbers indicate topography of the 200 decibar surface, in dynamic meters, relative to the 500 decibar surface; contour interval is 0.02 dynamic meter; darkened area along coast indicates appropriate benthic habitat for settlement (chart from Wyllie 1966).

Nearshore residence

The final hypothesized mechanism, and one perhaps most poorly known for *Sebastes*, is utilization of nearshore areas with minimum offshore dispersal. This has not been carefully investigated, because larvae are generally accepted to be important in offshore assemblages (Richardson & Pearcy 1977). Recent research on localized distributions of fish larvae (Marliave 1986) has resulted in new ideas about retention in the very nearshore zone, which is typically sampled poorly in ichthyoplankton investigations. Anderson (1983) suggested that certain nearshore species recruit to kelp canopy habitats as large larvae or very early juveniles at relatively young ages. This may also occur in Japanese species. Senta & Kinoshita (1985) noted the presence of small *S. inermis* in benthic nearshore stations. Many Japanese species are born at larger sizes than eastern North Pacific species; newly born *S. pachycephalus* are about 7 mm total length (TL) and are ready to settle to the bottom at an age of 25 days at 13 mm TL (Siokawa & Tsukahara 1961). This larger size at birth may facilitate the nearshore mechanism by minimizing the planktonic period.

Recruitment mechanisms

There is little question that *Sebastes* populations are characterized by significant interannual variability in recruitment strength, as suggested by abundance patterns of larvae (Fig. 5), juvenile recruitment (Mearns et al. 1980) and year-class strength differences after recruitment to the fishery (Norton 1987). The source of this recruitment variability could occur during several steps. First, reproductive output may vary from year to year within a species in response to food availability and environmental factors. Larson (1991) describes the dynamics of fat storage, which the female utilizes during the period of gestation (as opposed to the period of vitellogenesis observed in most fishes). Lenarz & Echeverria (1986) noted decreased fat deposition in El Niño years. Viviparous poeciliids may decrease the level of additional nutrition to embryos in times of adverse environmental conditions (Trexler 1985). This mechanism, if found in *Sebastes*, might explain either lower reproductive output or higher early mortality of smaller, less developed larvae, which would be consistent with the lower abundances of larvae during El Niño in the late 1950's (Fig. 5). The second source of recruitment variability would be mortality of larvae from either starvation or predation. Until improved species identification is possible, however, this source will be difficult to evaluate. Certainly species-specific responses to environmental and biotic effects differ (Norton 1987), and analysis based on generic-level characteristics will contribute relatively little to our understanding.

Advective sources of mortality for early larvae are suggested by the distant offshore distribution of *Sebastes* larvae and pelagic juveniles. There is some relationship between year-class strength variability and environmental conditions for at least some species; Norton (1987) suggested that successful year classes of widow rockfish, *S. entomelas*, may occur in years of increased onshore transport, possibly carrying pelagic larvae towards shore. This agrees with the ideas posed in Parrish et al. (1981). The vertical distribution of larvae, however, suggests that they are relatively rare in the shallow Ekman layer (Fig. 7) and may not be subject to offshore transport during upwelling. Moreover, the majority of offshore transport may occur through localized transport by jets (Mooers & Robinson 1984) or eddies (Simpson 1987). The latter may play an important role in the survival of *Sebastes* larvae and of other groundfishes that have been advected offshore. There is a remarkable overlap between the offshore field of mesoscale eddies (Lynn & Simpson 1987) and the zone of maximum concentration of copepod nauplii (Arthur 1977). As a result of high prey concentrations, larvae entrained to this zone could experience enhanced survival rather than increased mortality and offshore advection would be adaptive if linked with successful benthic recruitment of survivors. Further investigation of this hypothesis should focus on (1) the dynamics of phytoplankton, zooplankton and ichthyoplankton components of offshore eddies, (2) seasonal and interannual variations in the offshore eddy field and (3) the potential relationship of these variations with recruitment variations.

Localized eddies and other hydrographic features may be generated by headlands, seamounts and other complex topography (Boehlert & Genin 1987), and spawning in these areas might enhance retention of larvae. Hewitt (1981), for example, proposed that eddies play a role in speciation in the California Current region. On a smaller scale, potential retention areas associated with topography could result in subpopulations of some species (Iles & Sinclair 1982). If this mechanism exists for *Sebastes*, however, one would expect localized centers of enhanced or, conversely, depauperate benthic recruitment, as has been observed for sea urchins, *Strongylocentrotus purpuratus*, off the California coast (Ebert & Russell 1988). Studies of benthic juvenile recruitment will require a much broader geographic extent to evaluate this hypothesis.

Successful recruitment of pelagic juveniles to the benthic habitat may involve factors different from those affecting larvae. The pelagic juvenile phase may last several months to a year (Boehlert 1977). The broad distribution of pelagic juveniles relative to the area for possible settlement is evident in studies of albacore diets (Powell & Hildebrand 1950). Because the juvenile habitats of most species are poorly known, we cannot exclude the possibility that some species may have extended offshore distributions with concomitantly long pelagic juvenile phases. In purse seine collections, for example, Brodeur & Pearcy (1986) captured relatively large juveniles and adults of some species. Still, benthic recruitment of many species occurs with seasonal regularity (see Love et al. 1991) and thus is unlikely a stochastic process. Species such as *S. diploproa*, with a pelagic juvenile residence in surface waters, may use a shoreward transport mechanism such as that proposed by Shanks (1983). Species in midwater may use directed, shoreward swimming arising from avoidance of lower temperatures characteristic of fronts associated with passing internal waves, a mechanism suggested by Norris (1963) for *Girella nigricans*. Other directed movements such as orientation to magnetic or electric fields cannot be excluded. Comparative studies on species with different mechanisms will contribute a great deal to our understanding of settlement and recruitment in *Sebastes*.

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