Abstract.–Rockfish are among the most prevalent members of nearshore ichthyoplankton assemblages off central California, yet their abundance varies greatly from year to year. Warm events, like El Niño, can have pronounced effects on the success of a year class. We evaluate distribution, abundance, and species composition of rockfish larvae on small spatial and temporal scales in the upwelling center north of Monterey Bay during an extended El Niño (December 1991 through June 1993) relative to regional hydrography.

Anomalously warm, low-salinity water to depths greater than 50 m during much of our study was indicative of an onshore displacement of the California Current. Upwelling was reduced and delayed relative to other years. The two years differed, however, in the intensity, duration, frequency, and direction of wind events. Larval rockfish abundance was similar in both years of the El Niño, peaking in early February, and was among the highest when compared with estimates from CalCOFI surveys off central California (1951–84). Using larval ages, we determined that median birthdates of shortbelly rockfish were in early- to mid-February both years. Growth rates of larval shortbelly rockfish did not differ among months or between years. Relative to 1993, rockfish larvae were more abundant, and sizes of larval shortbelly were significantly greater at onshore stations in 1992. This coincided with onshore advection of water during the onset of the El Niño, suggesting retention of larvae nearshore. Initiation of upwelling in March and April 1993 and fewer larvae at onshore stations are indicative of greater offshore transport during the second year.

Juvenile rockfishes were extremely rare in summer of 1992; in 1993 they were twenty times more abundant and larger. Surviving juvenile shortbelly rockfish were born late during both years; upwelling occurred coincidentally during this period in 1993 but not in 1992. We suggest that substantially higher survival and recruitment of juvenile rockfishes in 1993 was due to increased offshore transport and perhaps lower predation during the larval stages.

Nearshore assemblages of larval rockfishes and their physical environment off central California during an extended El Niño event, 1991–1993

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Ocean conditions off central California are influenced seasonally by a variety of factors and processes that operate on a local scale (e.g. wind, upwelling, freshwater input, and bathymetry) and larger spatial scales (e.g. the California Current System and El Niño events). Prevailing winds from the northwest produce relatively intense upwelling, particularly near capes and headlands, typically during March through September (Kelly, 1985; Breaker and Broenkow, 1994; Rosenfeld et al., 1994a). An abrupt decrease in sea-surface temperature, occurring sometime between February and May, defines the spring transition to coastal upwelling, which is associated with increased nutrient concentration, primary production, and offshore transport of surface water. Because the coastal ocean environment can respond rapidly to changes in local wind speed, direction, and duration, onshore transport of water off central California can occur during periods of reduced equatorward winds and subsequent cessation of upwelling (Broenkow

and Smethie, 1978; Rosenfeld et al., 1994a). This transport is manifested nearshore by the occurrence of warm, relatively low salinity water representative of the offshore core of the California Current.

Point Año Nuevo (37.1°N, 122.3°W), to the north of Monterey Bay, has been identified as a distinct center of upwelling, associated with bifurcated plumes of cool, saline, nutrient-rich surface water that are advected both seaward and southward across Monterey Bay (Tracy, 1990; Schwing et al., 1991; Rosenfeld et al., 1994a). According to satellite and in situ data, these recurrent upwelling plumes can extend 10–100 km offshore and persist from days to weeks. As it flows equatorward, some of this upwelled water is advected into the bay.

Rockfishes (*Sebastes* spp.) are tremendously diverse, dominate coastal benthic fish assemblages and support heavily exploited recreational and commercial fisheries in California (Lea, 1992). Although rockfish larvae are among the most prevalent members of nearshore ichthyo-

plankton assemblages, especially off central California, annual abundance varies widely (Moser and Boehlert, 1991; Moser et al., 1993). Factors affecting survival of young fishes, including hydrographic conditions and associated transport processes, density of prey and predators, and spawning seasonality are potentially critical determinants of rockfish recruitment.

Rockfishes are viviparous, with larval release (parturition) occurring mainly from January to April for many of the species off central California (Wyllie Echeverria, 1987), just before and during the onset of upwelling. Duration of the pelagic larval and juvenile stages of many species is typically several months (Anderson, 1983; Woodbury and Ralston, 1991) but may be up to one year (Boehlert, 1977). The arrival and subsequent settlement of pelagic juvenile rockfishes in subtidal areas off central California may be associated with upwelling events and onshore transport during periods of wind relaxation (VenTresca et al., 1990; Larson et al., 1994). The recurring bifurcated plumes of upwelled water off Pt. Año Nuevo, a relatively unfished area that could serve as a source of larvae, interspersed with occasional periods of wind relaxation and onshore transport, may be important vehicles for transport of young rockfishes from upwelling centers into nearshore areas of Monterey Bay and farther south.

Warm events, often indicative of an El Niño, occur along the coast of California every 2–10 years (Norton et al., 1985) and persist for 1–3 years (Chelton et al., 1982). Strong events occurred coastwide in 1926, 1941, 1958, and 1983 (Ware, 1995). El Niño-like conditions can include 1) increased sea-surface temperature (SST) and depth of thermocline; 2) positive sea-level anomalies (Chelton and Davis, 1982); 3) reduced upwelling, nutrients, and primary and secondary production (Fiedler, 1984; McGowan, 1985; Miller et al., 1985); and 4) increased poleward and onshore flow of coastal water (Simpson, 1984; Hayward et al., 1994; Lynn et al., 1995). Significant increases in SST were noted off central California during winters of 1972, 1976, 1979, and 1983, which corresponded with El Niño episodes (Breaker et al., 1983).

Warm events like, but not restricted to, El Niño can have disastrous effects on year-class strength of rockfishes, a group with arctic to temperate affinities and distribution (Karpov et al., 1995; Lenarz et al., 1995; Ralston and Howard, 1995). Anomalously warm water and suppression of upwelling have been associated with large-scale reductions in the primary prey (e.g. euphausiids and smaller zooplankton) of juvenile and adult rockfishes (Mullin and Conversi, 1989). Reduced prey abundance may negatively affect the somatic and reproductive condition of adult rockfish (Lenarz and Wyllie Echeverria, 1986;

VenTresca et al., 1995), potentially disrupting the timing, location, and net output of reproduction. Changes in distribution and dispersal patterns of pelagic larvae, and altered production of their prey and predators, are expected during anomalous warm events (Bailey and Incze, 1985; Brodeur et al., 1985).

In this paper we evaluate distribution, abundance, and species composition of rockfish larvae and associated hydrography on small spatial (<20 km) and short temporal (biweekly to monthly) scales in an upwelling center north of Monterey Bay during an extended El Niño event (1991–93). From size, age, and estimated growth models, we compare birthdate distributions of early larvae and surviving pelagic juveniles of the most common species. We discuss potential larval transport and subsequent strength and timing of juvenile recruitment to nearshore areas along the central California coast.

Methods

Sampling

Ichthyoplankton surveys were conducted during daytime aboard the RV *Ricketts* (ca. 11 m long) at five stations along a northeast–southwest transect off Davenport, California (37°N, 122°10'W; Fig. 1). Sta-
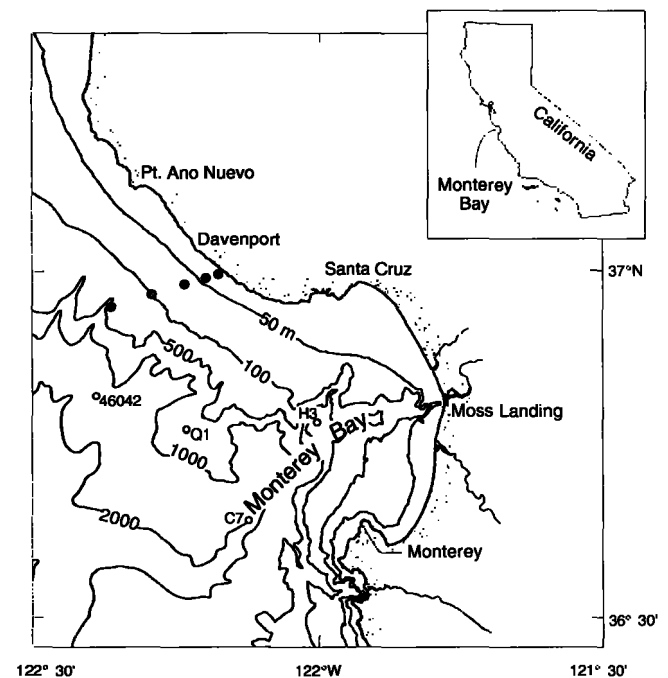
Figure 1

Monterey Bay study area and five stations (solid dots) sampled for larval fish off Davenport. Sites of wind measurements (46042) and 1989–91 CTD casts (H3, C7, and Q1) are indicated.

tions were located across the shelf at 1 km (15 m water depth), 3 km (30 m water depth), 7 km (60 m water depth), 13 km (100 m water depth), and 19 km (180–713 m water depth) from shore. During 1991–92, samples were collected at approximately two-week intervals from early December to April; less frequent sampling extended through June because of the absence of expected upwelling events during spring. Sampling between January and April 1993 was limited to monthly intervals by frequent storms and rough seas.

Larvae were sampled with two 70-cm (mouth diameter) open nets of 0.505-mm mesh, black Nitex fitted onto a bongo frame. Volume of water filtered (30–465 m^3 per net) was estimated from calibrated mechanical flowmeters positioned in the mouth of each net. Tows were made parallel to bathymetry at 1–3 k for 2–20 min (depending on depth) obliquely from near the bottom to the surface at nearshore stations and from 200 m to the surface at the offshore station. Three replicate tows were conducted at most stations (Table 1). Oceanographic data were collected

from near bottom to the surface at each station with a calibrated CTD (conductivity, temperature, and depth) profiler (model SBE 19 SEACAT, Sea-Bird Electronics). Daily wind speed and direction during the survey period in each year were calculated from daily averages of east and north wind components measured at the National Data Buoy Center moored buoy 46042 (Fig. 1).

Plankton samples were preserved at sea, one sample from each bongo pair in 5% buffered formalin and the other in 80% buffered ethanol. Rockfish larvae were sorted under a dissecting microscope from each paired sample for all replicates per station. Formalin-preserved rockfish from all replicates were enumerated for abundance estimates. Only one ethanol-preserved replicate per station was processed for species identification. Standard length (or notochord length for preflexion larvae) was measured to the nearest 0.1 mm for shortbelly rockfish, *Sebastes jordani*, and blue rockfish, *S. mystinus*, preserved in ethanol. Otoliths were removed for age determination from a subsample of these two dominant species; larval ageing methods (i.e. counting daily growth increments in otoliths) followed Yoklavich and Bailey (1990). Within the otolith microstructure of larval shortbelly rockfish, a well-defined increment is formed at parturition, which has been adequately resolved with optical microscopy at 1250× magnification (Ralston et al., 1996). Daily formation of increments in otoliths has been demonstrated in juvenile black rockfish (*S. melanops*; Yoklavich and Boehlert, 1987) and in shortbelly and brown rockfish (*S. auriculatus*; Laidig et al., 1991).

Birthdates of larval shortbelly and blue rockfishes were calculated by using a linear growth model (e.g. fitted from the aged subsample) to estimate age from length and by subtracting age from date of capture. Birthdate distribution estimated from larvae was compared with that estimated from older pelagic young-of-the-year shortbelly rockfishes collected from May to July, 1992 and 1993, near Monterey Bay (see Loeb et al.[1] for details of surveys). Ages of these pelagic juveniles were estimated from length by using linear growth models developed for this species and size range collected from central California during May and June 1992 and 1993 (Woodbury[2]). Birthdate distributions were corrected for age-specific mortality across all daily cohorts with rates modified from

Table 1

Dates of collection and number of replicate oblique bongo net tows conducted along an onshore–offshore transect off Davenport, California, during winter–spring months of 1991–93. Stations are defined by bottom depth (m) and distance from shore (km). "—" indicates no samples were taken.

| Date | Station depth (m) | | | | |
	15 (1 km)	30 (3 km)	60 (7 km)	100 (13 km)	200 (19 km)
1991–92					
02 December	3	3	2	3	3
18 December	3	3	3	3	3
09 January	3	3	3	3	3
23 January	3	3	3	3	3
06 February	3	3	3	3	3
21 February	3	3	3	3	3
12 March	3	3	3	3	3
02 April	3	3	3	3	3
04 May	—	—	—	1	1
16 June	—	3	3	3	—
Subtotal	24	27	26	28	25
1993					
29 January	3	3	3	3	3
12 February	—	—	3	3	3
07 March	—	3	—	—	3
06 April	—	3	—	3	3
Subtotal	3	9	6	9	12
Total	27	36	32	37	37

[1] Loeb, V. J., M. M. Yoklavich, and G. M. Cailliet. 1994. The importance of transport processes in recruitment of rockfishes (Genus *Sebastes*) to nearshore areas of Monterey Bay, California. Final Report, NOAA, California Sea Grant College, Project R/F-142, 25 p.

[2] Woodbury, D. 1996. Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Dr., Tiburon, CA 94920. Unpubl. data.

Ralston and Howard (1995): 0.1165, 0.10, 0.08, 0.06, 0.04, and 0.03/d for fish of age <15, 15–27, 28–42, 43–70, 71–100, and >100 d, respectively.

Larval identification

Preflexion and flexion rockfish larvae were identified primarily from melanistic pigment patterns, including: length of ventral midline series, occurrence of dorsal midline pigmentation, and occurrence of pectoral fin pigmentation. Distinctions among larvae with shared primary pigment patterns were based on secondary pigment characters (e.g. external dorsal midline pigment configuration, lower lip pigment, and pectoral fin size and pigment pattern), and on reproductive seasonality of adults (Wyllie Echeverria, 1987; Love et al., 1990).

Preextrusion, yolk-sac, and preflexion stages have been illustrated or described in some detail for 49 of the 52 species of rockfishes off central California (see Kendall [1991] for a general review). More advanced larval stages have been described for relatively few species of rockfish. We used serial descriptions of larvae from preflexion through flexion to identify shortbelly (Moser et al., 1977), blue (Moreno, 1993), cowcod (S. levis; Moser et al., 1977), bocaccio (S. paucispinis; Moser, 1967), and stripetail rockfish (S. saxicola; Laidig et al., 1996). All postflexion larvae with dorsal, anal, and pectoral fin rays were identified to species.

Squarespot rockfish, S. hopkinsi, were abundant as preflexion larvae and were identified cautiously from a description of their preextrusion stage (Moser et al., 1977). Two groups of species also were identified on the basis of shared pigment patterns. The "copper complex" informally is synonymous with the subgenus Pteropodus (Jordan et al., 1930; Kendall, 1991), and comprises copper (S. caurinus), gopher (S. carnatus), black-and-yellow (S. chrysomelas), grass (S. rastrelliger), china (S. nebulosus), and quillback (S. maliger) rockfishes. We include brown (S. auriculatus) and kelp (S. atrovirens) rockfishes in a "copper complex +" because their pigmentation is indistinguishable from members of Pteropodus. A "Sebastosomus +" group includes black, olive (S. serranoides), yellowtail (S. flavidus), widow (S. entomelas), and bank (S. rufus) rockfishes. Identification of this group is limited because yolk-sac and early preflexion larvae are indistinguishable from many other species, including most in the subgenus Sebastomus.

Data analysis

Larval abundance was calculated for each replicate at each station by multiplying the number of larvae by depth of tow and by dividing by the volume of water filtered per sample. Abundance was expressed as number of larvae per 10 m². Abundance data were examined for normality and were log-transformed where appropriate. Among-station and among-time differences in total abundance of larval rockfishes were tested for significance by using a 2-factor analysis of variance (ANOVA), including only those samples collected during the first eight periods in 1991–92 (i.e. those with three replicates per station and five stations per time period). Between-year comparisons of abundance were made with 2-factor ANOVA (i.e. factors were year and time) by using only those time periods and stations equally represented in both years. Specific time periods and stations that contributed to significant factors in the models were identified by using post-hoc pairwise multiple comparisons of cell means with Bonferroni-adjusted probabilities. Differences in mean size and growth rate of the two dominant species of larval rockfish among stations, collection times, and years were similarly analyzed.

## Results

The physical environment

Our 1991–93 study period off central California was characterized by a prolonged El Niño event. Anomalously warm, low-salinity water in nearshore areas during much of our study indicated an onshore displacement of the California Current, similar to that reported by Lynn et al. (1995) for this time period and by Simpson (1984) for the 1982–83 El Niño event. Upwelling was reduced and delayed relative to other years, and distinct persistent upwelling plumes were not evident within the survey area during the sampling periods. The two years differed, however, in the intensity, duration, frequency, and direction of wind events that affected transport processes.

Coastal winds off Monterey prior to the 1991–93 El Niño event were primarily from the northwest during December to April (Fig. 2A), as estimated from daily wind components measured at buoy 46042 (Fig. 1) and averaged from 1988 to 1991. Associated with this prevailing wind pattern was a steady shoaling of cold, high salinity water, indicative of upwelling, in the upper 200 m of the water column in the outer part of Monterey Bay, as measured by a total of 37 CTD casts from stations H3, C7, and Q1 (Fig. 1) during April 1989, December 1989–April 1990, and December 1990–March 1991 (Fig. 2, B and C; raw data from Rosenfeld et al., 1994b).

During winter 1991–92, daily wind speeds were largely greater than the average calculated during

the same period from 1988 to 1991, but wind direction reversed in late December and the greater part of February and March 1992, blowing predominantly from the southeast for 2–12 d at a time (Fig. 3A). Coincidentally, water in the upper 80 m was warmer and fresher following these periods of southeast winds (Fig. 3, B and C); water of 15°C and 33.2‰ occurred near

the surface by 2 April. Contoured vertical sections of temperature during the spring ichthyoplankton surveys off Davenport in 1992 indicated an increasingly stratified and warm water column at least to 19 km offshore (Fig. 4A); isohalines were similarly stratified. There was no evidence of upwelling (i.e. no shoaling of isotherms and isohalines near the coast) during winter–spring 1992. For comparison with the following year, note that the 10°C isotherm remained below 100 m during the 1992 sampling season.
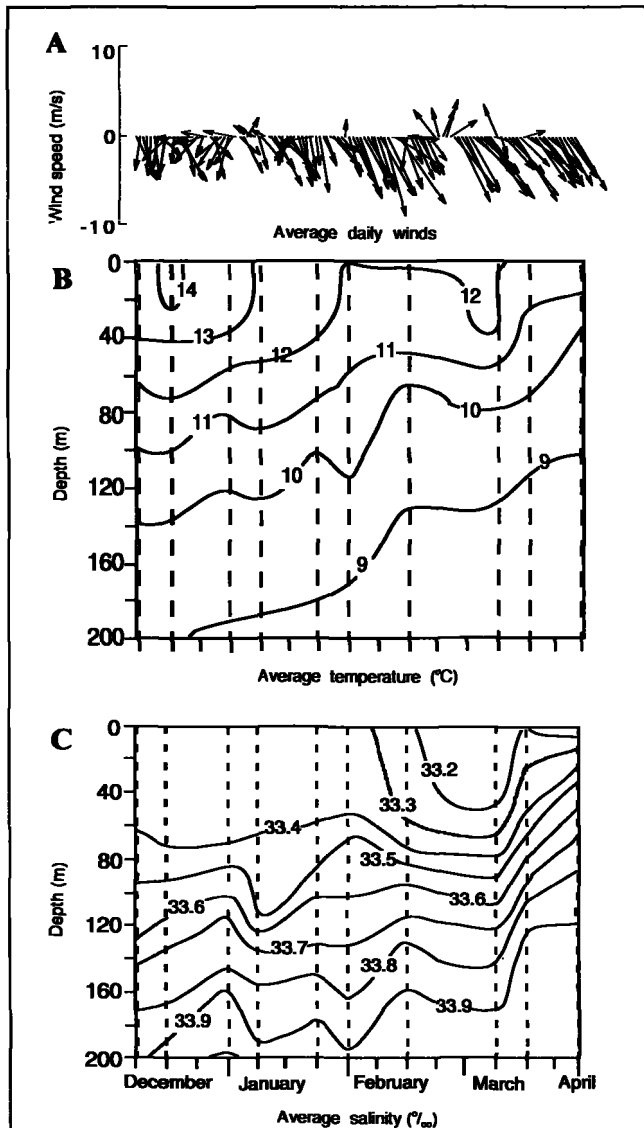
Figure 2

Wind, temperature, and salinity profiles for offshore Monterey Bay, California. (A) Wind vectors from December to April, as estimated from daily wind components measured at buoy 46042 and averaged from 1988 to 1991 (arrows point in the direction to which wind was blowing [north is toward top of page]); (B) weekly average temperature (°C); and (C) salinity (‰) in upper 200 m in the outer part of Monterey Bay during December to April, 1989–91. Weeks of CTD sampling are indicated with dashes. (Raw data from Rosenfeld et al., 1994b.)
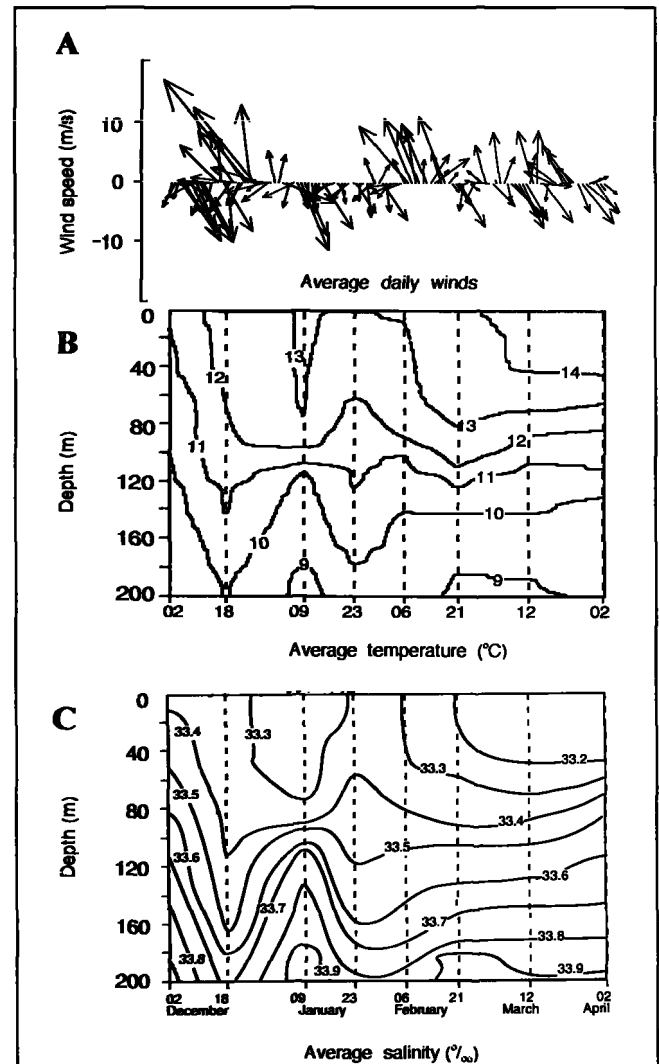
Figure 3

Wind, temperature, and salinity profiles for offshore Davenport, California. (A) Daily averaged wind vectors measured at buoy 46042 in Monterey Bay (arrows point in direction to which wind was blowing [north is toward top of page]); (B) temperature (°C); and (C) salinity (‰) in upper 200 m at an offshore station (19 km) during ichthyoplankton surveys 2 December 1991–2 April 1992. CTD sampling dates are indicated with dashes.

During winter 1993, a lens of warm surface water deepened from late January to mid-February, with 13.5°C water at 60 m along the transect line (Fig. 4B). Winds were variable, with no distinct periods of reversal. Unlike 1992, however, persistent wind from the northwest (favorable to upwelling) commenced in early March 1993 (Fig. 5A) and resulted in cooler water temperatures in the upper 80 m off Davenport by early April (Fig. 5B). This was the first evidence of upwelling during either year of the ichthyoplankton surveys, as indicated by the 10°C isotherm sloping up toward the coast from 19 km offshore in the 6 April 1993 CTD profile series (Fig. 4B).

Ichthyoplankton surveys

Patterns of distribution and abundance The 130 bongo-net tows made during ten ichthyoplankton surveys in 1991–92 (Table 1) contained 9,389 rockfish larvae; 39 tows made during four surveys in 1993 included 3,492 rockfish larvae. Rockfish larvae were collected during all surveys, occurring in 78.7% of all tows and in 100% of the tows made at the three stations 7–19 km from shore. Forty-seven percent of the rockfish larvae collected in 1992 and 66% in 1993 were identified as eight species or species-groups (Table 2). Shortbelly rockfish were numerically dominant both years, representing 46% of the total catch in 1993 and 29% in 1992. Shortbelly rockfish larvae occurred from late December to early May, largely in the offshore samples (13 and 19 km). Although much less numerous than shortbelly rockfish, blue, stripetail, and squarespot rockfish larvae also were relatively abundant each year (3–6% of the total). Although members of the "copper complex +" represented only 1–2% of the total catch and generally occurred in greater numbers offshore, they were the most abundant rockfish taxon identified at inshore stations (1 and 3 km).

Abundance of rockfish larvae varied among sampling dates and locations in 1991–92, with significant interaction between the two factors (ANOVA, $P<0.001$; Fig. 6A). Larvae were relatively abundant from January to April. Pairwise comparisons indicated that the large catches in early February 1992 at all stations were unique among all other time periods and that abundances across all stations early in the season (December and early January) were not significantly different from those that followed later (late-February, March, and April). Pairwise comparison of interstation abundance indicated two groups, one of stations closest to shore (1, 3, and 7 km) and another of the two offshore stations (13 and 19 km). The offshore stations had significantly greater abundance through time than did those in-

shore and, while abundance at most stations generally declined from a peak in early February, numbers of larvae remained relatively high through April at stations farthest from shore (13 and 19 km).

As with the 1991–92 collections, larval rockfish abundance varied significantly among sampling dates in 1993, with greatest abundances in February (Fig. 6B). Average abundances of larval rockfishes estimated at comparable stations and times from January through April were not significantly different between years (mean=602 larvae/10 m², SE=161 in 1992; mean=376 larvae/10 m², SE=179 in 1993; t-test, $P>0.383$), but distribution patterns differed. In contrast to the previous year, large catches of rockfish larvae occurred only at the two offshore stations in 1993. Significantly greater numbers of larvae occurred at the three stations closest to shore (1, 3, and 7 km) during January and February 1992, compared with the same months in 1993 (Kolmogorov-Smirnov tests, $P<0.05$).

Size, age, and birthdate distributions Size of larval shortbelly rockfishes collected on the same days in 1992 varied significantly among the 7, 13, and 19 km stations (ANOVA, $P<0.001$). Virtually all shortbelly rockfish larvae collected at the 7 km station were greater than 5 mm SL and significantly larger than those at the two offshore stations (Table 3). Shortbelly rockfish larvae were collected at the 7 km station only from early January to mid-March, and size composition remained similar throughout this period (overall mean=6.5 mm SL, SE=0.1). Size composition of shortbelly rockfishes did not differ significantly between the two offshore stations (overall mean=5.3 mm SL, SE=0.04), and the smallest larvae (<5 mm SL) were relatively abundant in all samples through early April.

Fewer samples and larvae collected at onshore stations in 1993 precluded among-station comparisons, although size composition of shortbelly rockfishes at the two offshore stations differed significantly (e.g. smaller larvae at the 13 km station compared with the 19 km station). The smallest larvae (<5 mm SL) were most abundant at the 13 km station in February and at the 19 km station in early April (Table 3).

Ages of 302 larval shortbelly rockfish collected in January–May 1992 and February–April 1993 were 1–28 d (Table 4). A least-squares linear model, *Length = a + b (Age)*, was fitted to separate sets of age-length data for each month in both years. Because no significant differences in growth rate were found among months (ANCOVA, $P>0.64$ [1992]; $P>0.73$ [1993]), age-length data were combined for each year. Moreover, there was no interannual difference in growth rate (ANCOVA, $P>0.90$). A least-squares linear model
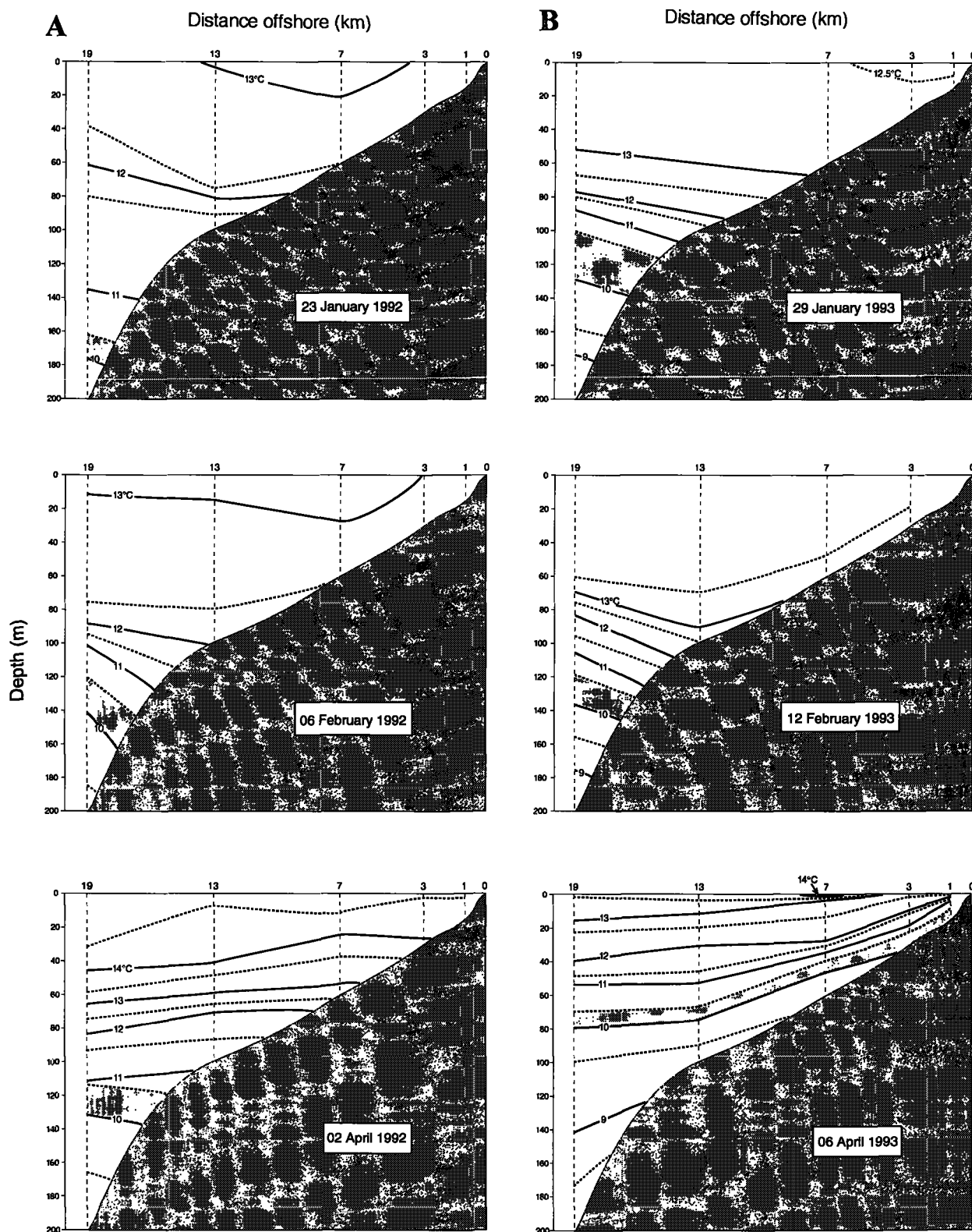
Figure 4

Vertical temperature profiles along the ichthyoplankton sampling transect off Davenport, California, during January, February, April, (**A**) 1992 and (**B**) 1993. The five CTD stations are indicated by distance offshore. Temperatures from 10.0 to 10.5°C are shaded for comparative purposes.

was computed for pooled age-length data because of the narrow age range (i.e. Length=4.63 + 0.20 [Age]; r^2=0.83; n=288). As an aside, the larval length at time of extrusion estimated by this model was 4.63 mm, which closely approximates the mean size of full-term

Figure 5

Wind, temperature, and salinity profiles for offshore Davenport, California. (A) Daily averaged wind vectors measured at buoy 46042 in Monterey Bay (arrows point in direction to which wind was blowing [north is toward top of page]); (B) temperature (°C); and (C) salinity (‰) in upper 200 m at the most offshore station (19 km) during ichthyoplankton surveys 29 January–6 April 1993. CTD sampling dates are indicated with dashes.

shortbelly rockfish larvae collected from females off central California (4.7 mm SL; Laidig et al., 1991).

Birthdate distributions were compared between shortbelly rockfish larvae collected early in the season and pelagic juveniles collected from May to July. According to larval ages and collection dates, birthdates of shortbelly rockfishes extended from December to early May (median=5 February) 1992, and January to early April (median=12 February) 1993 (Fig. 7). Birthdates estimated from juvenile shortbelly rockfishes occurred much later in both years (Fig. 7). The relatively few pelagic juveniles (2.3 fish/trawl, n=56 midwater trawls; see Loeb et al.[1] for survey results) collected in May–July 1992 had an extremely narrow range of birthdates from 8 April to 2 May (median=21 April). Greater numbers of surviving juvenile shortbelly rockfishes during May–July 1993 (75.1 fish/trawl, n=64 midwater trawls; see Loeb et al.[1] for survey results) had a broader range of birthdates from 24 January to 7 June (median=15 March).

Larval blue rockfish, the second most abundant of the identified species, had a much narrower range of lengths (2.8–6.9 mm SL) and, unlike shortbelly rockfish, were abundant only from late January to early February in both years (Table 3). Size of larval blue rockfishes, collected on the same days in 1992, varied significantly among the 7, 13, and 19 km stations (ANOVA, P<0.001), with larger larvae occurring at the innermost station (mean size=5.0 mm SL, SE=0.1; Table 3). As with shortbelly rockfish larvae, size composition of blue rockfishes was not significantly different between the two offshore stations (overall mean=4.5 mm SL, SE=0.1). Although 1993 collections were limited and comparisons not statistically significant, there was a continued trend of smaller blue rockfish larvae farther offshore.

Ages of 96 larval blue rockfish collected in January–February of 1992 and 1993 ranged from 2 to 21 d (Table 4); only 7 of these specimens were from 1993 because of problems with preservation. Because growth rates estimated over similar age ranges were not significantly different in January and February 1992 (ANCOVA, P>0.78), age-length data were combined and a least-squares linear model was calculated (i.e. Length=3.98 + 0.14 [Age]; r^2= 0.63; n=96). Birthdates were estimated for all blue rockfish larvae collected in 1992 and 1993 by using fish length and this growth model. Birthdate distribution was narrow in both years, ranging from 31 December 1991 to 21 February 1992 and from 12 January to 12 February 1993; the median birthdate was 27 January in both years. Birthdates could not be compared with those of pelagic juvenile blue rockfishes because no juveniles were collected in 56 midwater trawl
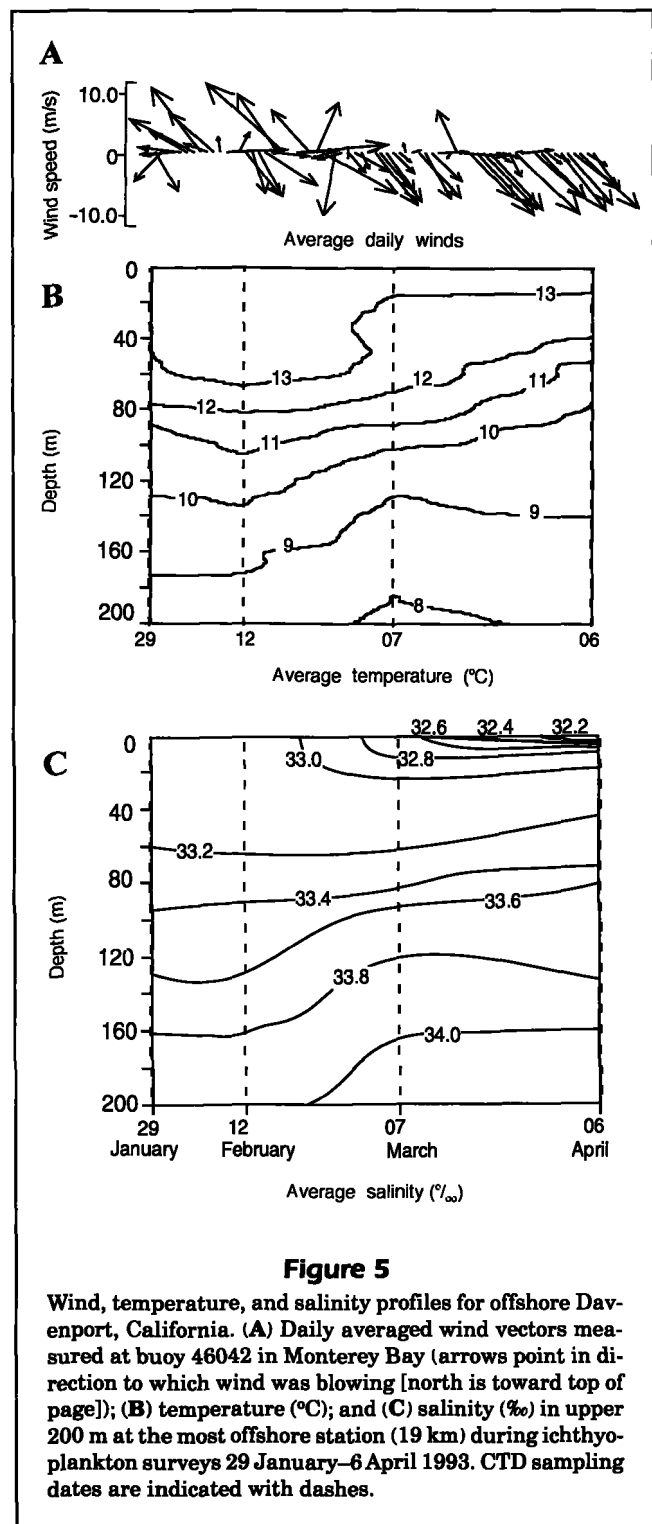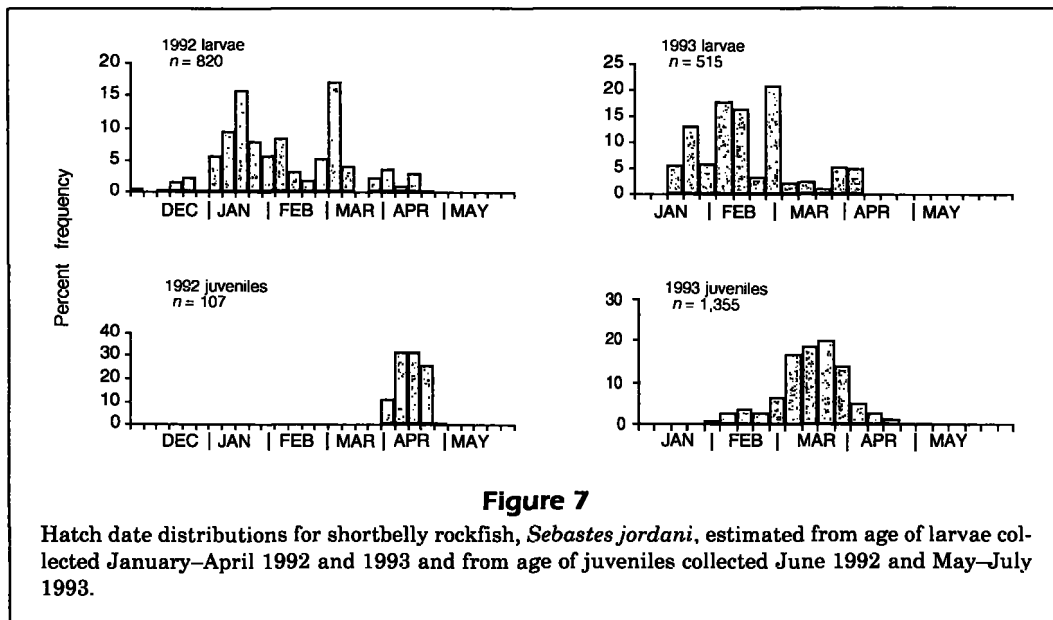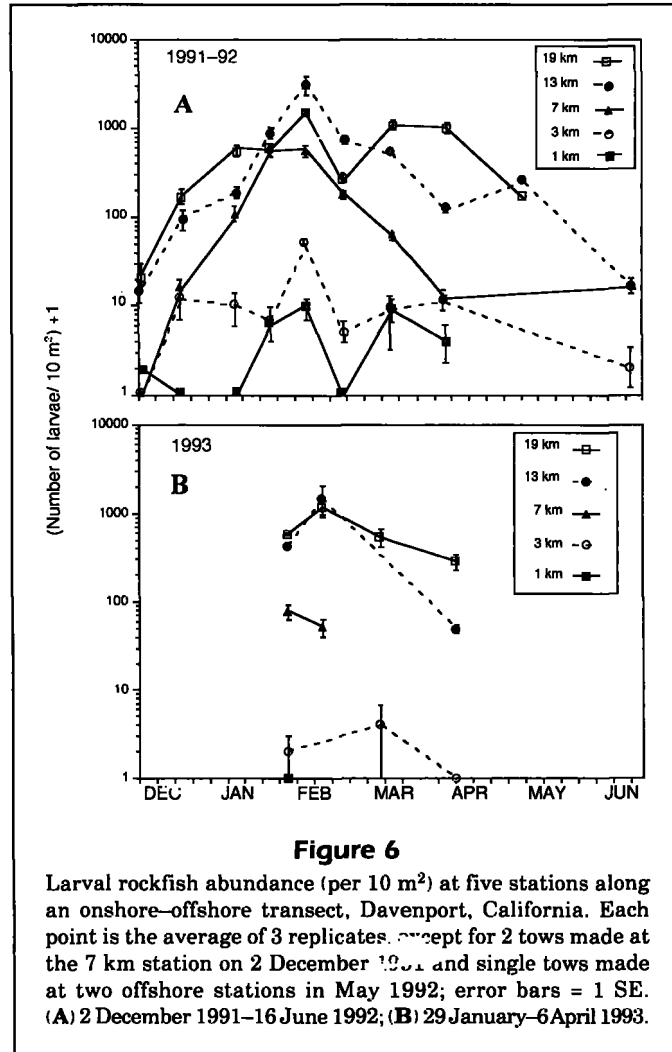
Table 2

Standardized abundance (number per 10 m²) of larval rockfishes in bongo-net tows collected off Davenport, California, December 1991–June 1992 and January–April 1993. "—" indicates that zero larvae were collected.

	2 Dec					18 Dec					9 Jan					23 Jan					6 Feb				
	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19
1991–1992																									
S. jordani	—	—	—	—	—	—	—	—	4	8	—	—	34	29	186	4	—	144	269	21	—	—	152	656	166
S. mystinus	—	—	—	—	—	—	3	—	—	—	—	7	15	—	38	2	4	85	21	109	—	—	109	180	90
S. hopkinsi (?)	—	—	—	—	—	—	3	12	12	—	—	—	49	4	34	—	—	25	25	11	—	—	67	46	54
S. saxicola	—	—	—	—	—	—	—	—	—	4	—	—	4	—	17	—	—	11	17	189	—	—	4	8	54
Copper complex +	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	7	—	4	3	4	38	17	27
S. paucispinis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	—	—	21	64	32	—	—	4	8	18
Sebastosomus +	—	—	—	—	—	—	—	8	—	—	—	—	4	—	—	—	—	—	—	4	—	—	42	—	36
S. levis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	4	—
Unidentified	—	3	—	13	37	4	8	19	56	62	—	3	42	69	169	8	4	113	191	186	3	61	160	3,127	714
Damaged	—	—	—	3	—	—	—	4	—	—	—	—	4	—	47	—	—	18	7	21	—	4	29	75	81
All *Sebastes* spp.	—	3	—	16	37	4	14	47	71	74	—	10	151	101	512	14	8	423	593	575	6	69	610	4,122	1,239

	21 Feb					12 Mar					2 Apr					4 May		16 Jun			Stand. abun.	Overall % abun.	Count (N)
	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19	13	19	3	7	13			
1992 (cont'd)																							
S. jordani	—	—	43	131	—	—	4	41	380	823	—	—	—	—	372	49	3	—	—	—	3,520	29	836
S. mystinus	—	—	9	26	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	719	6	183
S. hopkinsi (?)	—	—	43	33	18	—	—	4	23	14	—	—	—	—	4	4	3	—	—	—	487	4	121
S. saxicola	—	4	—	23	4	—	—	—	14	29	—	—	—	19	—	—	—	—	—	—	401	3	104
Copper complex +	—	—	17	3	4	8	4	8	—	—	6	7	4	27	—	—	—	—	10	4	207	2	52
S. paucispinis	—	—	—	3	13	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	189	2	50
Sebastosomus +	—	—	—	3	4	—	—	—	—	—	—	—	—	—	4	—	—	—	—	4	109	1	26
S. levis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	12	0.1	3
Unidentified	—	12	72	311	88	—	—	4	135	91	—	—	4	22	29	185	128	—	—	4	6,137	50	1,526
Damaged	—	—	26	7	9	—	—	4	28	29	—	—	—	—	—	—	—	—	—	—	394	3	94
All *Sebastes* spp.	—	16	208	540	162	8	8	62	585	987	6	7	7	68	410	238	138	—	10	12	12,175	100	2,995

	29 Jan					12 Feb			7 Mar		6 Apr			Stand. abun.	Overall % abun.	Count (N)
	1	3	7	13	19	7	13	19	3	19	3	13	19			
1993																
S. jordani	—	—	21	153	189	2	1,274	92	—	274	—	44	199	2,248	46	534
S. saxicola	—	—	—	32	76	—	91	70	—	9	—	—	4	282	6	62
S. mystinus	—	—	5	90	167	—	25	15	—	—	—	—	—	302	6	58
S. hopkinsi (?)	—	—	11	11	—	—	147	44	11	—	—	—	—	224	5	49
Sebastosomus +	—	—	—	48	11	—	45	19	—	7	—	—	—	130	3	28
Copper complex +	—	—	5	—	—	—	35	15	—	2	—	—	—	57	1	13
S. paucispinis	—	—	—	11	5	—	—	11	—	—	—	—	4	31	1	7
S. levis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified	—	8	53	99	156	25	395	282	—	126	—	39	188	1,371	28	343
Damaged	—	—	11	37	—	—	243	—	—	—	—	—	—	291	6	57
All *Sebastes* spp.	—	8	106	480	604	27	2,255	549	11	418	—	83	393	4,936	100	1,151

Figure 6

Larval rockfish abundance (per 10 m²) at five stations along an onshore–offshore transect, Davenport, California. Each point is the average of 3 replicates. except for 2 tows made at the 7 km station on 2 December 1991 and single tows made at two offshore stations in May 1992; error bars = 1 SE. (A) 2 December 1991–16 June 1992; (B) 29 January–6 April 1993.

Figure 7

Hatch date distributions for shortbelly rockfish, *Sebastes jordani*, estimated from age of larvae collected January–April 1992 and 1993 and from age of juveniles collected June 1992 and May–July 1993.

Table 3

Size (mean, SE, and n) of larval shortbelly and blue rockfish collected by standard oblique bongo-net tows at stations 7, 13, and 19 km off Davenport, California, December 1991–April 1993.

	1991–92									1993				
	18 Dec	9 Jan	23 Jan	6 Feb	21 Feb	12 Mar	2 Apr	4 May	Overall	29 Jan	12 Feb	7 Mar	6 Apr	Overall
Shortbelly rockfish														
7 km mean (mm)	—	6.6	6.3	6.7	6.2	6.1	—	—	6.5	4.8	6.3	—	—	5.1
SE	—	0.2	0.1	0.2	0.4	0.2	—	—	0.1	0.1	—	—	—	0.3
n	0	9	41	36	10	10	—	—	106	4	1	—	—	5
13 km mean (mm)	6.1	4.8	6.0	4.8	5.2	6.0	—	7.5	5.4	5.1	4.9	—	6.2	4.9
SE	—	0.1	0.1	0.1	0.1	0.1	—	0.4	0.1	0.1	0.1	—	0.4	0.1
n	1	8	77	155	39	82	—	11	373	31	233	—	9	273
19 km mean (mm)	7.0	5.6	5.5	5.0	—	5.0	4.7	6.5	5.0	5.6	6.3	5.8	5.3	5.7
SE	1.3	0.1	0.3	0.2	—	0.1	0.1	—	0.1	0.1	0.3	0.1	0.1	0.1
n	2	44	6	35	0	166	84	1	338	37	24	121	55	237
Blue rockfish														
7 km mean (mm)	5.8	5.0	4.8	5.3	5.4	—	—	—	5.0	4.1	—	—	—	4.1
SE	—	0.2	0.1	0.1	0.5	—	—	—	0.1	—	—	—	—	—
n	1	4	24	25	2	—	—	—	56	—	0	0	0	1
13 km mean (mm)	—	—	4.0	4.4	4.5	—	—	—	4.4	4.4	4.6	—	6.2	4.4
SE	—	—	0.2	0.1	0.1	—	—	—	0.1	0.1	0.2	—	0.4	0.1
n	—	0	6	43	7	—	—	—	56	19	5	0	9	24
19 km mean (mm)	—	4.7	4.4	4.9	4.3	—	—	—	4.6	4.2	4.4	—	5.3	4.2
SE	—	0.2	0.1	0.2	0.3	—	—	—	0.1	0.1	0.2	—	0.1	0.1
n	0	9	31	20	5	—	—	—	65	33	4	0	0	37

samples from May to July 1992 and only 29 individuals (0.5% of total catch) occurred in 65 midwater trawl samples from May to July 1993 (Loeb et al.[1]).

Discussion

Larval rockfish are a dominant group in the ichthyoplankton along the west coast of the United States, with relatively high abundances occurring seasonally in surveys off southern and central California (Barnett et al., 1984, Moser and Boehlert, 1991) and off northern California, Oregon, and Washington (Richardson and Pearcy, 1977; Richardson et al., 1980; Boehlert et al., 1985; Doyle et al., 1993). During our study, mean overall abundance of larval rockfish ranked second only to that of the northern anchovy (*Engraulis mordax*; 749 larvae/10 m^2) in 1992 and Pacific hake (*Merluccius productus*; 1,520 larvae/ 10 m^2) in 1993 (B. Daly, unpubl. data). Larval rockfishes are generally characterized as members of offshore assemblages; their abundance increased with distance from shore in our study as well as in the surveys cited above. Distribution of at least the youngest larvae is defined by the location of spawning adults, which for many rockfish species is principally over rock bottom along the edge of the continental shelf and submarine canyons. This is supported by the significantly greater numbers of small shortbelly rockfish larvae in samples collected at our most offshore station, located over Año Nuevo submarine canyon.

Declines in somatic and reproductive condition (VenTresca et al., 1995) and decreased fat storage (Lenarz and Wyllie Echeverria, 1986) in adult rockfish collected off central California during El Niño years likely are responses to reduction in primary prey biomass. Mullin and Conversi (1989) documented large-scale reductions in abundance of euphausiids and smaller zooplankton (e.g. the pri-

Table 4

Size, age, and number of larval shortbelly, *Sebastes jordani*, and blue, *S. mystinus*, rockfish included in age and growth estimates in 1992 and 1993.

	1992						1993				
	Jan	Feb	Mar	Apr	May	Overall	Jan	Feb	Mar	Apr	Overall
Shortbelly rockfish											
No. aged	54	60	34	15	12	175		47	36	44	127
Mean age (d)	8.4	8.2	6.3	2.6	11.6	7.6		6.7	7.2	4.5	6.1
SE	0.8	0.9	0.7	0.7	1.3	0.5		0.8	0.7	0.7	0.4
Range (d)	1–28	1–28	1–20	1–11	4–18	1–28		1–21	2–22	1–21	1–22
Mean SL (mm)	6.3	6.2	5.9	5.2	7.4	6.2		5.8	6.1	5.8	5.9
SE	0.2	0.2	0.2	0.2	0.4	0.1		0.2	0.2	0.2	0.1
Range (mm)	4.0–10.8	3.9–9.8	4.2–8.8	4.3–6.3	5.0–9.7	3.9–10.8		4.3–9.0	4.8–9.0	4.2–9.2	4.2–9.2
Blue rockfish											
No. aged	43	46				89	3	4			7
Mean age (d)	4.3	6.3				5.3	8.0	6.0			6.9
SE	0.3	0.7				0.4	4.0	1.6			1.8
Range (d)	2–14	2–21				2–21	4–16	2–10			2–16
Mean SL (mm)	4.7	4.8				4.8	5.1	4.5			4.8
SE	0.1	0.1				0.1	0.4	0.2			0.2
Range (mm)	3.4–6.1	2.8–6.9				2.8–6.9	4.4–5.9	4.0–5.0			4.0–5.9

mary prey of juvenile and adult rockfishes) during the 1958 El Niño. Poor condition of adult rockfishes could influence larval production and reproductive timing. Abundance of rockfish larvae in our study, however, was not significantly different between the two years of the extended El Niño event along the central California coast and was much greater than estimates from earlier ichthyoplankton surveys coastwide. Greatest mean abundance of rockfish off Oregon was 350 larvae/10 m² in May 1971 (Richardson and Pearcy, 1977), 199/10 m² in March 1972, and 176/10 m² in March 1973 (Richardson et al., 1980). Peak abundance of rockfish sampled during CalCOFI surveys in February 1951–81 averaged about 200 larvae/10 m² off northern and central California and 90 larvae/10 m² off southern California (Moser and Boehlert, 1991). Average larval rockfish abundance estimated from those CalCOFI lines (i.e. 63, 67, 70) and stations (i.e. 49–57) closest to our sampling sites was 486 larvae/10 m² in February, 1960–84. We estimated a mean abundance of 990 rockfish larvae/10 m² at the three offshore stations in February during our 2-year survey. This figure demonstrates that overall larval abundance was not negatively affected by an El Niño event and that the area north of Monterey Bay is a significant production ground for larval rockfishes. This finding is substantiated by the results of pelagic juvenile rockfish surveys along California, which indicate a center of distribution in this area (Larson et al., 1994).

Further, the El Niño event of 1991–93 did not seem to have caused a significant shift in overall timing of parturition, at least for the two species that dominated our ichthyoplankton surveys. Median hatch dates of shortbelly rockfish larvae collected during late winter and early spring of 1991–92 and 1993 were similar to each other (first and second week in February, respectively), and to the primary month of parturition (i.e. February) according to reproductive stages of this species off central California from 1977 to 1984 (Wyllie Echeverria, 1987). Release of blue rockfish larvae during our study likewise was as expected (i.e. January; Wyllie Echeverria, 1987). Absence of sampling in late December 1992 could have masked an unlikely peak of parturition earlier in the 1993 season.

Although reproductive timing and production seemingly were not influenced by the prolonged El Niño event, occurrence of juvenile rockfishes in trawl samples collected in late spring and summer was dramatically different between years. Extremely low numbers of pelagic juvenile rockfish were encountered during midwater trawl surveys (*n*=56 trawls) conducted from 4 May to 10 July 1992 north and south of Monterey Bay (Loeb et al.[1]). In contrast, pelagic juvenile rockfishes collected during the same time period in 1993 (*n*=65 trawls) were 20 times more abundant, comprised twice as many taxa, and were substantially larger than juveniles collected in 1992 (Loeb et al.[1]). Shortbelly, copper-complex, and kelp rockfishes dominated the relatively low numbers of

rockfish juveniles in 1992. The 1993 pelagic juveniles were dominated by shortbelly, squarespot, half-banded (*S. semicinctus*), and chilipepper (*S. goodei*) rockfishes, in that order. All of these species can produce larvae relatively late in the season.

Among the dominant species, only those shortbelly rockfish larvae released late in the season (March and April) were represented in the birthdate distributions of juveniles collected in the summer of both years of the El Niño. The few pelagic juvenile shortbelly rockfishes collected in May–June during the 1983 El Niño event also had late birthdates (Woodbury and Ralston, 1991). It is clear that the largest proportion of larval shortbelly rockfish production, >65% occurring prior to March during both years of the 1991–93 El Niño event, did not survive until the juvenile surveys conducted during the summers of 1992 and 1993. Blue rockfishes, largely produced in January and February and ranked second (1992) and third (1993) in larval catches, were not collected at all during pelagic juvenile surveys in May–July 1992 (56 midwater trawls; Loeb et al.[1]), and represented 0.5% (*n*=29 individuals) of the total catch of pelagic juveniles in May–July 1993 (65 midwater trawls; Loeb et al.[1]). Stripetail rockfish, another species whose parturition period is restricted to early in the year off central California (i.e. November–March with a peak in January [Wyllie Echeverria, 1987]), was relatively abundant in the plankton both years but rare in the pelagic juvenile collections (<0.1 and 0.5 fish per trawl).

In accordance with the results of the surveys by Loeb et al.,[1] subtidal observations along the central coast made by California's Department of Fish and Game Sportfish Project biologists indicated that few juveniles of nearshore rockfish species recruited to rocky and kelp canopy areas off the Monterey Peninsula during May–August 1992 (VenTresca[3]). Low abundance of pelagic juvenile rockfishes off central California also was noted during May–June 1992 surveys conducted by scientists of the NMFS Tiburon Laboratory (Lenarz et al., 1995; Ralston and Howard, 1995) and during previous El Niño events of 1983 and 1986 (Wyllie Echeverria et al., 1990). In contrast, overall abundance of pelagic juvenile rockfishes in 1993 was fourth greatest among the past eight years of NMFS-Tiburon surveys (Lenarz et al., 1995), and relatively high numbers, dominated by blue rockfishes, settled off Monterey during June–September 1993 (VenTresca[3]). Substantially greater abundance and larger sizes of pelagic juvenile rockfishes during

May–July 1993 indicated that recruitment was likely related to the timing of optimal environmental conditions during larval development. This is consistent with the dome-shaped relationship described by Ralston and Howard (1995) between interannual variability in winter SST's and estimates of year-class strength for blue and yellowtail rockfishes off central California collected from 1983 to 1992 (e.g. juvenile abundance was lowest when SST's were either exceptionally low or high during winter months of larval production).

Mortality of fishes during the larval stage has been attributed to starvation and predation; debate continues as to which factor is more significant for successful recruitment (Hunter, 1981; Bailey and Houde, 1989). There was no evidence from our ichthyoplankton samples that suggested that young rockfishes were starving in either year of the El Niño event. Growth of young shortbelly rockfishes was similar throughout the parturition period, no differences were detected between the two years, and growth in 1992–93 was similar to that estimated for this species from the central California during non-El Niño years (i.e. in 1989 [Laidig et al., 1991] and in 1991 [Ralston et al., 1996]). Moreover, blue rockfish, although relatively common in the ichthyoplankton, abruptly disappeared at young ages (i.e. when many were still dependent on yolk reserves) from samples collected in late January and early February and had very poor recruitment to the pelagic juvenile stage in 1992. This finding suggests acute mortality, perhaps coincident with onshore transport and increased encounter rates with predators.

Time of release of rockfish larvae can contribute to variation in year-class abundance by influencing the spatial and temporal coincidence of larvae, prey availability, predator abundance, and favorable environmental conditions, such as temperature, upwelling, and transport (Parrish et al., 1981; Methot, 1983; Checkley et al., 1988; Nyman and Conover, 1988). Rockfish larvae were more abundant and the dominant species (shortbelly rockfish) was significantly larger at onshore stations in 1992 than in 1993, indicating retention of larvae nearshore during the first year of the El Niño event. These occurrences coincided with onshore advection of water, as characterized by reversals in wind direction and by warmer, less saline water that occurred during peak larval rockfish abundance in February 1992.

Larval retention in nearshore areas could be responsible for heavy mortality, possibly through increased predation. Significant changes in zooplankton assemblages associated with wind relaxation and subsequent onshore transport have been noted along central California (Farrell et al., 1991), and abun-

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[3] VenTresca, D. 1995. California Department of Fish and Game, 20 Lower Ragsdale Dr., No. 100, Monterey, CA 93940. Unpubl. data.

dance of several potential larval fish predators can increase nearshore during these events. During the 1958 El Niño event, the California Current moved shoreward, and abundance of potential larval fish predators (siphonophores and chaetognaths) increased in inshore coastal waters (Smith, 1985). Mean zooplankton biomass, dominated by copepods, euphausiids, and chaetognaths, was significantly greater in nearshore than in offshore areas of Monterey Bay during the first year of the 1991–93 El Niño event (Baduini, 1995); this trend reversed after upwelling commenced in early April 1993. Limited information on chaetognaths (largely *Sagitta bipunctata*) collected in our ichthyoplankton samples (Bridges[4]) indicated extremely high numbers (e.g. up to 20,000 individuals/10 m^2 at 3 km from shore, which represented five times the greatest larval rockfish abundance) in early February 1992, coincident with the wind reversal, onshore transport of water, and peak abundance of larval rockfish. At least 20% of these animals were >11 mm in length, a size at which chaetognaths are capable of ingesting a larval fish (senior author, unpubl. data). The lack of upwelling and associated offshore transport during subsequent months could prolong nearshore retention and further reduce recruitment success.

Although predation on fish eggs and larvae has been generally characterized as a density-independent control on fish populations (Bailey and Houde, 1989), exceptions include co-occurrence of predators and prey concentrated in small areas (e.g. high density of herring larvae and scyphomedusae [Moller, 1984]) and prey-switching when preferred diet is not available (Pepin, 1987). Although small copepods are the preferred prey of larval fish and many of their invertebrate predators, reduction in this food source during El Niños (McGowan, 1985; Miller et al., 1985) could increase the likelihood of predation on small fish larvae. Several species of chaetognaths prey secondarily on young fish larvae (Kuhlmann, 1977), and an inverse relationship between larval fish abundance and chaetognath densities has been described from CalCOFI samples collected during the 1958 El Niño off California (Alvariño, 1980).

In contrast, increased upwelling intensity and offshore transport during March and April 1993 may have facilitated survival of larval stages for those species with broad periods of parturition by advecting them from nearshore areas. Although there is a

Standardized monthly abundance anomaly
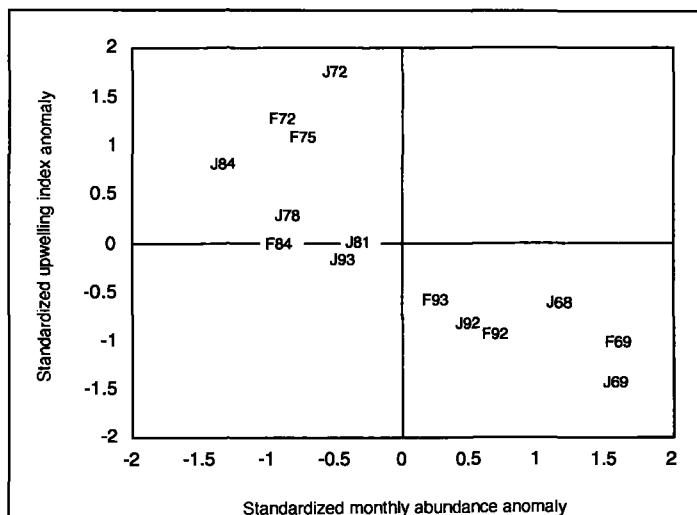
Figure 8

Comparison of mean monthly standardized anomalies of larval rockfish abundance in January (J) and February (F) of various years (indicated by last two digits of each year), with those of upwelling indices estimated at 36° and 39°N and averaged over a 4-day period prior to and including day of ichthyoplankton sampling. Estimates of larval abundance prior to our study are from CalCOFI ichthyoplankton surveys conducted inshore of station 60 along lines 63, 67, and 70 (Moser et al., 1993). Standardized anomalies were calculated by using data from our study and the CalCOFI surveys.

significantly negative relationship (r^2=0.63; P<0.001) between larval rockfish abundance and offshore Ekman transport (i.e. positive upwelling indices) during peak production in January and February (Fig. 8), dispersal mechanisms like upwelling seem to be important in determining recruitment to the juvenile stage (Ralston and Howard, 1995). Breaker (1983) characterized the spring transition from winter ocean conditions to the onset of upwelling and offshore Ekman transport as an abrupt decrease in SST (e.g. 0.38–0.59°C per day) off central California (36°26'N); dramatic spring transitions occurred in six of the twelve years (1971–83), with suppression of transition during El Niño events. According to examinations of daily SST's from the same station during the 1991–93 El Niño event (Schwing[5]), a spring transition did not occur at all in 1992 and a modest transition (0.34°C per day) was initiated in early April 1993, coinciding with the birthdate distribution of the surviving cohort of shortbelly rockfish juveniles.

In conclusion, the extended El Niño event of 1991–93 provided a unique opportunity to assess abundance and distribution of larval rockfishes during a

[4] Bridges, J. 1994. Department of Biology, University of California, Santa Cruz, CA 95064. Unpubl. data.

[5] Schwing, F. 1995. Pacific Fisheries Environmental Group, Natl. Mar. Fish. Serv., Pacific Grove, CA. Unpubl. data.

significant environmental perturbation, an opportunity that yielded some insight into the recruitment process. Characterizing the link between larval rockfish distribution and the hydrographically dynamic environment of the central California coast required finer-scale spatial and temporal sampling than has been achieved previously. Rockfish larvae were more abundant and larger at onshore stations in 1992, coinciding with onshore advection of water during the onset of the El Niño event and suggesting retention of larvae nearshore; abundance of juvenile rockfishes in nearshore areas later in that year was extremely low. Initiation of upwelling in March and April of 1993 and the occurrence of fewer rockfish larvae at onshore stations suggest greater offshore transport during the second year; juvenile rockfish abundance was greater than the previous summer. From these data, we suggest that substantially higher survival and recruitment of juvenile rockfishes in 1993 likely are due to increased offshore transport and dispersal, and possibly lower predation, during the larval stages.

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