

RECRUITMENT OF THREE SPECIES OF JUVENILE ROCKFISH (*SEBASTES* SPP.) ON SOFT BENTHIC HABITAT IN MONTEREY BAY, CALIFORNIA

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ABSTRACT

A number of ecologically and economically important species of rockfishes recruited to soft benthic habitats in Monterey Bay, California, during 1995–96. *Sebastes elongatus*, *S. saxicola*, and *S. levis* were the most abundant and, although caught throughout the depth range (40–100 m) of our survey, had highest densities from 60 to 100 m. Densities of *S. elongatus* and *S. saxicola* were greater than that of *S. levis*. Peak settlement followed ocean upwelling. Size–frequency analysis indicated that, once settled, juvenile rockfish ontogenetically moved toward adult depths. Growth rates ranged from 0.17 to 0.32 mm/d, with growth declining during months of highest sea-surface temperature. Peaks in distribution of back-calculated birthdates corresponded with periods of increased upwelling. Significant emigration from the sampling area occurred during the onset of winter storms.

INTRODUCTION

At least sixty-two species of rockfishes (*Sebastes* spp.) inhabit waters off the Pacific coast of North America (Eschmeyer and Herald 1983). Most of these species are important in both commercial and recreational fisheries. A major problem in managing rockfish resources is the difficulty in predicting year-class strength of these populations (Mearns et al. 1980). Studying the magnitude and timing of recruitment (defined in our study as the time of settlement of pelagic juvenile rockfish to benthic habitats) of young-of-the-year (YOY) fishes, and the processes that affect their survival, may be critical for understanding and predicting the relative size of the year-class when it enters the fishery.

Rockfishes exhibit unique reproductive and early life-history characteristics. Fertilization occurs internally, embryos develop within paired ovaries, and larvae are released into the water column 1–2 months after fertilization (Boehlert and Yoklavich 1983; Eldridge et al. 1991; Moser and Boehlert 1991). Larvae and pelagic juveniles of many rockfish species live in the upper 100 m

of the water column (Lenarz et al. 1991; Larson et al. 1994) for one to several months before settling to benthic habitats (Boehlert 1977; Moser and Ahlstrom 1978; Moser and Boehlert 1991).

Once settled, juvenile rockfish move gradually over several years into adult habitats (Love et al. 1991). Although abundance varies tremendously from year to year, numbers of older, pelagic juveniles have been significantly correlated with the abundance of settled juveniles, indicating decreased mortality during late pelagic and benthic stages (Ralston and Howard 1995; Adams and Howard 1996). Thus, a close relationship may exist between year-class strength and the number of juveniles that survive to the benthic stages.

Seasonal and annual changes in environmental conditions, such as timing and intensity of upwelling, are thought to influence survival of young rockfishes (Mearns et al. 1980; Larson et al. 1994; Ralston and Howard 1995). Upwelling centers are located just north of Monterey Bay at Point Año Nuevo and to the south at Point Sur (Breaker and Broenkow 1994; Rosenfeld et al. 1994). Upwelling is generally characterized by high nutrient concentrations, low temperatures, and offshore transport. While Parrish et al. (1981) hypothesized that offshore transport could be detrimental to the survival of early pelagic stages of fishes in the California Current, others have suggested that upwelling might benefit larval and juvenile rockfish through increased food resources and decreased predation by nearshore predators (Ainley et al. 1993; Larson et al. 1994; Yoklavich et al. 1996).

The influence of ocean conditions on interannual variation in juvenile rockfish abundance can be evaluated by comparing indicators of ocean conditions with the distribution of birthdates of fishes that survive the pelagic stage. Birthdate distributions have been estimated by subtracting age from the date of collection (Yoklavich and Bailey 1990; Woodbury and Ralston 1991; Yoklavich et al. 1996). These birthdate distributions for surviving juveniles can be compared with the time of spawning as predicted from the literature or from early larval surveys. Corresponding environmental conditions can be examined for possible influence on survival and growth of rockfishes during their early developmental stages.

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Several studies have examined rockfish recruitment to rocky bottom and kelp beds in Monterey Bay (Anderson 1983; Hoelzer 1988; Carr 1991; unpubl. data from D. VenTresca, Calif. Dep. Fish and Game, 20 Lower Ragsdale Dr., Monterey, CA 93940). Rockfish recruitment to soft benthic habitats has been documented in southern California (Boehlert 1977; Mearns et al. 1980). Approximately 80% of Monterey Bay is shallower than 100 m, and most of this area is soft-sediment habitat (Eittreim et al., in press). This habitat may be important for the recruitment of some rockfish species, but recruitment to this habitat has not previously been examined.

The 1996 amendments to the Magnuson-Stevens Fishery Conservation and Management Act (16 U.S.C. 1801 et seq.) require the description and identification of essential fish habitat (EFH), defined as those waters and substrata necessary for fish to spawn, breed, feed, or grow to maturity, as well as the implementation of measures to conserve and enhance this habitat. For many species, identifying EFH is difficult because of a lack of scientific information about habitat utilization. In order to fulfill the EFH mandate for rockfishes, habitat-specific information for all species and life stages is needed.

The purpose of this study was to describe spatial and temporal patterns in recruitment of dominant species of newly settled rockfishes to soft benthic habitats within Monterey Bay, California, and to examine growth and survival of these species. Specifically, we (1) determined species composition of juvenile rockfish on soft sediments; (2) analyzed spatial patterns in distribution of juvenile rockfish density and size; (3) assessed the timing and magnitude of rockfish recruitment to soft benthic habitats during 1995; (4) determined age and growth of the three dominant species during the benthic juvenile stage; and (5) interpreted birthdate distributions of these three species in terms of corresponding oceanographic conditions during the parturition period.

MATERIALS AND METHODS

Collections

Monterey Bay is located along the central California coast between 36.5°N and 37°N (fig. 1). The Monterey submarine canyon divides the bay more or less evenly into northern and southern sectors.

Fishes were collected with a small otter trawl (bridle length of 22.9 m, mouth width of 8.3 m, body mesh size of 3.8 cm, and cod-end mesh size of 1.0 cm) deployed from the RV *Ed Ricketts* on soft seafloor sediments in Monterey Bay. The mesh size of our otter trawl is efficient at sampling fishes as small as 19 mm (NMFS unpubl. data). Each tow lasted approximately 20 minutes. Sampling began in March 1995 and continued

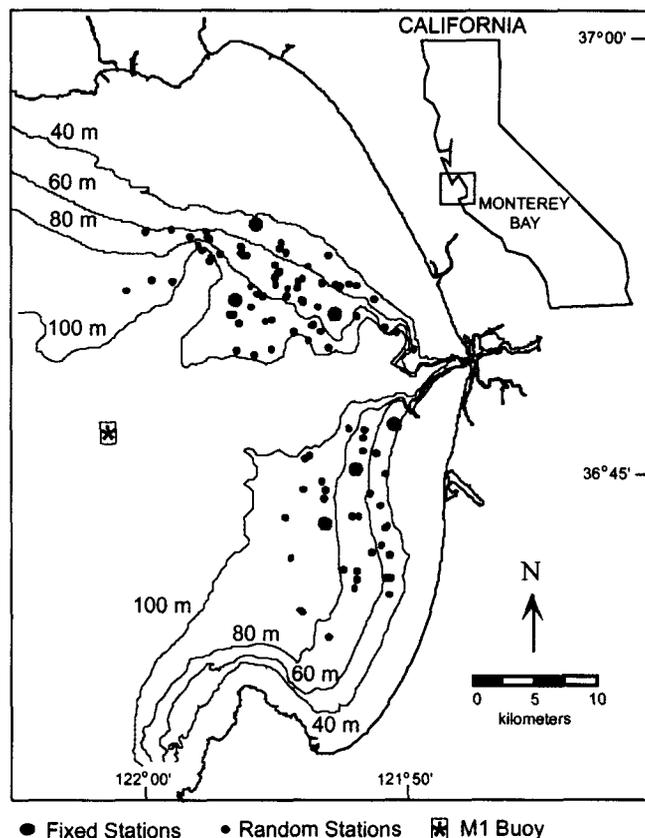


Figure 1. Otter trawls were used to sample juvenile rockfish almost weekly at stratified random and fixed stations between March 1995 and February 1996 in Monterey Bay, California. The M1 buoy is the source of sea-surface temperature data obtained from the Monterey Bay Aquarium Research Institute.

weekly, as weather permitted, through February 1996. Sampling stations were located within three depth strata: 40–60 m, 60–80 m, and 80–100 m (fig. 1). Minimum and maximum depths were based on gear constraints. Depth was stratified to ensure that the entire range was sampled and to facilitate comparisons of fish density among depths. Random samples were collected to evaluate spatial variations in abundance and size of rockfishes; samples at fixed stations were used to describe temporal changes in these variables. Locations for random stations, one per depth stratum, were determined before each weekly sampling. Six fixed sampling stations (two within each depth stratum) were determined prior to the first collection, and were sampled repeatedly throughout the survey period.

Fifty-six tows were completed in the 40–60 m depth stratum (30 at fixed stations, 26 at random stations); 72 tows were completed in the 60–80 m depth stratum (36 each at fixed and random stations); and 69 tows were completed in the 80–100 m depth stratum (30 at fixed stations, 39 at random stations).

All rockfishes (*Sebastes* spp.) were identified to species by means of a guide by Laidig and Adams (1991).

Standard length (SL) was measured to the nearest millimeter. Ages were determined from subsamples of sagittal otoliths of *S. elongatus* (greenstripe rockfish), *S. saxicola* (stripetail rockfish), and *S. levis* (cowcod) with techniques described by Stevenson and Campana (1992). Subsamples represented fishes from all months of sampling and the entire size range.

Daily growth increments in a thin frontal section of the otolith were enumerated at 1000 \times magnification with a compound microscope. Counts were made along the longest and clearest path from the nucleus to the otolith edge. The otoliths were read twice, with results from the first read unknown for the second read. There was a high degree of ageing precision and reproducibility for all three species as determined with the average percent error (APE; Beamish and Fournier 1981), coefficient of variation (CV), and index of precision (D; Chang 1982; see fig. 8).

Fish length and age data were fit to growth models by means of Systat (1992). We chose the Gompertz growth model because it best describes fish growth during early life stages, and has been used to describe juvenile growth in other rockfish species (Laidig et al. 1991; Woodbury and Ralston 1991). For *S. saxicola*, larval age data from Laidig et al. 1996 were included in the Gompertz model to help define the lower portion of the growth curve. The nonlinear Gompertz model was forced through a given size at parturition (4.5 mm for *S. elongatus*, 5 mm for *S. saxicola* and *S. levis*) as reported by Laidig et al. (1991). By using the inverse of the Gompertz equation, we determined ages for all individuals sampled within the size range of aged fishes, for each of the three species. Age was subtracted from the date of capture for each individual specimen to provide a distribution of birthdates for the surviving juveniles. We used a linear regression model to calculate a growth rate in mm/day for each species.

Distribution

All tows were standardized by area swept, that is (distance traveled) \times (net width), calculated as hectares (ha). In order to determine distance traveled, we recorded latitude and longitude by using a differential global positioning system (dGPS) immediately following the deployment of the trawl and again immediately before retrieval of the trawl. To maximize trawl contact with the bottom, and to insure accuracy and precision of distance estimates, constant vessel speed and direction were maintained as much as possible. Catch from each tow was considered one sample. Fish density (# fish/ha) at each station was plotted with a geographic information system (GIS) software program, MapGrafix (ComGraphix Inc, ©1994). Size data were plotted in histograms and reported as mean SL \pm one standard error.

Catch data from random stations were used to describe the spatial distribution of juvenile rockfishes in Monterey Bay. The Kruskal-Wallis nonparametric one-way analysis of variance was used to determine if there were significant differences in density with depth. A nonparametric analysis was necessary because of unequal sample sizes and nonnormal data. The Games and Howell modification of Tukey's pairwise comparison (Day and Quinn 1989) was used *post hoc* to test differences in means between depth strata. This method accounts for unequal variances and unequal sample sizes. We compared standard lengths of fishes from random stations among depth strata by using the Kolmogorov-Smirnov test (Zar 1984).

A standardized Morisita's index (I_d ; Krebs 1989) was used to describe dispersion patterns in density for each of the three dominant species. This index ranks the distribution of density of a given species from -1 to 1 , with 0 indicating random dispersion, positive numbers indicating clumped dispersion, and negative numbers indicating uniform dispersion. The statistical significance of I_d was determined with methods described in Elliot (1971).

Catch data from fixed stations were used to describe timing of recruitment and changes in density for juvenile rockfishes over time. Frequencies of density grouped by month for each depth stratum were compared graphically versus time for *S. saxicola*, *S. elongatus*, and *S. levis*. Size distributions, including catches from both fixed and random stations, were graphed by depth stratum and month to describe changes over time.

Oceanographic Conditions

Wind data can be used to compute offshore Ekman transport due to wind stress (Bakun et al. 1974). The Pacific Fisheries Environmental Laboratory of NOAA/NMFS provided daily averages of the offshore component of Ekman transport based on wind velocity recorded at 36°N off central California. Sea-surface temperature (SST) data were collected at a buoy station near Monterey Bay (M1: 36°45.25'N, 122°01.10'W) and obtained from the Monterey Bay Aquarium Research Institute.

Sea-surface temperature and offshore Ekman transport were graphically compared with timing and magnitude of recruitment in order to identify possible influences of transport on recruitment. Specifically, comparisons were made to determine whether offshore transport during upwelling and onshore transport during periods of relaxed upwelling might be related to rockfish recruitment in nearshore habitats. Distribution of birthdates estimated from ages of fish at the time of collection can define periods of successful parturition of surviving juveniles. Oceanographic data were graphically compared to birthdate distributions to identify possible influences of ocean condition on survival of recruits.

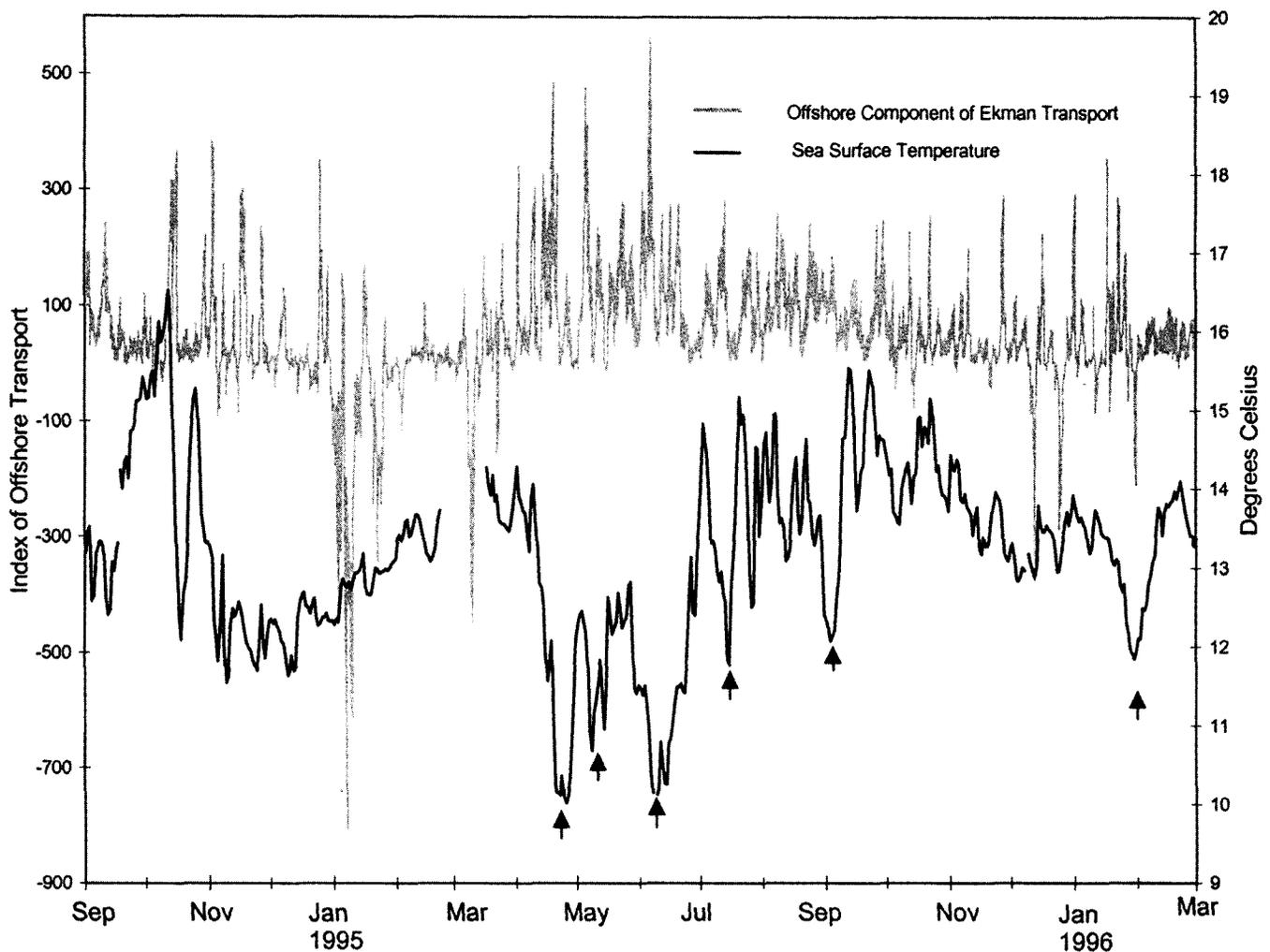


Figure 2. Upwelling off central California from September 1994 through February 1996, as represented by daily averages of sea-surface temperature and offshore component of Ekman transport. Arrows indicate distinct periods of upwelling. Data were obtained from the Monterey Bay Aquarium Institute (M1 buoy) and the Pacific Fisheries Environmental Laboratory of NOAA/NMFS.

RESULTS

Oceanographic Conditions

Upwelling, as represented by high offshore transport and low SST, occurred at intervals between April and September 1995 off central California (fig. 2). SST rapidly dropped from approximately 14°C in March 1995 to 10° at the end of April, indicating the onset of upwelling. SST generally increased through July (with a peak of 14.3°) as summer progressed, but suddenly dropped to 11.8° in mid-July and again in the beginning of September. These periods of relatively low SST generally were associated with increased offshore transport and can be characterized as upwelling.

Temperatures peaked in mid-September and generally remained above 14°C through October. At the same time, offshore transport declined, and periods of onshore transport were evident (negative indices in fig. 2). Another drop in SST occurred at the end of January.

Species Composition and Spatial Distribution

A total of 4,193 fishes from fifteen species of rockfishes were caught in 197 tows completed during 42 cruises (table 1). Three species—*Sebastes elongatus*, *S. saxicola*, and *S. levis*—accounted for over 90% of the total rockfish catch. Each remaining rockfish species accounted for less than 5% of the total catch of rockfish.

The densities of all three dominant species had clumped distributions, with low catches in the shallow depth stratum (table 2). Density of *S. elongatus* (range = 0–144 fish/ha; fig. 3A) and of *S. saxicola* (0–90 fish/ha; fig. 3B) differed significantly among the three depth strata ($p = 0.045$ and 0.001 , respectively). No significant ($p > 0.05$) differences were found in *post hoc* pairwise comparisons of density among the three depth strata for either species. Density of *S. levis* (0–24 fish/ha) was much lower than that of the other two species (fig. 3C), and did not differ among depth strata.

TABLE 1
**Abundance and Length of Juvenile Rockfishes Caught with an Otter Trawl
 on Soft Benthic Habitat in Monterey Bay, California, March 1995–February 1996**

Species	Common name	Abundance		Standard length (mm)	
		Total	% of total	Range	Mean ± SE
<i>Sebastes elongatus</i>	Greenstripe rockfish	1,810	43.2	30–85	41.2 ± 1.0
<i>S. saxicola</i>	Stripetail rockfish	1,736	41.4	32–116	65.8 ± 1.6
<i>S. levis</i>	Cowcod	289	6.9	49–104	66.3 ± 3.9
<i>S. goodei</i>	Chilipepper	182	4.3	65–152	92.5 ± 6.9
<i>S. semicinctus</i>	Halfbanded rockfish	83	2.0	50–140	85.1 ± 9.3
<i>S. crameri</i>	Darkblotched rockfish	37	0.9	48–139	70.2 ± 11.5
<i>S. diploproa</i>	Splitnose rockfish	31	0.7	44–78	57.3 ± 10.3
<i>S. wilsoni</i>	Pygmy rockfish	8	0.2	40–95	57.0 ± 20.2
<i>S. paucispinus</i>	Bocaccio	6	0.1	85–111	94.5 ± 38.6
<i>S. miniatus</i>	Vermilion rockfish	4	0.1	85–102	92.0 ± 46.0
<i>S. hopkinsi</i>	Squarespot rockfish	3	0.1	43–108	85.0 ± 49.1
<i>S. pinniger</i>	Canary rockfish	1	*	94	—
<i>S. jordani</i>	Shortbelly rockfish	1	*	84	—
<i>S. eos</i>	Pink rockfish	1	*	22	—
<i>S. entomelas</i>	Widow rockfish	1	*	92	—
Grand total		4,193	100		

*Less than 0.05% of total rockfish catch.

TABLE 2
**Mean Density and Size by Depth Stratum of *Sebastes elongatus*, *S. saxicola*, and *S. levis*
 Caught over Soft Benthic Habitat in Monterey Bay, California, March 1995–February 1996**

Species	Depth (m)	Density (fish/ha)		Standard length (mm)		
		Mean	S.E.	Mean	S.E.	Range
<i>S. elongatus</i> ($I_d = 0.54^*$; $n = 40$)	40–60	3.5	2.1	40	0.2	32–51
	60–80	23.5	10.6	42	0.1	31–54
	80–100	12.1	2.9	42	0.5	30–85
<i>S. saxicola</i> ($I_d = 0.51^*$; $n = 81$)	40–60	2.6	1.5	50	1.1	32–88
	60–80	10.2	3.7	62	0.5	32–90
	80–100	15.5	3.5	74	0.7	36–116
<i>S. levis</i> ($I_d = 0.54^*$; $n = 77$)	40–60	1.4	1.0	64	1.3	52–76
	60–80	4.1	1.5	65	0.6	49–85
	80–100	0.9	0.3	70	1.2	53–104

I_d is a measure of fish distribution patterns among (n) samples.

* $p < 0.05$.

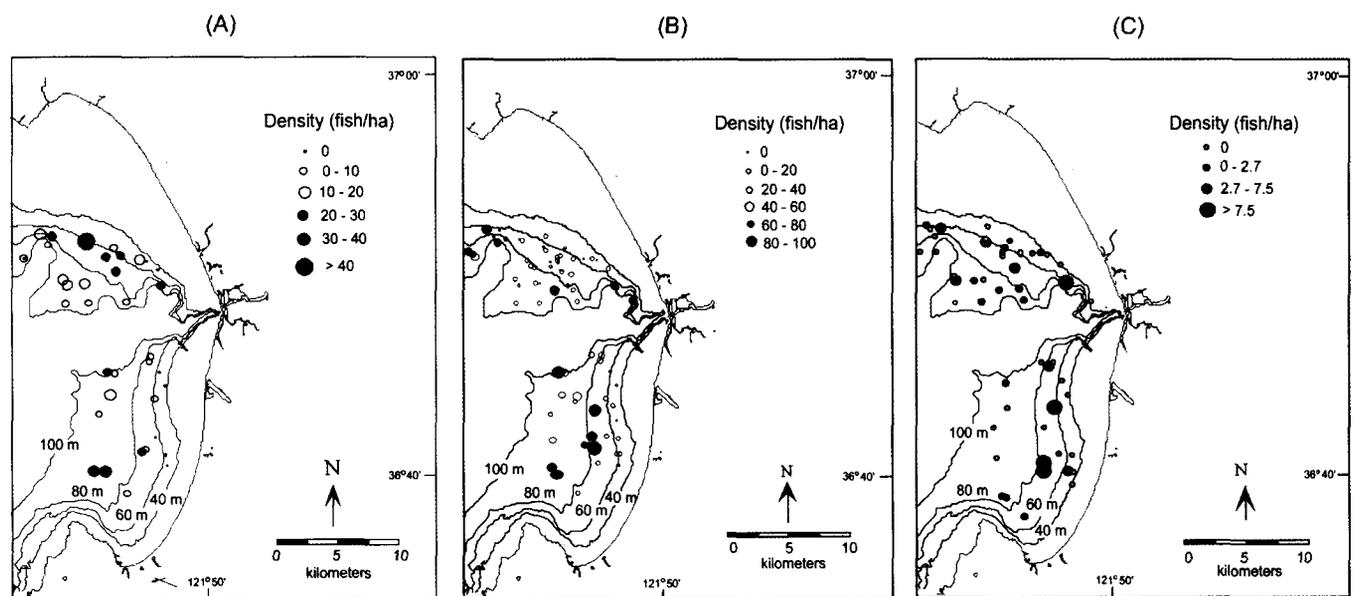


Figure 3. Spatial distribution of *Sebastes elongatus* (A), *S. saxicola* (B), and *S. levis* (C) caught over soft benthic habitat in Monterey Bay, California, between March 1995 and February 1996.

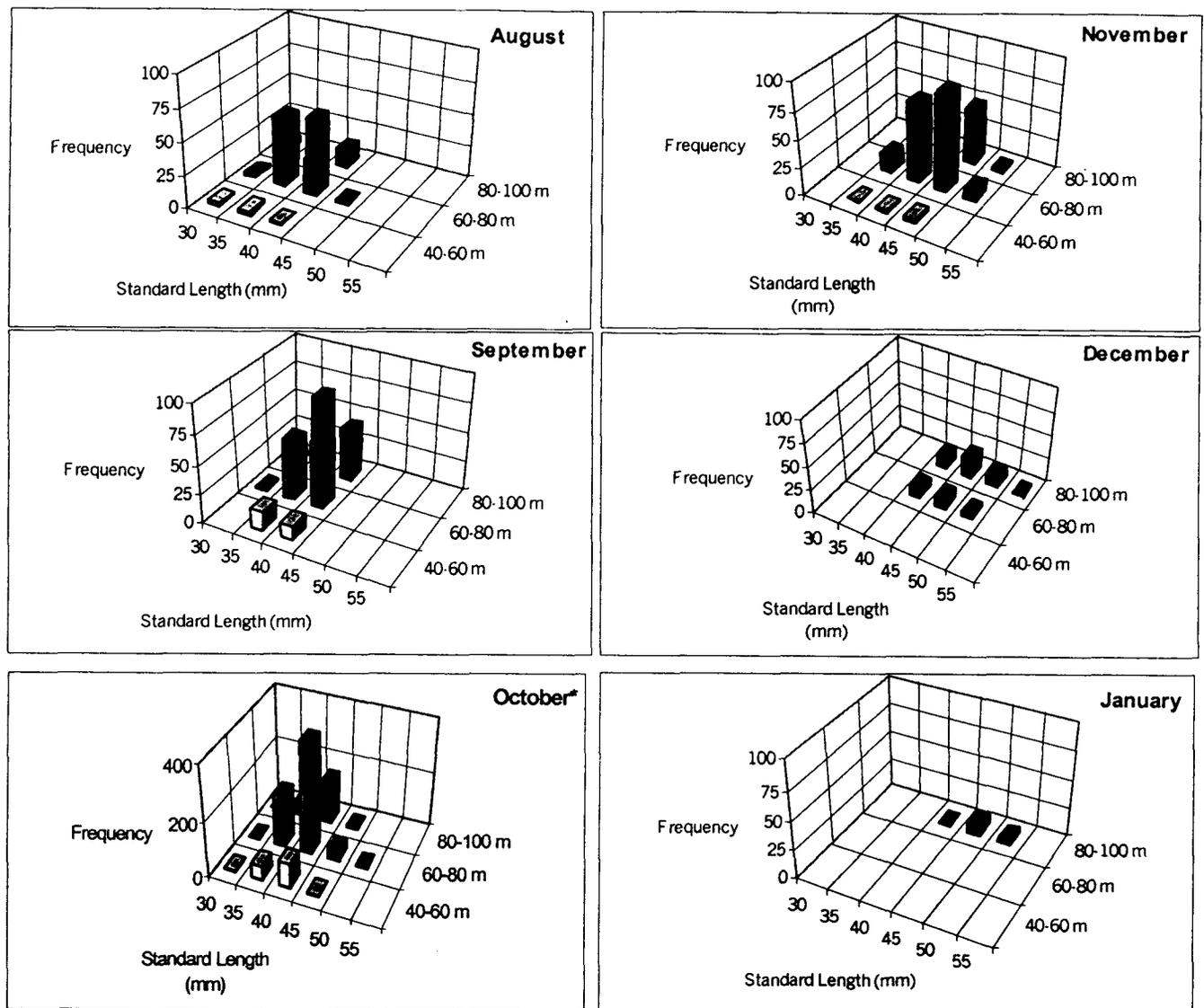


Figure 4. Length frequency of *Sebastes elongatus* by depth stratum (40–60 m, 60–80 m, 80–100 m) by month. Fish were caught at random and fixed stations over soft benthic habitat in Monterey Bay, California. Each depth range was sampled at least monthly between March 1995 and February 1996. (* Note difference in scale for October.)

Size of all three dominant species differed significantly among depth strata ($p < 0.05$; table 2). Only one sample of *S. elongatus* with a mean length >50 mm was collected (in December) in 100 m depth (fig. 4). All samples of the largest *S. saxicola* (mean >90 mm; fig. 5) came from a depth of 100 m. All samples of the largest *S. levis* (mean >80 mm; fig. 6) came from depths >60 m.

Temporal Distribution

In all depth strata, *S. elongatus* first occurred at fixed stations on 23 August, following a long period of high SST that corresponded with a period of relaxation of upwelling (fig. 7). *Sebastes elongatus* were caught only at the deep stations in December and January; none were caught in February. *Sebastes saxicola* was first caught at

deep stations in April, but did not appear at the shallow stations until June. They were still present through February. Relatively large numbers of *S. levis* occurred in early August. They were not collected at the deep stations until September, but were still present at relatively high density through February.

Mean density of all three species was generally highest at the deep stations and lowest at the shallowest depth (fig. 7). All three species increased in abundance simultaneously, with peak density in September and October. This corresponded to a period of relatively high SST, relaxed upwelling, and decreased offshore transport, with periods of moderate onshore transport (fig. 2). Density of all three species declined in November and early December during a period of heavy winter storm ac-

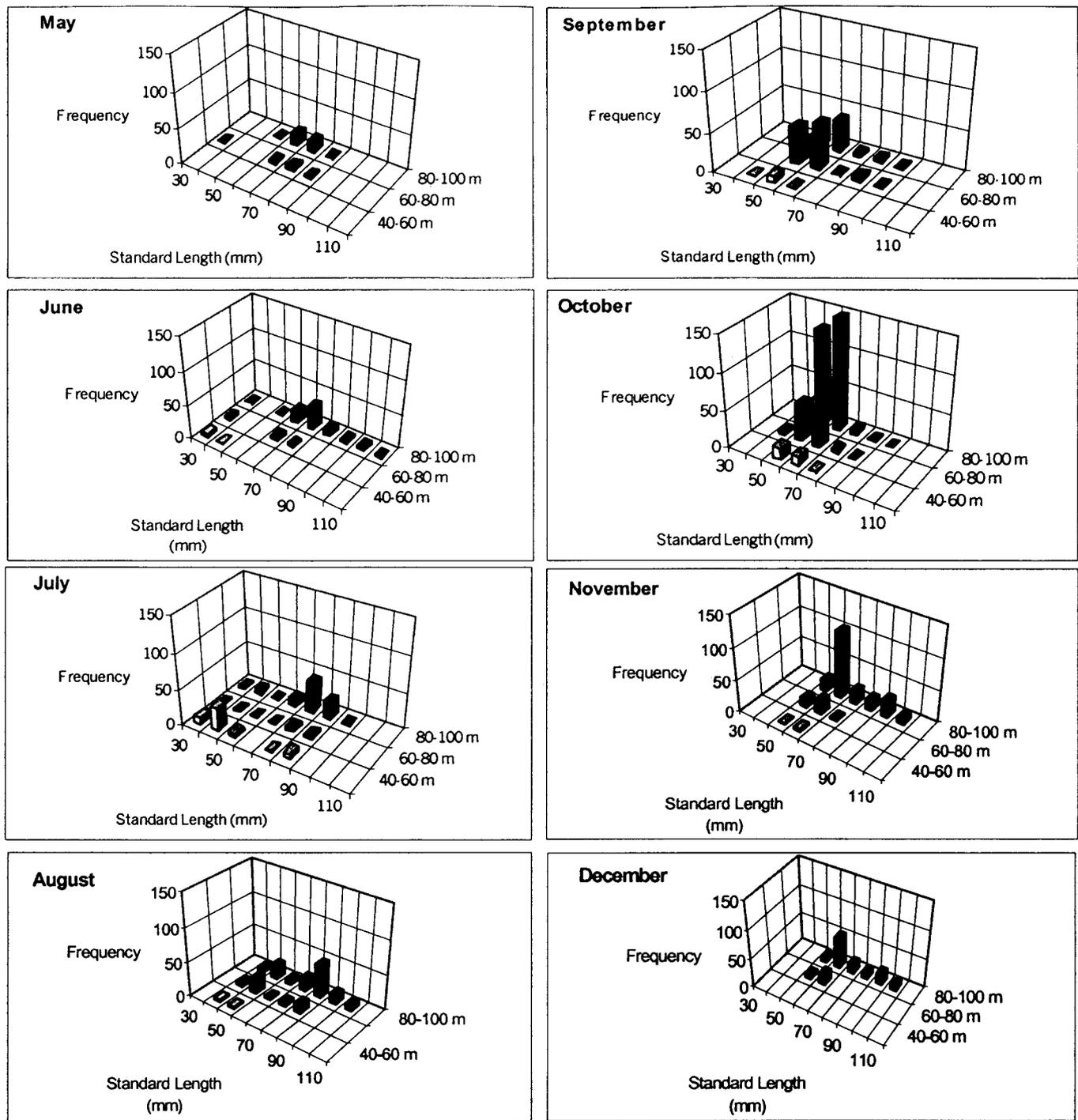


Figure 5. Length frequency of *Sebastes saxicola* by depth stratum (40–60 m, 60–80 m, 80–100 m) by month. Fish were caught at random and fixed stations over soft benthic habitat in Monterey Bay, California. Each depth range was sampled at least monthly between March 1995 and February 1996. *Sebastes saxicola* were caught during each month sampled, but only results from May through December 1995 are shown here.

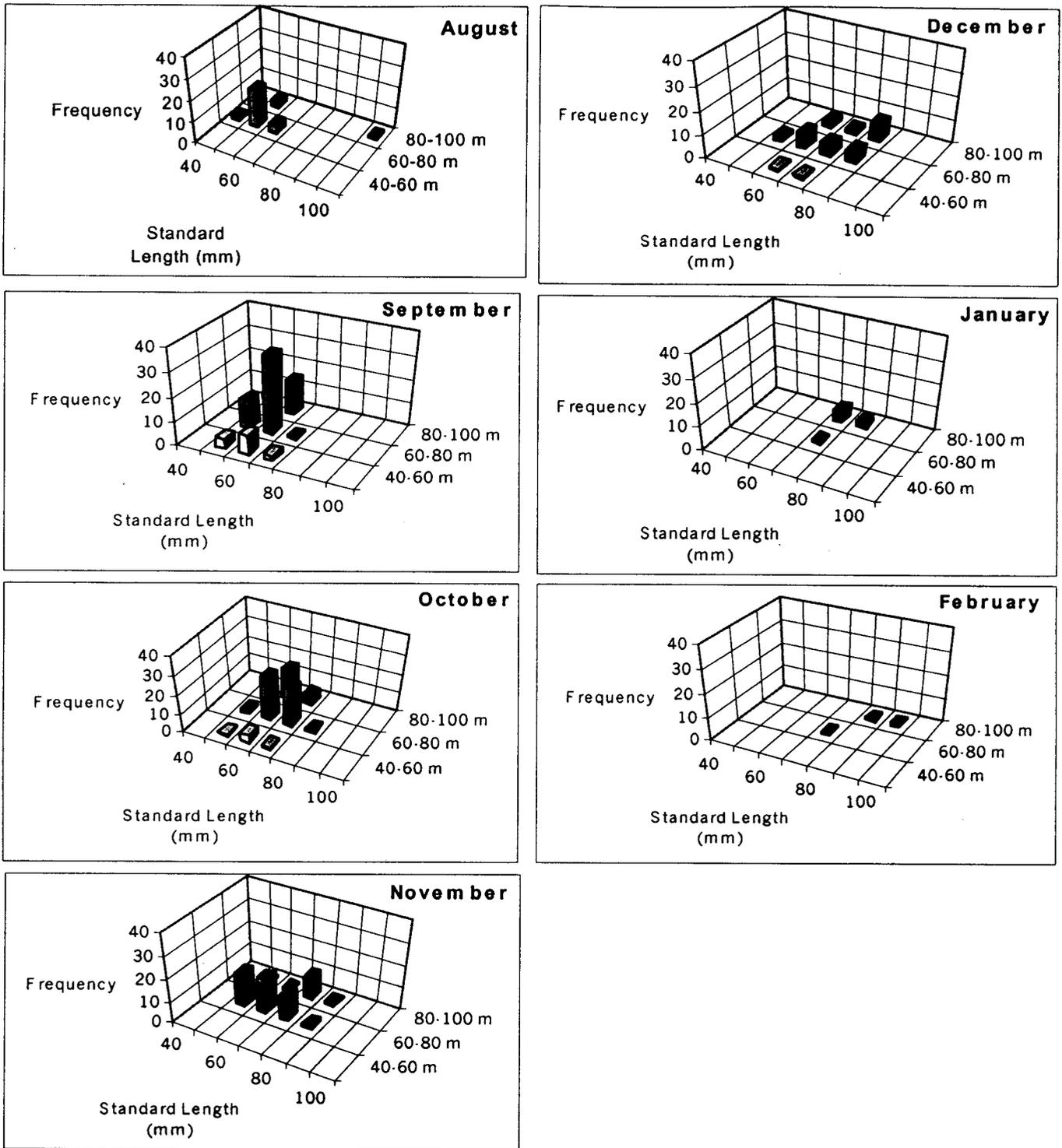


Figure 6. Length frequency of *Sebastes levis* by depth stratum (40–60 m, 60–80 m, 80–100 m) by month. Fish were caught at random and fixed stations over soft benthic habitat in Monterey Bay, California. Each depth range was sampled at least monthly between March 1995 and February 1996. *Sebastes levis* were caught each month between June 1995 and February 1996, but a total of only 3 individuals was caught in June and July.

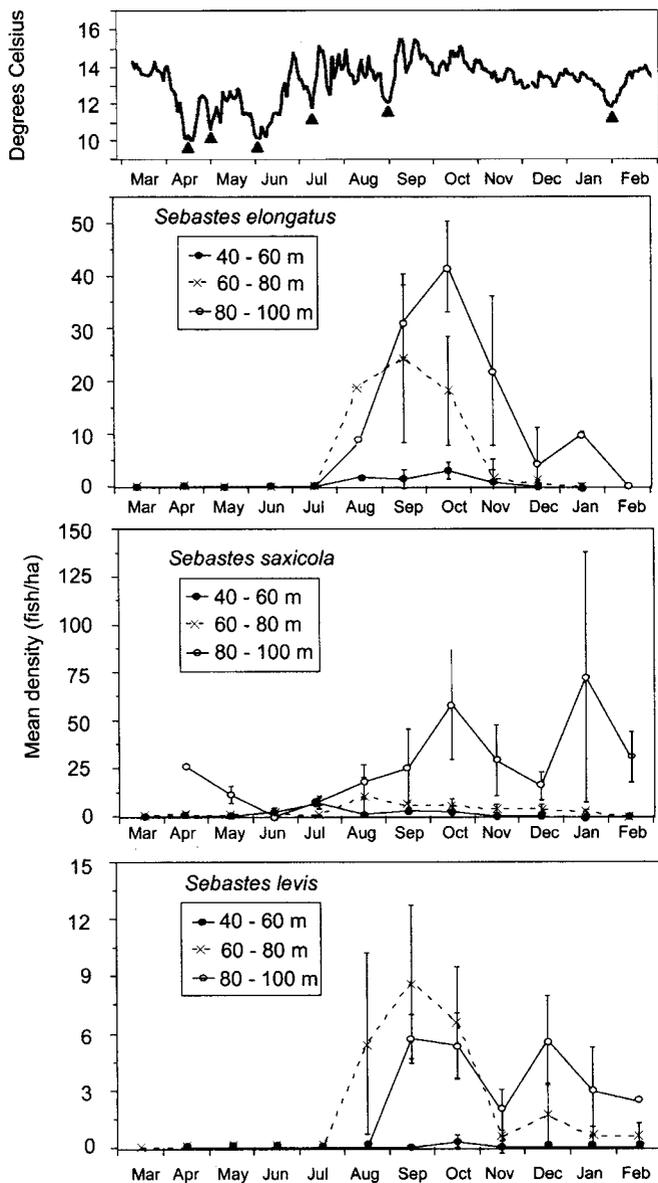


Figure 7. Sea-surface temperature and mean density (fish/ha) of juvenile *Sebastes elongatus* ($n = 634$), *S. saxicola* ($n = 897$), and *S. levis* ($n = 148$) at fixed stations by month. Two to five tows were completed per depth stratum per month. Error bars are one standard error. Arrows in sea-surface temperature denote distinct periods of upwelling. (Note difference in scale among graphs.)

tivity, then increased again in late December and January. This second peak also corresponded to a period of relatively high SST, relaxed upwelling, and increased on-shore transport, with two major periods of onshore transport.

For all three species, size (i.e., modal, minimum, and maximum SL) increased steadily from recruitment to the end of our survey. *Sebastes elongatus* increased in size from August (mean = 38 ± 0.2 mm) to January (mean = 48 ± 0.6 mm; fig. 4). A first cohort of *S. saxicola* (50–80 mm SL) was collected from April through May (fig. 5).

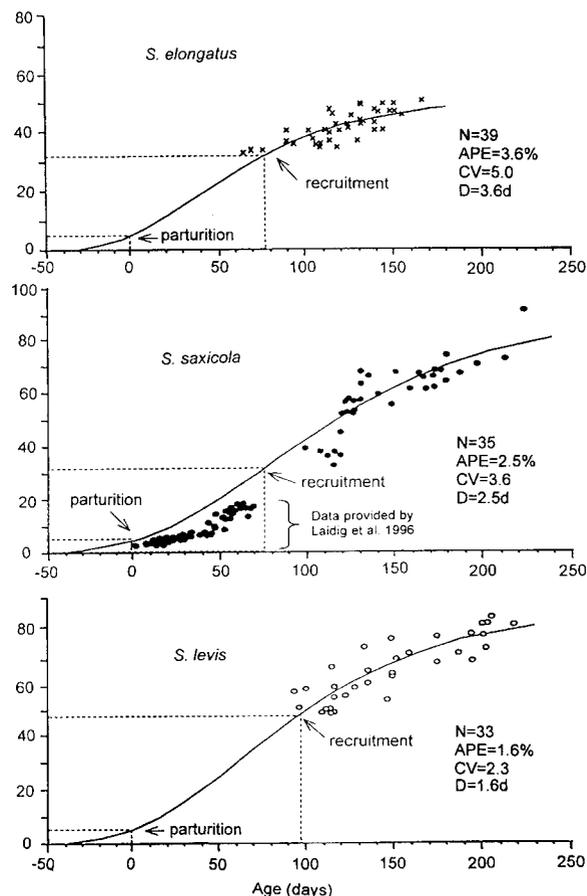


Figure 8. Predicted Gompertz growth functions and size-at-age data for benthic juvenile *Sebastes elongatus*: $L_t = 4.5 \times e^{3.81} [1 - e^{(-0.011t)}]$; *S. saxicola*: $L_t = 5.0 \times e^{2.84} [1 - e^{(-0.016t)}]$; and *S. levis*: $L_t = 5.0 \times e^{2.31} [1 - e^{(-0.021t)}]$. Specimens were caught over soft benthic habitat between 40 and 100 m in Monterey Bay, California, from March 1995 through February 1996. Ages were estimated from daily growth increments of the sagittal otoliths. Sample size, average percent error (APE), coefficient of variation (CV), and index of precision (D) of age estimates are provided for each species.

This cohort increased in catch and size through August and was gone by November. In mid-June, during a period of intense upwelling, a second cohort of small fish (30–40 mm SL) was caught. Density of the second cohort peaked in October. This cohort increased to 70 mm SL and was still present in samples through January. Size of *S. levis* increased from August (mean = 56 ± 0.6 mm) to January and February (mean = 79.9 ± 1.8 mm; fig. 6).

Growth

Growth rates were different among each of the three species (fig. 8). Growth of *S. elongatus* after recruitment, as determined by linear regression, was estimated to be 0.17 mm/day ($r^2 = 0.68$, MSE = 8.35). The growth rate of the second cohort of *S. saxicola* was estimated to be 0.32 mm/d ($r^2 = 0.65$, MSE = 47.35). Estimated growth rate of juvenile *S. levis* was 0.25 mm/day ($r^2 = 0.76$, MSE = 30.71).

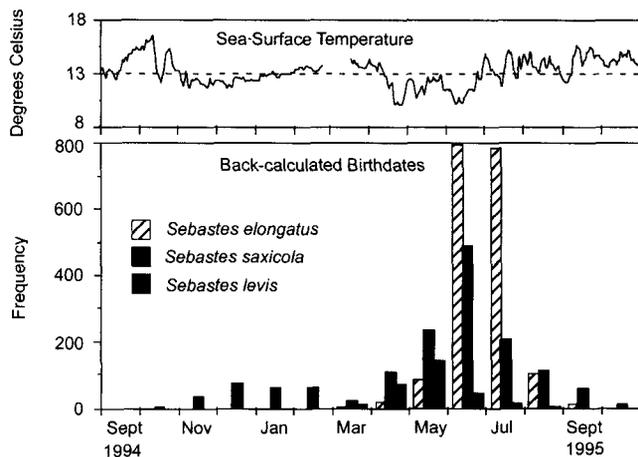


Figure 9. Timing of back-calculated birthdates for *Sebastes elongatus*, *S. saxicola*, and *S. levis* in relation to sea-surface temperature. Fish were caught over soft benthic habitat in Monterey Bay, California, between March 1995 and February 1996.

From the Gompertz growth curves for all three species, including both the data from this study and the larval data from Laidig et al. (1996) for *S. saxicola*, parturition was estimated to occur approximately 30–35 days after fertilization (fig. 8). On the basis of the smallest individuals caught, the initial age at recruitment was approximately 60 days following parturition for *S. elongatus*, 80 days for *S. saxicola*, and 100 days for *S. levis*. The Gompertz model predicted age at recruitment to be 75, 75, and 97 days, respectively.

Birthdate Distributions

Sebastes elongatus birthdates ranged from March through September (fig. 9). However, 98% of the birthdates were between May and August, with a peak in late June and early July. *S. saxicola* birthdates ranged from September 1994 to October 1995, with two peaks in frequency from December through February 1994 and in June 1995. Back-calculated birthdates for *S. levis* ranged from February to August 1995, with a peak in May. For all three species, peaks in back-calculated birthdates corresponded to periods of low SST (fig. 9).

DISCUSSION

Species Composition and Spatial Distribution

Several researchers have examined the recruitment of juvenile rockfish in complex rock habitats along central California. Nearshore fish communities in shallow (generally <25 m water depth) kelp beds and other rocky areas have been the focus of extensive surveys by the California Department of Fish and Game (CDFG) along the central coast from 1987 to 1999 (unpubl. data, D. VenTresca, CDFG, 20 Lower Ragsdale Dr., Monterey, CA 93940). Others have investigated species composi-

tion, development, and food habits of juvenile rockfish recruiting to central California kelp beds (Anderson 1983; Singer 1985; Hoelzer 1988; Carr 1991). Soft sediments in Monterey Bay traditionally have not been sampled for juvenile rockfish, but we collected fifteen species in this habitat at water depths of 40–100 m. Significant recruitment—particularly of *Sebastes elongatus*, *S. saxicola*, and *S. levis*—seems to occur in low-relief sediment on the shelf in Monterey Bay.

Rockfishes develop strong associations with specific substrata throughout different stages of their life (Larson 1980; Carlson and Straty 1981; Richards 1987; Matthews 1990; Carr 1991; Love et al. 1991). The type of habitat varies greatly among species. The adults of all three of the most abundant species in our survey are relatively deep dwelling, but not strictly associated with soft substrata. *Sebastes elongatus* commonly are found from 100–250 m depth, are relatively small (maximum length 43 cm), and associate with mud-cobble substrata near the edges of rocky areas along much of the U.S. West Coast (Percy et al. 1989; Stein et al. 1992; Yoklavich et al. 2000). Adult *S. saxicola* (maximum length 41 cm) are most abundant at 100–200 m (the larger, older adults at deepest depths) and occur predominantly on soft sediments after settlement (Yoklavich et al. 2000). These two relatively small species might not require the shelter and protection provided by high-relief rock habitats. Adult *S. levis* occur most commonly at depths >150 m in high-relief rocky areas, sometimes intermixed with soft mud (Yoklavich et al. 2000). Some of the largest rockfishes (up to 1 m total length), adult *S. levis* are found in rock crevices and under overhangs.

Some of the highest densities for all three species were found at two distinct locations in the southern half of Monterey Bay. Sidescan sonar surveys of the seafloor in southern Monterey Bay identified isolated areas of low-relief granite basement rocks and sedimentary outcrops, bounded by flat mud and sand at about 80–90 m water depth (Greene et al. 1995). Within and around this rocky habitat are linear scarps of cobble and sand patches. Juvenile *S. elongatus* and *S. saxicola* have been observed in these cobble and sand patches from submersibles (pers. observation by M. Yoklavich) and at shallower depths (R. Larson, San Francisco State Univ., 1600 Holloway Ave., San Francisco, CA 94132, pers. comm.). Newly settled *S. levis* have been seen on fine sand and clay sediments as well as over shell mounds and other complex substrata around the base of oil platforms (M. Love, Univ. Calif., Marine Science Institute, Santa Barbara, CA 93106, pers. comm.). It is likely that we sampled within low-lying patches of sand and cobble or along the sand-mud interface around low-relief rock outcrops, resulting in the clumped distributions of these species throughout the bay.

Temporal Distribution

The timing, duration, and magnitude of rockfish recruitment are related to timing of parturition, and to survival and transport of the pelagic stages. These processes are dynamic and result in high interannual and interspecific variation in recruitment (Anderson 1983; Kendall and Lenarz 1987; Carr 1991; Moser and Boehlert 1991). Benthic recruitment of rockfish to shallow (<30 m) nearshore habitats in central California typically occurs between April and August, with peak abundances in summer (Anderson 1983; D. VenTresca, CDFG, 20 Lower Ragsdale Dr., Monterey, CA 93940, unpubl. data). Recruitment of rockfishes to soft benthic habitat in water depths >40 m in Monterey Bay began during June in 1995, and abundance peaked in late summer and early fall. Strong upwelling conditions were still evident during this period, as in earlier months, but there also were periods of relaxed upwelling, with warmer sea-surface temperatures and onshore transport.

The timing and magnitude of recruitment could be influenced by either passive ocean transport or active swimming of pelagic or newly settled juveniles. It is possible that juvenile rockfish reach an ontogenetic stage during which they undergo biological or behavioral changes and begin to move toward shore. Pelagic juveniles are large enough to actively swim toward nearshore environments (Moser and Ahlstrom 1978; Larson et al. 1994) and also may change their position in the water column to minimize the effects of offshore transport and maximize the effects of onshore transport. Pelagic juveniles of many rockfish species, including *S. saxicola*, occur typically between 50 and 100 m, the zone of shoreward flow in an upwelling cell (Lenarz et al. 1991).

The dependence of recruitment on onshore transport was not clear for each of the dominant species. Although the highest recruitment of *S. saxicola* occurred during relaxed upwelling, a few small individuals started to appear in mid-June following a period of distinct upwelling. Similar appearances of larger pelagic *S. saxicola* in nearshore waters of Monterey Bay during heavy upwelling were reported by Larson et al. (1994). This suggests that the trigger for onshore movement by pelagic juveniles is internal and that larger pelagic juveniles may actively move toward nearshore habitats, possibly by regulating their vertical distribution in the water column, even in the presence of offshore advection of the Ekman layer during upwelling. Passive transport by onshore currents would work in concert with these active efforts, resulting in high recruitment during periods of both passive and active transport (Anderson 1983; Carr 1991; D. VenTresca, CDFG, 20 Lower Ragsdale Dr., Monterey, CA 93940, unpubl. data). Peak recruitment of all three species between August and September during this study could have been a result of active transport triggered by

some internal biological signal coupled with oceanographic conditions favorable to onshore transport.

Juveniles of some species of rockfish may take several weeks to a year to reach benthic habitats (Ahlstrom 1961; Boehlert 1977) or may remain in midwater before settling even after they have reached nearshore habitats (Larson et al. 1994). The smallest *S. saxicola* collected during our study was 32 mm, with the majority between 45 and 60 mm. Because of the mesh size of our net, we assume that the smallest benthic fishes were being sampled. Anderson (1983) observed benthic juveniles between 27 and 53 mm in length as early as April on soft sediment at the outer edges of kelp beds in Monterey Bay. Pelagic juveniles caught off central California in midwater trawls during 1984–95 were mostly between 20 and 40 mm, but a few were as large as 52 mm (R. Larson, San Francisco State Univ., 1600 Holloway Ave., San Francisco, CA 94132, pers. comm.). These pelagic juveniles may take some time to reach benthic habitats, but the overlap in size between pelagic and benthic juveniles suggests that they do not settle into intermediate habitats before recruiting to the area sampled in our study.

Pelagic juveniles of *S. levis* are not abundant in samples collected by midwater trawls in May and June off central California: only 30 individuals (SL = 15–58 mm) were caught from 1988 to 1996 (Echeverria et al. 1990). In our study, *S. levis* began recruiting to soft sediments at approximately 50–60 mm in length. The overlap in pelagic and benthic juvenile sizes suggests that *S. levis* does not settle in an intermediate habitat before recruiting to the soft sediments surveyed in this study.

Once juveniles of *S. elongatus*, *S. saxicola*, and *S. levis* recruited to the seafloor, the time they were present in the study area varied. *Sebastes elongatus* recruited at a small size, and remained in the area for approximately three months, with abundances declining sharply for fishes over 50 mm in length. The few specimens that were over 50 mm were caught along the edge of the submarine canyon. *Sebastes saxicola* and *S. levis* recruited at larger sizes, used the area until reaching a much larger size and for a longer time, and attained larger sizes than *S. elongatus* on this habitat. Juveniles of all three species underwent ontogenetic movements to deeper waters, with density and size of fishes increasing with depth, during the course of this study.

Movement to deeper waters could be triggered by a number of physical or biological factors, including temperature, size, age, food conditions, and photoperiod (Boehlert 1981; Boehlert and Yoklavich 1983; Haldorson and Richards 1987). In this study, declining density corresponded to a period of increased winter storms in November and early December. When wind and swell were high, fewer numbers of all fishes, not just rockfishes,

were caught in the trawl, suggesting lower efficiency of sampling gear or lower availability of the fish. After storms, density increased, but only in the deep stratum.

Growth

Daily growth increments in sagittal otoliths of *S. elongatus*, *S. saxicola*, and *S. levis* were not directly validated in this study. However, they have been validated for a number of fishes (Brothers et al. 1976; Butler 1989; Stevenson and Campana 1992), including juvenile black rockfish (*S. melanops*) held in the laboratory (Yoklavich and Boehlert 1987). As is the case for several species of rockfishes (Penney and Evans 1985; Laidig et al. 1991; Ralston et al. 1996), a distinct growth increment formed at extrusion. For all analyses of growth and birthdate distributions of *S. elongatus*, *S. saxicola*, and *S. levis*, growth increments were assumed to be daily.

Growth rates of most benthic rockfish juveniles range from 0.20 to 0.31 mm/d (Carlson and Haight 1976; Matthews 1990; Love et al. 1991); higher growth rates have been estimated for *S. jordani* (0.59 mm/d) and *S. paucispinis* (0.72 mm/d; Woodbury and Ralston 1991). During our study, mean growth rates ranged from 0.17 mm/d for *S. elongatus* to 0.32 mm/d for *S. saxicola*.

Birthdate Distributions

Birthdate distributions back-calculated from daily growth increments have been used to evaluate yearly survival of juvenile rockfish (Woodbury and Ralston 1991; Yoklavich et al. 1996). Depending on the time of sampling, birthdate distributions back-calculated from juveniles are often skewed toward newer recruits, because older fish have been subject to more age-specific mortality (Yoklavich et al. 1996). Distributions can be adjusted if size-specific rates of mortality during larval and pelagic juvenile stages can be estimated. For this study, the mortality rates are unknown. Once fish have settled they are subject to a substantially lower rate of mortality than at earlier stages (Campana and Jones 1992); therefore, correction for mortality that has occurred after settlement should not be necessary.

The peak in birthdates for all three dominant species corresponded to a pronounced drop in SST and increase in offshore transport, which occurred during summer 1995. For *S. elongatus* this period matches the narrow range of timing of parturition (Echeverria 1987). This supports our interpretation of daily increments in the otoliths. Also, because birthdates for *S. elongatus* were similar to expected months of parturition, the timing of recruitment might be typical of other years.

For *S. saxicola* a small peak in the distribution of back-calculated birthdates matches the peak months of parturition (November–March; Echeverria 1987). However, a much larger peak occurred between April and August,

completely outside the predicted range. All *S. levis* birthdates fell beyond the predicted dates for parturition. Moser and Boehlert (1991) also reported *S. levis* larvae as late as July in one of five CalCOFI sampling years between San Francisco and Baja California. This timing of parturition for surviving benthic rockfish is most likely a result of higher survival of those individuals born between April and August. Alternately, if growth increments were not produced on a daily basis, individuals would be older than estimated, and birthdates would fall within predicted dates. However, there is no evidence to suggest that growth increments in rockfish otoliths are not daily.

Juvenile rockfish spawned late in the season, after the onset of upwelling, had the highest survival rate. During the end of 1994 and beginning of 1995, temperatures in the California Current were anomalously high, with conditions characteristic of an El Niño year (Hayward et al. 1996). There is successful early parturition for rockfishes during years with normal upwelling intensity (Woodbury and Ralston 1991). During years with reduced or delayed upwelling, successful parturition occurs later in the season; these are years when cumulative survival is poor (Woodbury and Ralston 1991).

Highest survival of *S. mystinus* (blue rockfish) and *S. flavidus* (yellowtail rockfish) occurred when SST and upwelling were at intermediate levels, with low survival during years of extreme temperatures (Ralston and Howard 1995). During a two-year El Niño event, only larvae released late in the year were represented in birthdate distributions of juveniles of *S. jordani* (Yoklavich et al. 1996). The high temperatures early in the 1994–95 parturition season, coupled with late successful parturition as predicted from the birthdate distributions, match findings of these previous studies. Larvae born after the transition to upwelling experienced lower mortality rates and higher survival, possibly because of increased food, growth, and offshore transport away from nearshore predators.

Another explanation for higher abundance of those born late in the season is that juveniles from earlier periods of parturition either survived to the stage of settlement and perished after settlement, or all settled outside of Monterey Bay. In March 1995, unusual flood conditions in the Salinas Valley affected nearshore conditions in the bay. The Salinas and Pajaro Rivers, which typically have low flows, poured large amounts of water, silt, and debris into Monterey Bay. Waters throughout Monterey Bay were brown and turbid. Unusual amounts of silt, mud, and debris were present in our samples, and fewer fish of all species were caught during this time. These conditions could have been unsuitable for juvenile rockfish survival. Assuming juveniles born earlier in the year settle at the same size and age as those that set-

tle later in the year, juveniles born during peak periods of spawning for *S. saxicola* and *S. levis* would have been recruiting to benthic habitats during these conditions of poor water quality. This could explain survival of only those individuals born later in the season, when conditions for recruitment had improved.

CONCLUSIONS

Our study suggests that soft benthic sediments provide important habitat for recruitment of some relatively deep-dwelling rockfishes. This habitat, along with near-shore rock outcrops and kelp forests, could be considered essential fish habitat—nursery areas that are particularly important to the survival of rockfish populations. Furthermore, oceanographic conditions could influence both the timing of juvenile recruitment and the survival of recruits during larval and pelagic juvenile stages.

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