Abundance and distribution of rockfish (Sebastes) larvae in the Southern California Bight in relation to environmental conditions and fishery exploitation

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ABUNDANCE AND DISTRIBUTION OF ROCKFISH (*SEBASTES*) LARVAE IN THE SOUTHERN CALIFORNIA BIGHT IN RELATION TO ENVIRONMENTAL CONDITIONS AND FISHERY EXPLOITATION

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ABSTRACT

In this study we describe seasonal, interannual, and long-term changes in the larval abundance of six rockfish (*Sebastes*) taxa in relation to spawning biomass and to variability in the ocean environment. We used rockfish larvae from a total of 11,472 CalCOFI plankton tows taken in the Southern California Bight from 1951 to 1998. Species included in the study were bocaccio (*S. paucispinis*), cowcod (*S. levis*), shortbelly rockfish (*S. jordani*), aurora rockfish (*S. aurora*), and splitnose rockfish (*S. diploproa*). Interannual trends in occurrence and abundance are described for each species in relation to biomass trends of adults and to changes in the ocean environment caused by ENSO events and by the cool and warm regimes of the Pacific Decadal Oscillation (PDO). Larval abundance of *S. paucispinis* and *S. levis* declined abruptly during the shift to a warm regime and continued to decline, as did the adult biomass. Abundance of *S. jordani* larvae declined during the regime shift but increased after the 1982–83 El Niño, reaching the peak value for the time series in 1991. Within each regime, minor declines in larval occurrence and abundance were associated with ENSO episodes. The tightly grouped series of three La Niña events in 1970–76 immediately preceded the shift from the cool to the warm regime late in 1976 and may have contributed to the marked decline in larval occurrence and abundance that, for most species, continued through the 1982–83 El Niño. The decline in larval rockfish abundance during the regime shift may be a consequence of the decline in rockfish populations caused by the expanding rockfish fishery; however, the ocean environment may be a causal factor, because larvae of *S. jordani*, an unexploited species, underwent declines similar to those of fishery target species during that period.

INTRODUCTION

Sebastes, with over 65 species, is the most speciose genus of fishes of the west coast of North America, from Cabo San Lucas, Baja California Sur, Mexico, to the Bering Sea. The genus is well represented in the north-

western Pacific, with at least 25 species in addition to the several (e.g., *S. aleutianus, S. alutus, S. borealis*) that occur on both Asian and North American coasts (Masuda et al. 1984). Numbers of species decrease to the south of California, and only one, *S. macdonaldi*, continues into the Gulf of California from the Pacific coast. Six other species are restricted to the gulf, and at least two species are found off the temperate coasts of Chile, Argentina, and South Africa (Chen 1971, 1975, 1986; Rocha Olivares 1999a, b). Similarly depauperate is the North Atlantic, with only four species representing the genus (Eschmeyer 1998). The Southern California Bight (SCB), with its continental borderland, offers prime habitat for more than 50 rockfish species (Miller and Lea 1972; Eschmeyer et al. 1983). Found here are southern representatives of rockfish species whose distributions are primarily to the north; northern representatives of more southern species; and a large number of species whose distributions are centered off southern California.

In addition to a large species complement and extraordinary diversity of size, form, and color, *Sebastes* is characterized by viviparous reproduction (Boehlert and Yoklavich 1984), relatively slow growth rates for most species (Phillips 1964; Love et al. 1990; Lea et al. 1996), and variable recruitment with occasional dominant year-classes (Ralston 1998). The type of viviparity found in rockfishes ensures a high reproductive potential. Fecundity is relatively high (e.g., >2 million young per brood in large species); some species produce more than one brood per year; and the young are nurtured within the ovarian cavity of the mother. The brood is released at the first-feeding larva stage, thus avoiding the mortality associated with the egg and yolk-sac larva stages of oviparous fishes (Moser 1967a, b; Boehlert and Yoklavich 1984; Wyllie Echeverria 1987; Moser and Boehlert 1991; Wourms 1991).

On the west coast of the United States, rockfishes have supported commercial and recreational fisheries since the latter half of the nineteenth century and have continued as a mainstay of fresh fish markets since that time (Lenarz 1987). Total rockfish landings in California were approximately 7,000 metric tons (t) per year from 1950 to the mid 1970s, when they increased sharply,
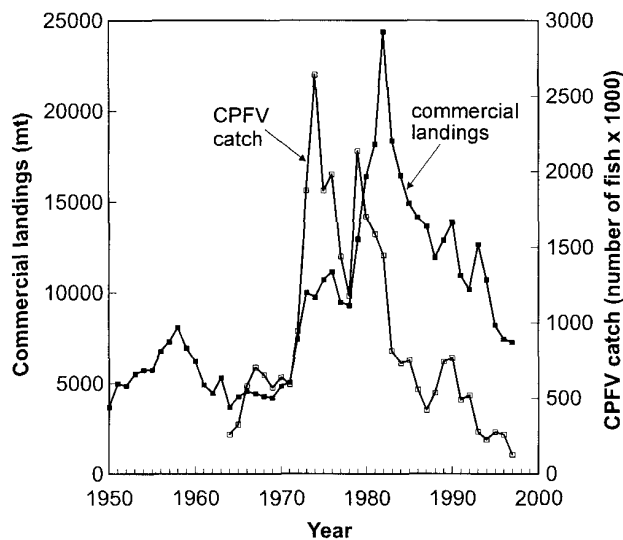
Figure 1. Total California rockfish landings by the commercial fleet in California and total commercial passenger fishing vessel (CPFV) catch for southern California. Data for commercial landings are from Thomas Barnes, California Department of Fish and Game (pers. comm.); data for CPFV catch are from California Department of Fish and Game CPFV logbooks (see Hill and Barnes 1998). CPFV catch is approximately one-half of the total recreational catch.

peaking at >24,000 t in 1982, and subsequently declined at a steady rate to the present (fig. 1). A similar trend was evident in rockfish catches of the commercial passenger fishing vessel (CPFV) fleet off southern California (fig. 1). Often an occasional highly successful year-class becomes the primary component of the fishery for that species for many years, as illustrated by the 1970 year-class of widow rockfish (S. entomelas; Lenarz and Gunderson 1987; Ralston and Pearson 1997) and the 1977 year-class of S. paucispinis (MacCall et al. 1999).

Rockfish typically are the third or fourth most abundant category of fish larvae taken on annual CalCOFI plankton surveys (Moser et al. 1993). Identification of Sebastes larvae to species is difficult because of the large number of species and the relatively few unique characters available for distinguishing the larvae (Matarese et al. 1989; Moser 1996). We routinely identify larvae of seven Sebastes species in CalCOFI plankton tows and now have assembled complete time series for four of these: bocaccio (S. paucispinis), cowcod (S. levis), aurora rockfish (S. aurora), and shortbelly rockfish (S. jordani). The time series are for the SCB region (present survey pattern) from 1951 to 1998.

Despite the high reproductive potential, decreasing catches indicate that stocks of most rockfish species have declined markedly over the past three decades. The decline is so severe for some species (e.g., S. paucispinis, S. levis) that extensive stock rebuilding measures are required (MacCall et al. 1999; Butler et al. 1999). The generally poor condition of rockfish stocks, documented

by assessments of individual species, points to a crucial need for comprehensive management of eastern Pacific rockfishes (Ralston 1998). In addition to overfishing, poor reproduction and recruitment have been suggested as causal factors in this decline.

The role that ocean environment may play in the decline of rockfish stocks has only recently been investigated (Lenarz et al. 1995; Ralston and Howard 1995; Yoklavich et al. 1996; Love et al. 1998) but may be important when considering future management options. Environmental change is the hallmark of the eastern Pacific, which is well known for its distinct high-frequency and low-frequency oscillations in ocean temperature. The El Niño–Southern Oscillation (ENSO) produces a series of alternating warm (El Niño) and cold (La Niña) episodes in the equatorial Pacific with durations of two to seven years. When these equatorial events are particularly intense and persistent they may affect temperature and other aspects of the ocean environment as far north as the Bering Sea. Hollowed et al. (1998) coined the term "Niño North" for El Niño events that result in maximum warming at higher latitudes, and identified five of these (1957–58, 1963, 1982–83, 1993, and 1997) in the last half-century. Although there have been almost as many La Niña as El Niño events in the past 50 years, fewer of these have affected higher latitudes of the northeastern Pacific. Particularly important is the 1954–56 event, which produced cold ocean conditions throughout the northeast Pacific, and the tightly grouped series of La Niña events between May 1970 and March 1976, which caused prolonged cold ocean temperatures north of the tropics for a half-decade. A moderate La Niña occurred in 1988–89 and a stronger one began in mid-1998. Its effects in the California Current region remained through 1999.

The low-frequency oscillation in the North Pacific known as the Pacific Decadal Oscillation, or PDO, is related to basin-scale changes in atmospheric pressure and particularly to the intensification and position of the Aleutian Low Pressure System (Mantua et al. 1997). The result is a 20–30-year cycle of alternating cool and warm ocean regimes. The northeastern Pacific was anomalously cool in 1900–1924, warm in 1925–1946, cool in 1947–1976, and warm from 1977 to 1999. Among the apparent biological consequences of these regime shifts are basinwide changes in primary and secondary production and in the abundance of eastern Pacific fish stocks. Plankton production in the central Pacific and in the Gulf of Alaska increased dramatically after the regime shift of 1977, while the opposite was true for west coast waters from northern Baja California to Washington (Venrick et al. 1987; Brodeur and Ware 1992; Polovina et al. 1995; Roemmich and McGowan 1995a, b; Ware 1995; Hayward 1997; McGowan et al.
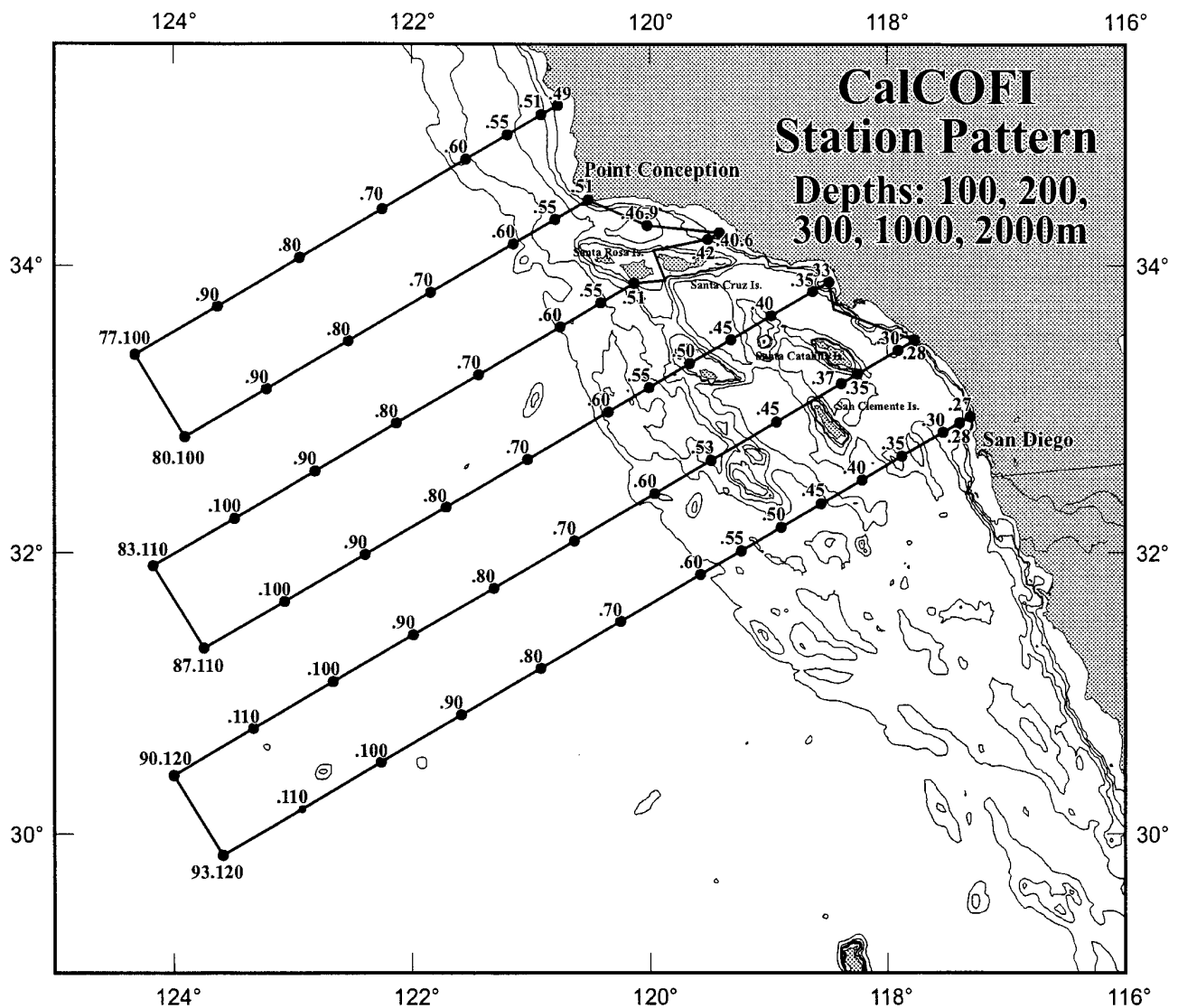
Figure 2.   Station pattern for CalCOFI survey cruises from 1985 to the present, and bathymetry of the survey region. Isobaths are 100, 200, 500, 1000, and 2000 m.

1998). Groundfish and salmon stocks increased markedly in the Gulf of Alaska and neighboring Bering Sea, whereas these stocks generally declined markedly in west coast waters (Francis and Hare 1994; Mantua et al. 1997; Francis et al. 1998; Hollowed et al. 1998).

In this study we describe seasonal, interannual, and long-term changes in the larval abundance of six rockfish taxa in relation to adult biomass trends and to variability in the ocean environment, and we present information on the role that these factors may play in the dynamics of rockfish populations.

METHODS

We used larval rockfish counts from a total of 11,472 CalCOFI plankton tows taken in the area of the present CalCOFI survey pattern, which is essentially the SCB (fig. 2). This included all standard survey tows taken since 1985, when occupancy of the present pattern was initiated on a quarterly basis. Tows used prior to 1985 are a subset from wider-ranging surveys, conducted on a monthly or quarterly basis, typically from central California to southern Baja California (Hewitt 1988; Moser et al. 1993, 1994). Ichthyoplankton and station data for all cruises are summarized in a series of data reports (see Charter et al. 1999 and previous reports in the series). Hydrographic data from these surveys are published by the Scripps Institution of Oceanography (see Univ. of Calif., SIO 1999 and previous reports in the series).

Standard oblique tows from 1951 through 1968 employed a 1 m ring net towed to a depth of 140 m. Begin-

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ning in 1969 the nominal tow depth was increased to 210 m, and the 71 cm bongo net (McGowan and Brown 1966) replaced the ring net from the last cruise in 1977 to the present. Silk mesh (0.55 mm opening), used from 1951 to 1968, was replaced by nylon mesh (0.505 mm opening) in 1969. Detailed descriptions of gear and methods are given by Kramer et al. (1972) and Smith and Richardson (1977). Ohman and Smith (1995) summarized historical CalCOFI zooplankton methods and calibration factors for the various gear types.

Samples were preserved in 5% formalin aboard ship and returned to the laboratory, where zooplankton displacement volumes (expressed as ml per 1000 m^3) were determined, and the fish eggs and larvae were removed (Kramer et al. 1972). Rockfish larvae were identified as a composite taxon from 1951 to 1969. Beginning in 1972 larvae of *S. aurora*, *S. jordani*, *S. levis*, *S. macdonaldi*, and *S. paucispinis* were identified; identification of *S. diploproa* began in 1987. Archived CalCOFI samples for the years 1951–68 were reexamined in 1997 and 1998 in order to obtain complete time series for these species. Only those stations represented in the current survey pattern were examined for these years, and *S. goodei* was added to the list of identified larvae. Thus, complete time series for 1951–98 are available for *S. aurora*, *S. jordani*, *S. levis*, *S. macdonaldi*, and *S. paucispinis*. There is a gap in the series for *S. diploproa* from 1972 through 1986, and data on *S. goodei* larvae are available only for the years 1951–69. Methods used for identifying the species in this study are documented in Moser 1996 and Sakuma and Laidig 1995.

Larval abundance is expressed as the number of larvae per 10 m^2 of surface area determined by multiplying the larval count by the standard haul factor (SHF = [(tow depth/volume of water filtered) · 10]) determined for each tow. Larval occurrence is expressed as the proportion of positive tows for a given species. All 11,472 tows were used to calculate the proportion of positive tows or mean abundance if larvae of a given taxon occurred over the entire present survey pattern and during all months. A subset of the total tows was used when a taxon's distribution was limited to a portion of the survey pattern or was seasonally limited. Temperatures used in this study (surface bucket temperature or 10 m temperature, depending on which was available) were those associated with each of the net tow stations. Temperatures were available for 70% of the stations in the study, and plankton volumes were available for all stations.

RESULTS

Areal Distribution

The inner third of the current CalCOFI survey pattern overlies the continental borderland off southern California, a region of complex topography that includes the mainland continental shelf and slope, approximately 13 deep-water basins, and numerous islands and banks (submerged islands) and their shelves and slopes (fig. 2). This region offers a wealth of habitats for rockfish species, as reflected in the abundance of larvae at these stations (figs. 3 and 4). The ocean overlying the continental borderland is higher in surface nutrients and chlorophyll in comparison to the offshore region and is physically and biologically complex (Hayward and Venrick 1998). The distinct mesoscale oceanographic features of the region and the complex topography with which they interact form a uniquely dynamic and productive habitat.

Sebastes paucispinis larvae had relatively high average abundances in the Point Conception and Channel Islands areas on lines 77 to 90 out to station 60, the margin of the continental borderland (fig. 3A). Low average numbers of larvae were present on all lines seaward of station 60, out to station 90, and larvae occurred as far seaward as station 83.110 (~200 nmi from the borderland slope margin). Approximately 76% of the occurrences and 88% of the total larvae were in an area bounded by station 60 on lines 77 to 90. Station 83.55, southwest of Santa Rosa Island, had the highest average count (11.3 larvae per 10 m^2) for the time series, followed by relatively high counts at station 87.50, northeast of San Nicholas Island, and 80.55, southwest of Point Conception.

Sebastes levis larvae, the rarest species in this study, had a somewhat more restricted distribution than *S. paucispinis*, with highest average numbers at a cluster of stations in the northern Channel Islands area (fig. 3B). Approximately 68% of the occurrences and 76% of the larvae were in an area bounded by lines 80 and 87, seaward to station 55. The peak average abundance (0.29 larvae per 10 m^2) was at station 83.42 in the Santa Barbara Channel; however, four other Channel Islands stations (82.46.9, 83.55, 87.40, and 87.50) had average values nearly as high. There were only four positive tows seaward of the borderland margin. After the regime shift, larvae occurred at only three stations in the Santa Barbara Channel (station 82.46.9) and Point Conception area (80.51 and 80.55).

Highest average larval abundances of *S. aurora* larvae were found at a group of stations (stations 51–70 on line 77, stations 55 and 60 on line 80, and station 83.60) in the Point Conception area, with the highest average value on station 77.55 (fig. 3C). On lines south of line 83, larvae were relatively evenly distributed at stations seaward to station 60, although average values were low on shelf stations nearest the coast. The distribution of *S. diploproa* larvae was similar to that of *S. aurora*, with highest average values in a cluster of stations in the Point Conception area and a relatively even distribution over the remainder of the survey pattern out to station 60
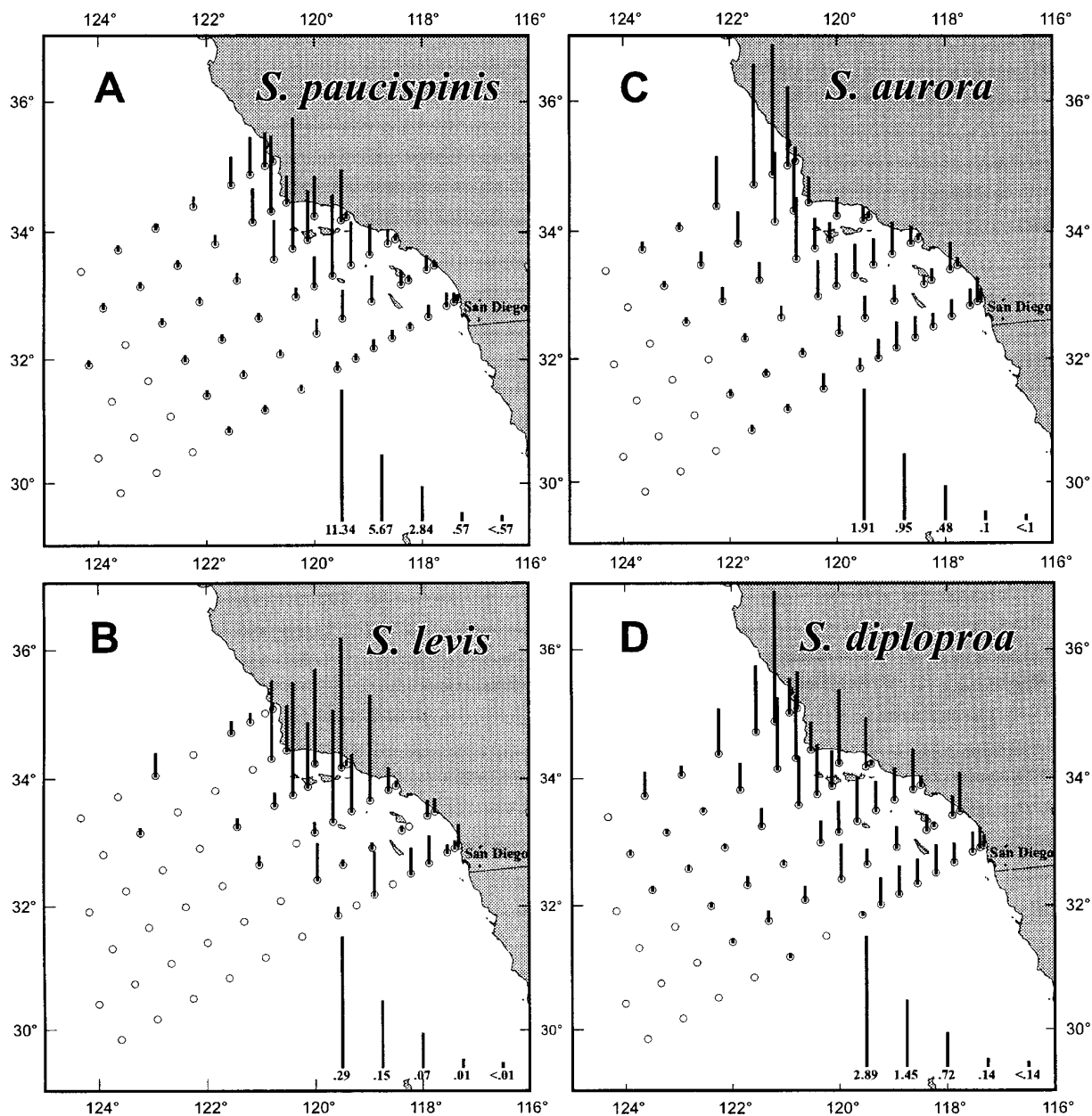
Figure 3.   Average abundance of *Sebastes* larvae at nominal CalCOFI stations from 1951 to 1998. *A, S. paucispinis,* bocaccio; *B, S. levis,* cowcod; *C, S. aurora,* aurora rockfish; *D, S. diploproa,* splitnose rockfish. Length of vertical bars indicates average larvae per 10 m^2 scaled proportionally from the station with the highest value.

(fig. 3D). As for *S. aurora*, larvae extended relatively farther seaward (at least to station 70 on lines 77–83) in the region of the Point Conception plume. Larval *S. diploproa*, in contrast to *S. aurora*, had relatively higher average values at stations nearest the mainland coast.

S. *jordani* larvae, the most abundant species in this study, were concentrated closer to the coast compared to other species (fig. 4A). Peak abundance was at station

77.51 north of Point Conception; other stations with relatively high average abundance were proximal to, or shoreward of, the Channel Islands. Occurrences, with low average abundance, were recorded at most stations seaward to station 90.

Larvae of *Sebastes* spp. (unidentified *Sebastes* larvae in aggregate, constituting 76% of total rockfish larvae in the samples) occurred at nearly all stations in the survey
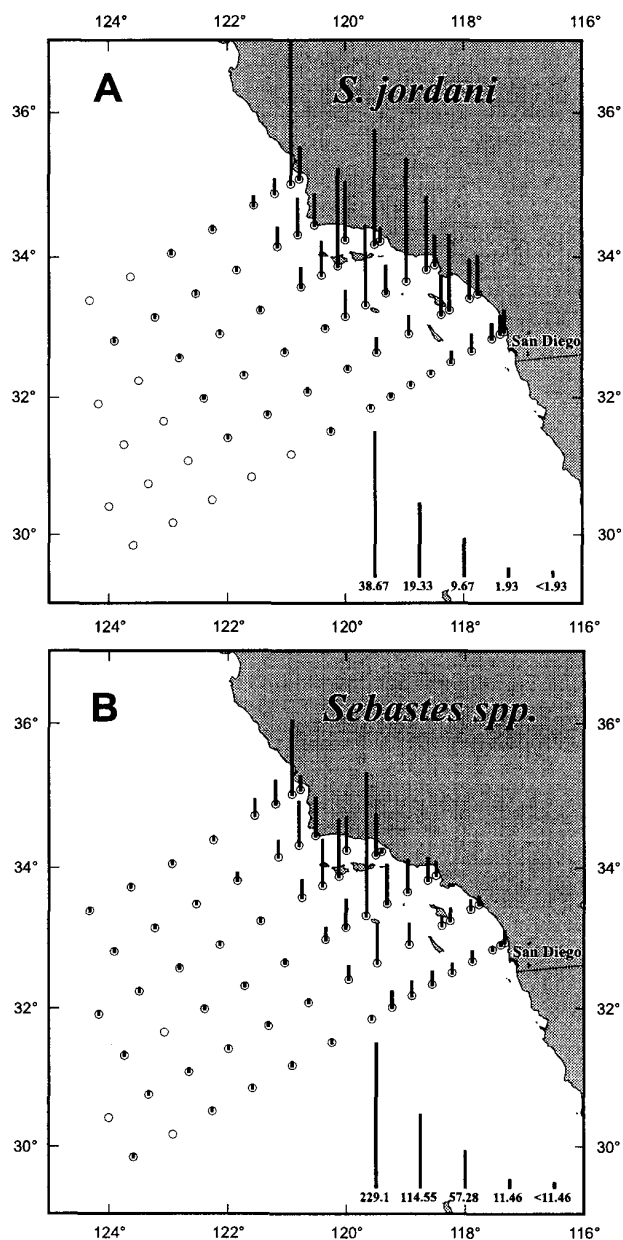
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Figure 4. Average abundance of *Sebastes* larvae at nominal CalCOFI stations from 1951 to 1998: *A, S. jordani*, shortbelly rockfish; *B, Sebastes* spp., unidentified rockfish larvae. Length of vertical bars indicates average larvae per 10 m² scaled proportionally from the station with the highest value.

pattern, but the highest average abundances were at stations in the Point Conception and northern Channel Islands area (fig. 4B). Approximately 79% of the total *Sebastes* spp. larvae were in the region bounded by station 55 on lines 77–90, although only 40% of the total occurrences were in this region. Station 87.50, just northwest of San Nicholas Island, had the highest average abundance (229.1 larvae per 10 m²).

Seasonal Larval Occurrence and Abundance

Most of the rockfish larvae taken in CalCOFI oblique net samples are early-stage larvae; in a sample of 11,633 larvae, more than 90% were smaller than 7 mm (Moser and Butler 1987). Thus, larval abundance provides information on reproductive seasonality and could be used as an index of larval production.

Most rockfish species give birth to their broods of larvae during winter and spring (fig. 5A). After a period of low larval production during the summer, average larval abundance begins to increase in November and December, reaches a peak in January–March, and then declines during spring months. Larvae of *S. paucispinis* are essentially absent from summer and early fall samples but begin to appear in November and increase to peak abundance in January, after which their abundance declines steadily (fig. 5B). Larvae of *S. levis* have a similar seasonal pattern: some larvae appear in late fall, and there is a distinct peak in January–March, followed by a sharp decline through spring and early summer (fig. 5C). The parturition season for *S. jordani* off southern California begins in January, with larval abundance peaking sharply in February, and then declining rapidly through March and April (fig. 5D).

Sebastes aurora and *S. diploproa* have different seasonal patterns than most other rockfish species (figs. 5E, F). Larvae of *S. aurora* are infrequent in late summer and essentially absent during early fall. Numbers begin to increase in late fall and through the winter, reaching a peak in May–June (fig. 5E). Larvae of *S. diploproa* are present during the entire year, with lowest average abundance in March, after which there is a steady increase to a peak in October, then a sharp decline in November and a more gradual decline through February (fig. 5F).

Temperature and Zooplankton Volume

Average annual temperatures for the stations included in this study clearly show the well-documented cool regime prior to 1976 and the warm regime in effect since 1977 (fig. 6). Within the survey area the average temperature for 4,428 stations during 1951–76 was 15.4°C vs 16.4° for 3,523 stations from 1977 to 1998. Average winter (January–March) and summer (July–September) temperatures for the cool regime were 14.1° and 17.2°. Average winter and summer temperatures for the warm regime were 14.9° and 18.1°. The prominent contiguous La Niña and El Niño events of the mid-1950s were evident in the data from this study. Average annual temperature decreased in 1954 and further in 1956, then increased abruptly in 1957 to a peak in 1959 (fig. 6). A moderate average decrease in 1960–62 was followed by a sharp increase in 1963 in response to the short-lived 1963 El Niño. Although this El Niño lasted
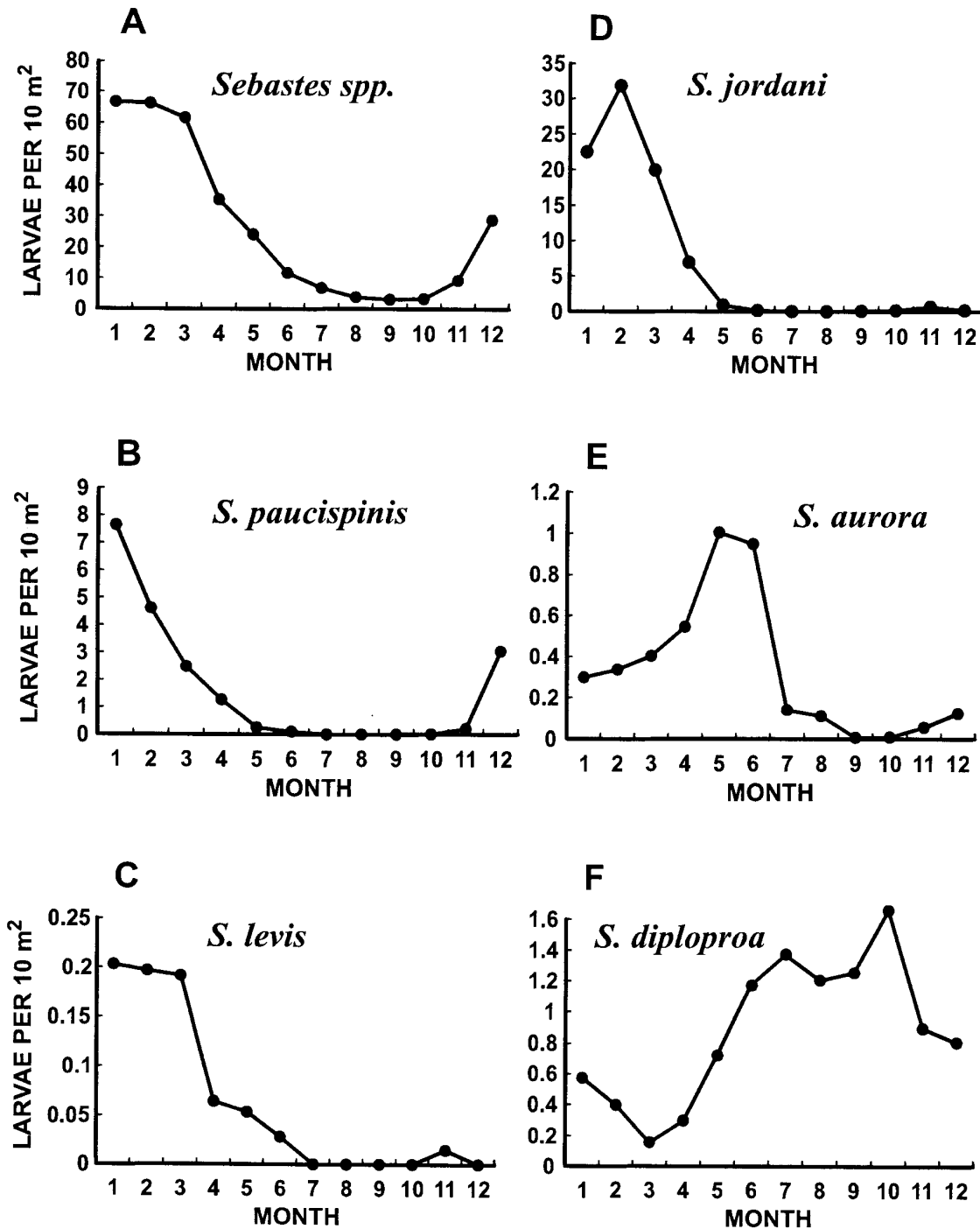
Figure 5. Seasonal abundance (average number per 10 m²) of larvae of six *Sebastes* taxa from the CalCOFI time series. *A, Sebastes* spp., unidentified rockfish larvae; *B, S. paucispinis,* bocaccio; *C, S. levis,* cowcod; *D, S. jordani,* shortbelly rockfish; *E, S. aurora,* aurora rockfish; *F, S. diploproa,* splitnose rockfish.

less than a year, it produced sustained anomalous warm conditions in the Gulf of Alaska (Hollowed et al. 1998). A series of closely grouped La Niña events from May 1970 to March 1975 resulted in anomalously cold conditions in the study area. The CalCOFI record is incomplete because the surveys were triennial during this

period, but the low average temperatures for surveys in 1972 and 1975 clearly demonstrate the generally cold conditions for these years (fig. 6).

The shift to a warm regime in late 1976 was not documented by CalCOFI because of the cruise hiatus during 1976–77; however, the regime shift is clearly ap-
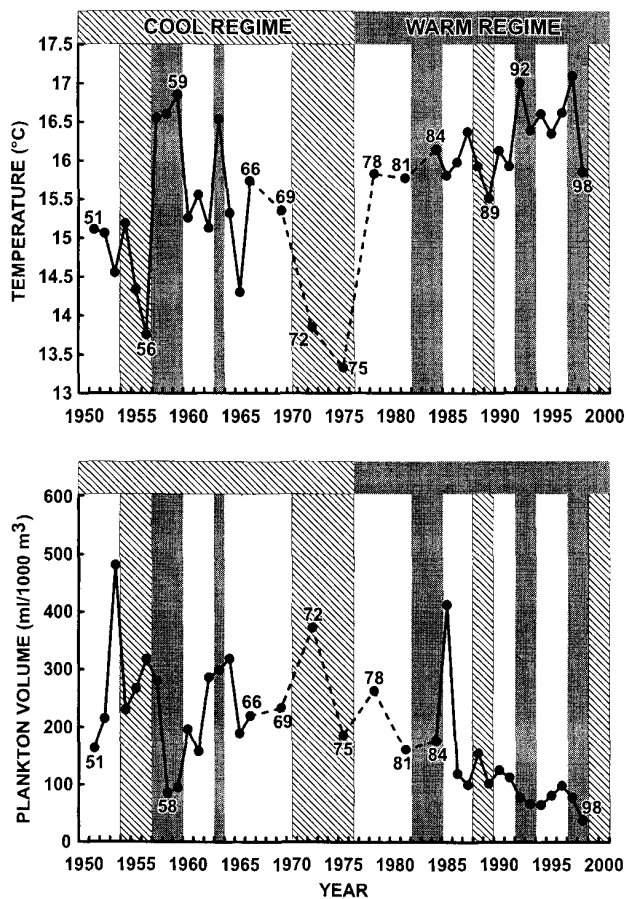
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Figure 6. Average annual temperatures (upper panel) and zooplankton volumes (lower panel) for CalCOFI stations included in this study. Cool and warm regimes of the Pacific Decadal Oscillation (PDO) are indicated above each graph, and Southern Oscillation (ENSO) events are indicated by vertical bars (El Niño, shading; La Niña, hatching; the wide hatched bar represents a series of three consecutive La Nina events between May 1970 and March 1976). Dashed line indicates the period of triennial CalCOFI surveys.
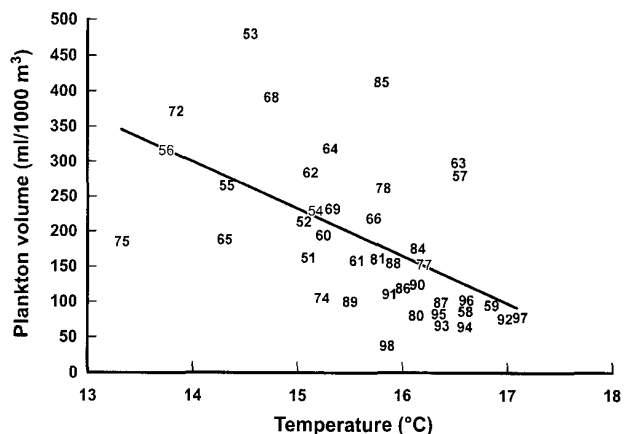

Figure 7. Plot of average annual temperature versus average annual zooplankton volume for CalCOFI surveys from 1951 to 1998. Equation for the regression line: $y = -67.545x + 1245.8$; $R^2 = 0.319$.

Average plankton volumes for the warm regime were 90.0 in winter and 130.0 in summer. A peak in average plankton volume of almost 500 ml per 1000 m³ preceded La Niña of 1954–56 (fig. 6). The effect of the 1957–59 El Niño is clearly evident in the low average volumes during 1958–59. The next high value was in 1972, and after the regime shift average values declined steadily, except for a spike in 1985 (fig. 6). The inverse relationship between temperature and plankton volume for the stations included in this study is apparent when average values for each year are plotted (fig. 7).

Annual and Interannual Changes in Larval Occurrence and Abundance

Sebastes paucispinis. The proportion of net tows positive for *S. paucispinis* larvae declined about 60% from the cool to the warm regime (table 1). During the cool regime the proportion of positive tows peaked in 1954, the beginning of a La Niña event, and then declined in 1955–56, the remaining years of La Niña (fig. 8). An increase in 1957, a transition year to El Niño, was followed by a sharp decline during 1958–59, the remaining years of El Niño. Then followed a general increase to relatively high values from 1966 to 1972. The decline between 1975 and 1978 was abrupt, and generally low values were typical of warm regime years, except for the relatively high average value during the 1988–89 La Niña.

Average larval abundance declined 52% from the cool to the warm regime (table 1), with annual trends (fig. 8) similar to trends in the proportion of positive tows. Values were unusually high in 1969–75, then decreased precipitously in 1978 after the regime shift. The unusually high average value for 1981 is the result of a single large sample of 622 larvae from station 87.50 on cruise 8101. Without that station, average abundance for 1981 would

parent in the abrupt increase in average temperature in 1978 and the consistently high temperatures in the years immediately following, including the major El Niño of 1982–83 (fig. 6). A short-lived La Niña in 1988–89 was evident in the low average temperature for 1989, and this was followed by El Niño events in 1992–93 and 1997.

Historically, in the California Current region plankton volume has been higher during cold ocean conditions than during warm conditions, and the decline in zooplankton volume in the recent warm regime is well documented (Roemmich and McGowan 1995a, b; McGowan et al. 1998). In this study, average plankton volume for 6,809 stations in the cool regime was 228.2 ml per 1000 m³ vs 123.8 ml per 1000 m³ for 4,663 stations during the warm regime, an overall reduction of 46%. Average winter and summer plankton volumes for the cool regime were 186.8 ml per 1000 m³ (January–March) and 287.4 ml per 1000 m³ (July–September).

TABLE 1
Average Occurrence (Proportion of Positive Tows) and Abundance (Larvae per 10 m²) for Larvae of
Six *Sebastes* Taxa during Cool (1951–76) and Warm (1977–98) Regimes in the Southern California Bight Region

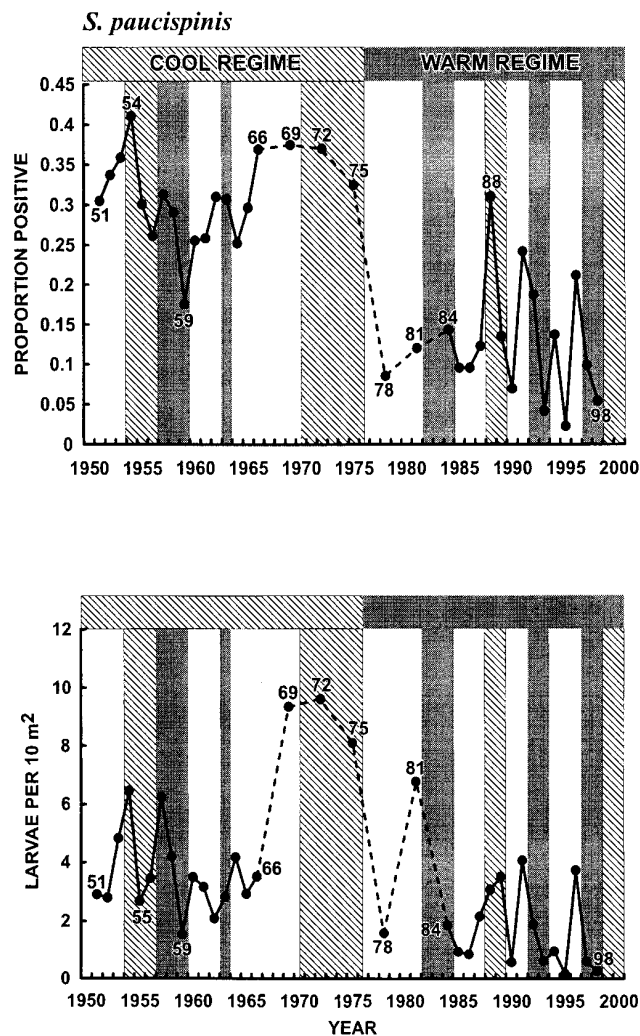| | Proportion of positive tows | | | Average larvae per 10 m² | | |
Taxon	Cool regime	Warm regime	Percentage change	Cool regime	Warm regime	Percentage change
Sebastes spp.	0.56	0.43	−23.2	27.65	30.79	+11.4
S. paucispinis	0.31	0.12	−61.3	4.69	2.24	−52.2
S. levis	0.04	0.002	−95.0	0.18	0.03	−83.3
S. jordani	0.39	0.22	−43.6	17.41	13.77	−20.9
S. aurora	0.09	0.03	−66.7	0.50	0.36	−28.0
S. diploproa	0.14	0.05	−64.3	0.99	0.55	−44.4

Figure 8.   Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes paucispinis*, bocaccio, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². Cool and warm regimes of the Pacific Decadal Oscillation (PDO) are indicated above each graph, and Southern Oscillation (ENSO) events are indicated by vertical bars (El Niño, shading; La Niña, hatching; the wide hatched bar represents a series of three consecutive La Nina events between May 1970 and March 1976). Dashed line indicates the period of triennial CalCOFI surveys.

follow a trend similar to the trend for average occurrence. Sharp declines were associated with El Niño events during both regimes, and the value for 1998 is 6% of the average abundance during the cool regime.

Sebastes levis.   In CalCOFI samples *S. levis* larvae were relatively rare: a total of 117 positive tows produced 550 larvae. The trends in occurrence and abundance for *S. levis* larvae were similar to those for *S. paucispinis*, with a 95% decline in proportion of positive tows and an 83% decline in abundance from the cool to the warm regime (table 1; fig. 9). The peak in 1969 was followed by abrupt decline in 1972 and 1975 for both occurrence and abundance. Except for a few larvae taken in the early 1990s, *S. levis* larvae were absent from CalCOFI tows during the warm regime.

Sebastes jordani.   In this study *S. jordani* larvae were the most abundant of the identifiable rockfish larvae. During peak years, they accounted for about 15% of the total rockfish larvae and occurred on about half of the total stations in the study area. Their average occurrence declined 44%, and their average abundance declined 21% from the cool to the warm regime (table 1). The difference between the mean abundances for the two regimes is not significant statistically ($p = >0.05$), and variability in larval abundance was greater than for the other species in this study. There was a slight decline associated with La Niña years 1955–56 and an abrupt decline during the subsequent El Niño (fig. 10). The decline just before the regime shift was sustained after the shift to a low point in 1984. Average proportion of positive tows declined from 0.4 in 1972 to 0.014 in 1984, and average abundance declined from 28.4 larvae per 10 m² in 1969 to 0.2 larvae per 10 m² in 1984. Equally remarkable was the increase in occurrence and abundance that followed the low values in 1984. The proportion of positive tows increased steadily to 0.43 in 1992, and average abundance peaked at 63 larvae per 10 m² in 1991, when there were five tows with >400 larvae per 10 m². The increase in proportion of positive tows was almost linear, whereas the increase in abundance was interrupted by a decline during and imme-
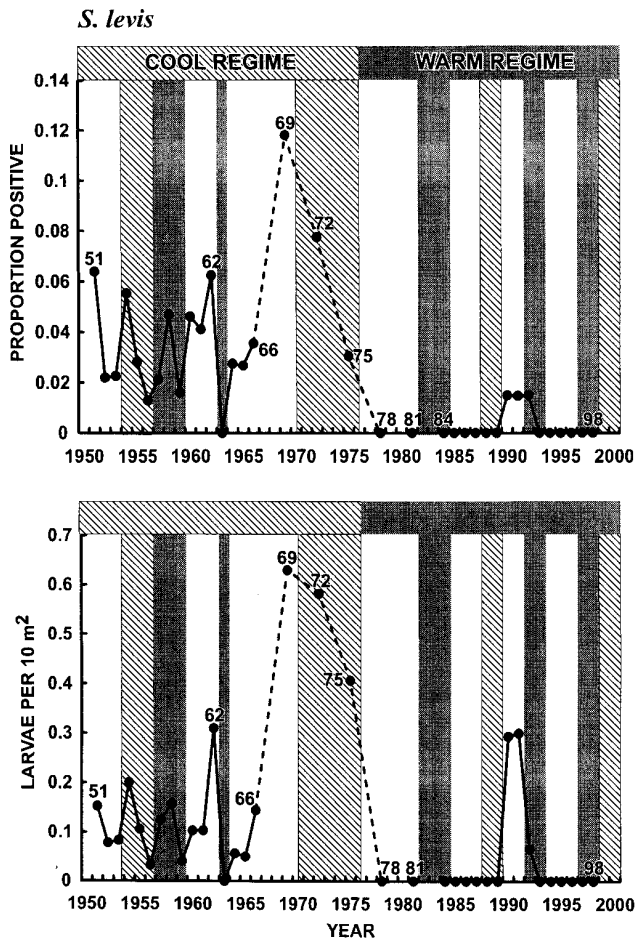
S. levis

S. jordani

Figure 9. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes levis*, cowcod, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.

Figure 10. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes jordani*, shortbelly rockfish, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.

diately following the 1988–89 La Niña. Both occurrence and abundance declined sharply during the 1992–93 El Niño, beginning a downward trend that continued through 1998.

Sebastes aurora. From the cool to the warm regime *S. aurora* larvae declined 67% in proportion of positive tows and 28% in abundance (table 1). There was a decline in occurrence in 1956, the last year of a La Niña event, and a more pronounced decline associated with the 1957–59 El Niño (fig. 11). The proportion of positive tows generally increased after 1961 to high values in 1966–69. Occurrence declined markedly in 1972 and 1975, increased slightly in 1978, and then declined to zero in 1985. Following this low point, occurrence generally increased to a peak in 1991, dropped sharply during the 1992–93 El Niño, then increased slightly up to 1995, after which it decreased. The increase between 1985 and 1991 was interrupted by a decline in 1989, the last year of the 1988–89 La Niña. Trends in abun-
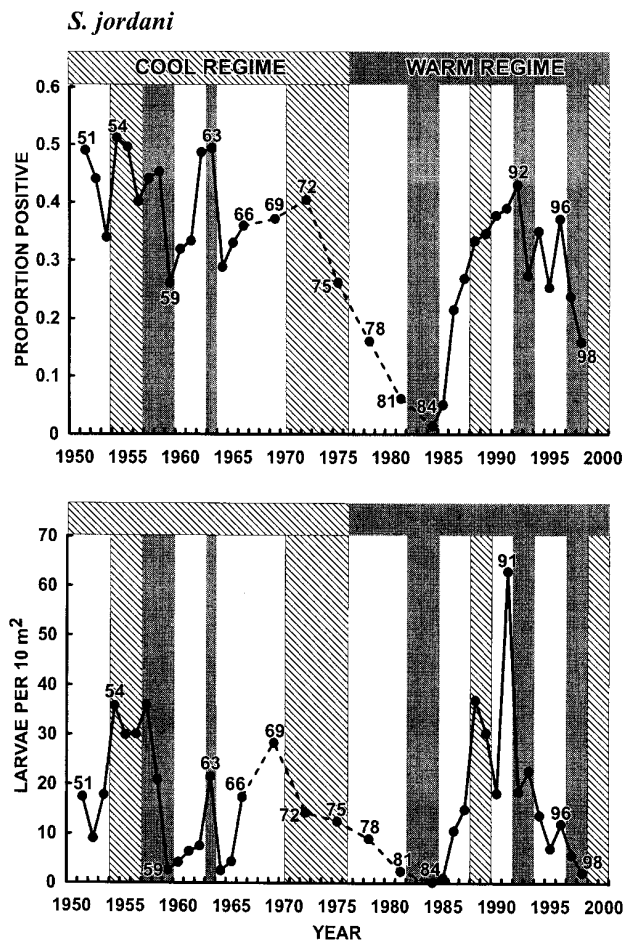
dance were similar to those of occurrence, except that 1966 was the peak year in the cool regime, and the average number of larvae was high in 1978.

Sebastes diploproa. Trends in occurrence and abundance of *S. diploproa* larvae were similar to those for *S. aurora* (fig. 12). There was a general decline associated with the contiguous ENSO events of the 1950s, followed by an increase during the 1960s. We lack data for the period from 1972 to 1986, but average occurrence declined 64% and abundance declined 44% from the cool regime to the warm regime (table 1). During the warm regime, declines in occurrence and abundance were associated with the 1988–89 La Niña and the subsequent two El Niño events.

Sebastes spp. The proportion of positive tows for unidentified rockfish larvae declined 23% from the cool to the warm regime; however, average abundance increased 11% (table 1). In the cool regime, there was a general decline in proportion of positive tows during
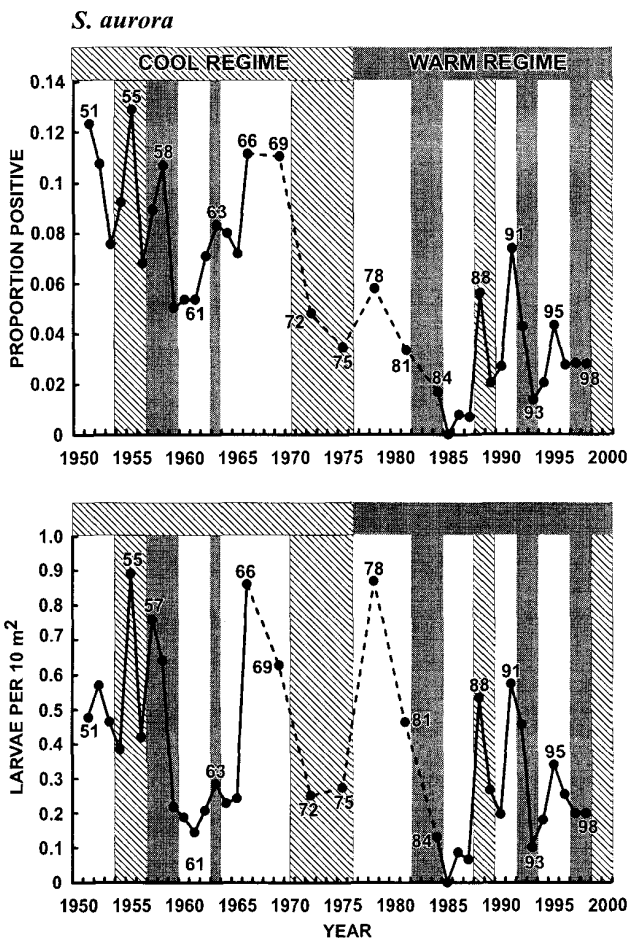
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S. aurora

S. diploproa

Figure 11. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes aurora*, aurora rockfish, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.
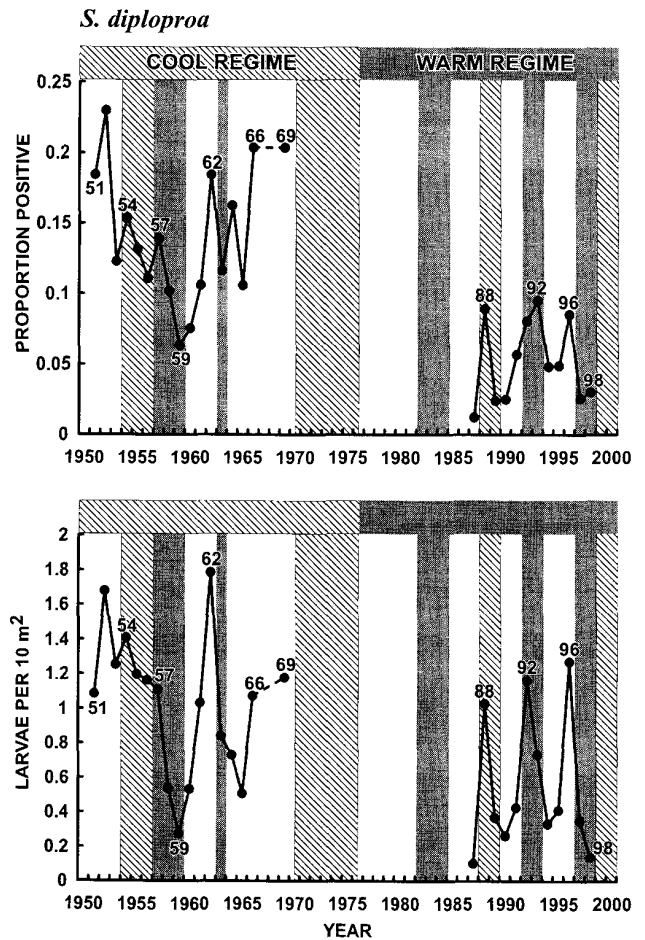
Figure 12. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes diploproa*, splitnose rockfish, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.

the contiguous ENSO events of the 1950s, followed by a general increase to a peak in 1972 (fig. 13). Following this was a gradual downward trend in proportion of positive tows to a low in 1998. Abundance trends were less gradual, declining in association with the ENSO events of the 1950s, followed by gradual increases up to 1966, and then abrupt increases in 1969 and 1972. The trend of abruptly declining abundance to a low value in 1984 was interrupted by an unusually high value in 1981. Abundance increased again during the late 1980s, and declined during the 1990s.

DISCUSSION

Fishery Trends

Interpretation of trends in occurrence and abundance of larval rockfishes in the CalCOFI time series depends on knowledge of adult biomass trends and larval pro-

duction for these species over the same time span. Despite the history of severely declining catches for most species over the past several decades, comprehensive stock assessments have been produced for relatively few rockfish species (Ralston 1998; Pacific Fishery Management Council 1999). Most of these assessments have revealed a history of overfishing and, for some species, a dire need for stock rebuilding. Estimates of total biomass are available for only two species in this study: *S. paucispinis* and *S. levis* (MacCall et al. 1999; Butler et al. 1999). For the other three species, catch data give limited insight into the status of the populations.

Historically, *S. paucispinis* has been one of the most important species in trawl, setnet, and hook-and-line fisheries off California and has received much attention from fishery biologists and managers (Bence and Hightower 1990; Bence and Rogers 1992; Ralston et al. 1996; MacCall et al. 1999). Annual landings in
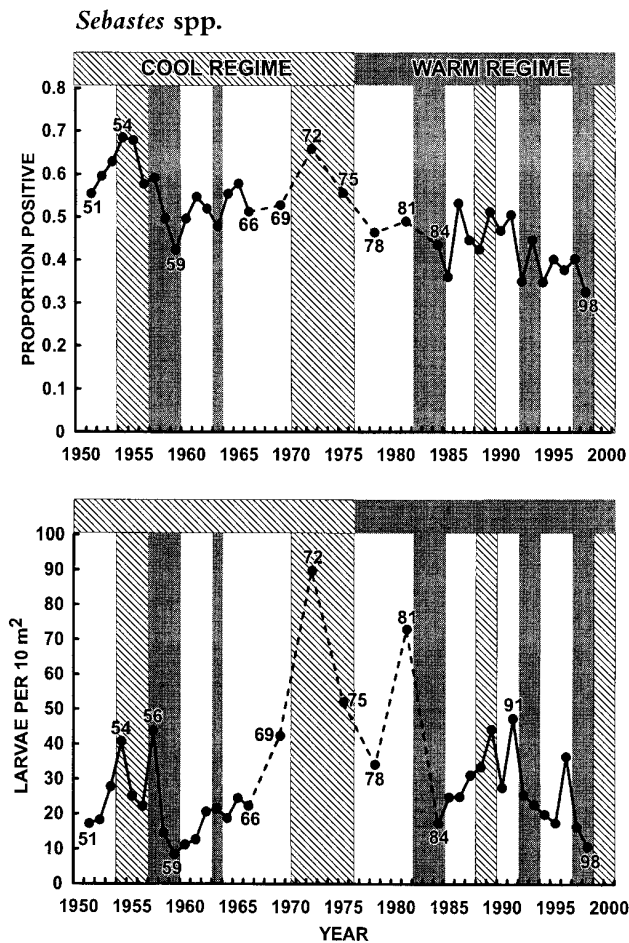
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Sebastes **spp.**

Figure 13. Average annual occurrence (*upper panel*) and average annual abundance (*lower panel*) of *Sebastes* spp., unidentified rockfish larvae, from CalCOFI stations used in this study. Occurrence is expressed as proportion of tows positive for the species, and abundance is expressed as larvae per 10 m². See figure 8 for explanation of graph format.

Figure 14. Estimated biomass of *Sebastes paucispinis*, bocaccio (from MacCall et al. 1999) and of *S. levis*, cowcod (from Butler et al. 1999).

California averaged ~2,500 t during the 1960s, increased sharply in the early 1970s, varied between ~4,000 and 7,000 t from 1973 to 1983, and then dropped abruptly from the mid 1980s to the present (MacCall et al. 1999). MacCall et al. (1999) estimated a steady reduction of biomass from about 70,000 t in the early 1970s to about 1,200 t in 1999, <7% of the unfished biomass (fig. 14).

Sebastes levis is a large, predatory species with a distribution centered in the SCB. Historically, it has supported a substantial commercial fishery, and has been a prize species in recreational fisheries. Trends in catch are similar to those of *S. paucispinis*. Total annual catch averaged ~76 t in the 1960s and increased to ~140 t in the 1970s, peaking at 194 t in 1976. The catch began to decline in the 1980s, precipitously so after 1989, to a low of 19 t in 1997 (Butler et al. 1999). Butler et al. (1999) estimated a decline in total biomass from ~2,700
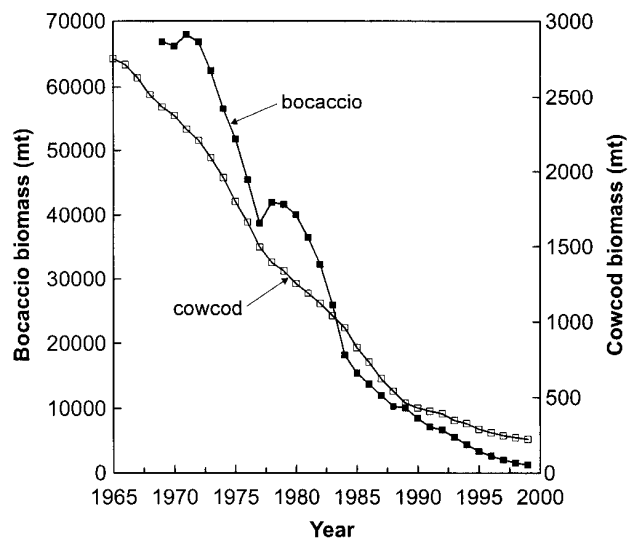
t in the 1970s to ~238 t in 1998, <5% of the virgin biomass (fig. 14).

Sebastes jordani is a relatively small species whose biomass may approach 500,000 t and is essentially unexploited commercially (Pearson et al. 1991). Annual catches since 1980 usually were <10 t; exceeded 20 t only in 1985, 1996, and 1997; and fell far short of the present allowable biological catch of 13,900 t (fig. 15). Nearly all of the historical catch has been off central California (Pacific Fishery Management Council 1999). The lack of fishery interest in this species, despite its huge biomass, relates primarily to the relatively small size of adults and associated problems in processing and marketing. *Sebastes jordani* is important ecologically; it is a major prey species for piscivorous fishes, including other rockfishes, marine mammals, and seabirds, and it occupies an important part of the food web of coastal California and northern Baja California.

Sebastes aurora live on and around deep reefs, are rarely encountered by recreational anglers, and prior to the 1980s were taken incidentally with other rockfish in the commercial fishery. Catches of *S. aurora* (fig. 15) increased during the early 1980s, in association with the rapidly expanding set-line and setnet fishery for blackgill rockfish (*S. melanostomus*), reaching a peak of slightly more than 100 t in 1990 (Butler et al. 1998). The catch then declined steadily to ~20 t in 1998. In the 1970s and 1980s the catch was predominantly from northern and central California, but after 1992 the fishery shifted to southern California.

Sebastes diploproa is a moderately important trawl species along the entire west coast, and catches off California remained relatively stable—between 200 and
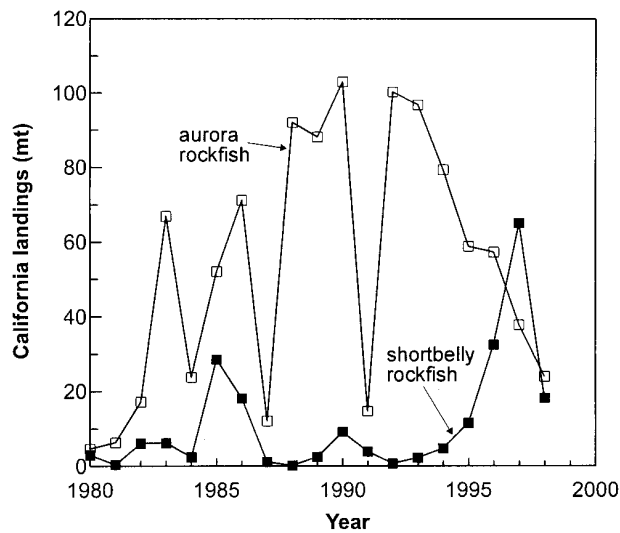
Figure 15. Total California landings for *Sebastes jordani*, shortbelly rockfish, and *S. aurora*, aurora rockfish, during 1980–98. Data from CALCOM database (see Pearson and Erwin 1997).
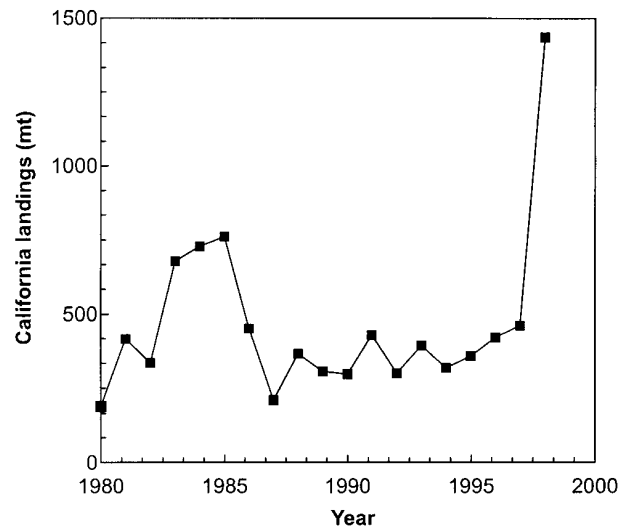

Figure 16. Total California landings for *Sebastes diploproa*, splitnose rockfish, during 1980–98. Data from CALCOM database (see Pearson and Erwin 1997).

800 t—from 1980 to 1997 (fig. 16). It, like *S. aurora*, has been managed as part of the *Sebastes* complex and has not had a formal stock assessment. The catch increased to 1,400 t in 1998 as a result of increased effort directed to "large aggregations of splitnose [rockfish] suddenly becoming available to the fishery," primarily off central California (Pacific Fishery Management Council 1999). This resulted in separate management recommendations for this species.

Larval Trends

Comparison of trends in biomass for *S. paucispinis* and *S. levis* with interannual trends in their larvae suggest that spawner biomass and biomass-specific reproductive effort are the major factors determining the level of larval abundance. There is roughly an order of magnitude difference between the abundance of *S. jordani* and *S. paucispinis* larvae, and another order of magnitude difference between *S. paucispinis* and *S. levis*. Estimates of peak spawner biomass for these species (500,000, 70,000, and 2,700 t) also differ by roughly an order of magnitude. Since most of the rockfish larvae captured in plankton nets are small, recently-born individuals, their incidence and abundance are primarily measures of the reproductive effort of the stock. The most important factors affecting larval production are biomass of the adult stock and the reproductive effort for the year. The latter is closely tied to the amount of energy that is available for reproduction during egg maturation and gestation of the young. Declines in larval abundance most likely reflect declines in adult abundance due to fishery harvest or previous recruitment failures. Short-term fluctuations are most likely related to episodes of high or

low reproductive output, since rapid biomass changes would not be expected.

Larval abundance of *S. paucispinis*, *S. levis*, *S. jordani*, and *Sebastes* spp. (unidentified rockfish larvae) increased markedly during the late 1960s, reaching peak values just before or during the extended period of unusually cold ocean conditions that marked the end of the cool regime. Larval abundance of these taxa declined during the cold period and continued to decline through the regime shift. Assigning some role in this decline to environmental conditions during this period of major ocean change is confounded by the fact that this was precisely the time when the fishery was expanding in the study area. Gear and technical improvements in the fishery, particularly the use of gill nets, increased both harvest efficiency and the number of species harvested. Arguing for the role of ocean climate as a contributing factor in rockfish larval decline during this period is the fact that the larvae of *S. jordani*, an essentially unexploited species, underwent a decline similar to those of fishery target species during the period of the regime shift. If fishery removals were the principal factor in rockfish larval decline, one would not expect *S. jordani* larval abundance to decline in relation to the regime shift in a manner similar to the exploited species.

The wide variability in larval *S. jordani* abundance, and the remarkable recovery of the larval population during the warm regime suggest that something besides the regime shift (or fishery) has a strong influence on their abundance. The steep rise in larval abundance during the late 1980s may reflect an abrupt increase in biomass due to an unusually successful recruitment during the early 1980s. Such intermittent large year-classes are

typical of rockfishes, and the early age of maturity—50% at age two and 100% by age four (Pearson et al. 1991)—would favor a rapid population response. A similar increase in biomass of one or more small, nonexploited species could account for the average increase of 11% in larval abundance of *Sebastes* spp. from the cool to the warm regime and for the abrupt increase in *Sebastes* spp. abundance during the late 1980s. The rapid decline in larval abundance of *S. aurora* during the series of cold episodes prior to the regime shift and the marked increase in abundance in 1978 after the regime shift may be related to the fact that the reproductive peak for this species comes in late spring, when water temperatures are increasing. A similar response in larval abundance could be expected of *S. diploproa*, a species with a summer-fall spawning peak, but larval data are not available for the period from 1972 to 1986.

How might changes in ocean condition alter larval rockfish production? Lenarz and Wyllie Echeverria (1986) showed that visceral fat volume in yellowtail rockfish (*Sebastes flavidus*) was significantly lower during 1983, an El Niño year, compared to 1980, a non–El Niño year; this correlated, to some extent, with differences in gonad volumes for the two years. Also, Lenarz et al. (1995) showed that condition factors for adults of chilipepper (*S. goodei*), blue rockfish (*S. mystinus*), and *S. flavidus* were lower during the 1982–83 and 1992–93 El Niño events than during associated non–El Niño years, and VenTresca et al. (1995) showed that adult condition and gonad indices in *S. mystinus* were depressed during these two El Niño events. Recently, Woodbury (1999) has shown that growth rates of adult *S. entomelas* (widow rockfish) and *S. flavidus* were depressed during El Niño conditions in 1983 compared to other years between 1980 and 1987.

These studies suggest that reduced ocean productivity during El Niño events and the associated effects on female rockfish condition could lower larval production. Likewise, the prolonged decline in ocean productivity associated with the recent warm regime may have caused a prolonged depression in larval rockfish production. This does not explain why larval abundance declined during La Niña conditions, when presumably primary and secondary production and trophic conditions were generally enhanced. Clarification of the relation between ocean conditions and rockfish reproduction will require a thorough study of maternal condition and larval production in a variety of rockfish species in relation to ocean climate.

Is survival of early-stage rockfish larvae a significant factor in the decline in larval abundance associated with the regime shift and with ENSO episodes? Because rockfish are viviparous, the condition of the pregnant female affects fetal-maternal exchange and particularly brood nutrition. The relatively poor condition of female rockfishes during El Niño episodes could be reflected in the condition of intraovarian young and could result in poor survival immediately after birth. The well-documented decline in ocean productivity associated with El Niño events may play an important role in the survival of first-feeding larvae and in subsequent larval stages. If declines in larval rockfish abundance were due to starvation, early larvae should show histological evidence of starvation as demonstrated for larvae of jack mackerel (Theilacker 1986) and northern anchovy (O'Connell 1980). Such a study has yet to be conducted for rockfish larvae.

Yoklavich et al. (1996) presented evidence contradicting the notion that starvation during El Niño conditions reduces survival of rockfish larvae. They found no evidence of starvation in rockfish larvae collected during the 1992–93 El Niño, and growth rates in *S. jordani* larvae from their samples were similar to growth rates of *S. jordani* larvae from non–El Niño years in the same region (Laidig et al. 1991; Ralston et al. 1996). Yoklavich et al. (1996) concluded that reduced survival of larval rockfish in their samples taken during the 1992–93 El Niño was due to predation following transport of the larvae to near-coastal waters, where chaetognath populations were extremely high. Their suggestion that upwelling conditions led to offshore transport of rockfish larvae and enhanced larval survival contradicts Parrish et al. (1981), who hypothesized that offshore transport of the larvae of demersal fishes in the California Current region is generally detrimental to larval survival.

It is obvious that much more research is needed to provide a basis for a thorough evaluation of the survival of larval rockfish in relation to environmental variation, especially if Ralston and Howard (1995) are correct in concluding that year-class strength in rockfishes is determined largely during the larval period.

ACKNOWLEDGMENTS

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