

Distributions of larval rockfishes *Sebastes* spp. across nearshore fronts in a coastal upwelling region

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ABSTRACT: We sampled larval fishes along cross-shelf transects off Granite Canyon, California, USA, during the upwelling seasons of 1993 and 1994 to determine whether coastal upwelling fronts affect the cross-shelf distribution of larval rockfishes *Sebastes* spp. during the earliest period of planktonic life. Rockfish larvae occurred in relatively high densities near surface fronts and were distributed in patches oriented along sloping pycnoclines contiguous with surface fronts. Qualitative comparisons between observed distributions of larval rockfishes in relation to hydrographic structure and predictions from models of plankton distributions at convergent fronts support the hypothesis that convergent circulation contributes to observed distributions. Our results indicate that (1) coastal upwelling fronts influence larval rockfishes at an earlier life history stage than has previously been documented, and (2) the influence of upwelling fronts on distributions of larval rockfishes is similar to the influence of hydrographic fronts on distributions of larval fish reported for a variety of oceanographic settings. In light of the plausible effects of upwelling fronts on larval transport and ecology, our findings suggest that upwelling fronts merit further investigation for their potential role in translating variability in upwelling dynamics into fluctuations in recruitment to coastal rockfish populations along the west coast of North America.

KEY WORDS: Larval fish distribution · Coastal upwelling · Upwelling fronts · Recruitment mechanisms · Rockfishes · *Sebastes*

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INTRODUCTION

Wind-driven upwelling exerts a strong influence on the productivity and circulation of the coastal ocean in eastern boundary current systems (Brink & Cowles

1991). Variability in recruitment of coastal fishes and invertebrates that undergo a planktonic larval phase has been linked to variability in upwelling intensity over a range of spatial and temporal scales (Bailey 1981, Cury & Roy 1989, Farrell et al. 1991, Roughgarden et al. 1991, Ainley et al. 1993, Lenarz et al. 1995, Ralston 1995, Ralston & Howard 1995, Shkedy et al. 1995, Wing et al. 1995a,b, Morgan et al. 2000).

Among the taxa affected by upwelling, rockfishes *Sebastes* spp. exhibit early life histories that are in many ways functionally intermediate to life histories typified by intertidal invertebrates and coastal pelagic fishes: like pelagic fishes, rockfishes undergo substantial growth and development in the pelagic habitat,

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developing from small (3 to 7 mm) larvae into pelagic juveniles 20 to 70 mm in length prior to settlement to benthic habitats, yet, like intertidal invertebrates, many species of rockfishes must return to nearshore habitats to complete the life cycle (Love et al. 1991, Moser & Boehlert 1991). Empirical relationships between rockfish recruitment and upwelling intensity (Norton 1987, Ainley et al. 1993, Ralston & Howard 1995) exhibit characteristics of both dome-shaped relations indicative of optimal conditions for larval feeding (Cury & Roy 1989), and inverse relations indicative of the effects of transport on larval supply to adult habitats (Farrell et al. 1991, Roughgarden et al. 1991, Shkedy et al. 1995, Wing et al. 1995a,b). Presently, however, little is known about specific mechanisms through which variability in upwelling might translate into recruitment variability.

Hydrographic fronts have been hypothesized to have an important role in determining recruitment to fish populations, presumably through their influence on larval ecology and transport (Grimes & Kingsford 1996). Densities of larval fishes in frontal zones are commonly greater than in adjacent water masses, although specific distributions vary considerably among taxa (Kjørboe et al. 1988, Grimes & Finucane 1991, Kingsford et al. 1991, Govoni & Grimes 1992, Munk et al. 1995, Kingsford & Suthers 1996a, Sabatés & Olivar 1996, Lochmann et al. 1997). Plausible mechanisms for the generation and maintenance of elevated densities of larval fishes at fronts include (1) concentrated spawning in frontal zones (Shelton & Hutchings 1982), (2) concentration of larvae by hydrodynamic convergence at fronts (Govoni & Grimes 1992, Lochmann et al. 1997), and (3) improved feeding success, condition and growth deriving from elevated productivity at fronts (Munk 1993, Lang et al. 1994, St John & Lund 1996; see Powell et al. 1990 for an exception) which might abbreviate periods of vulnerability to predation (Meekan & Fortier 1996). However, notwithstanding the potential benefits for larvae at fronts of improved feeding success and partial protection in a dense field of alternative prey (Kean-Howie et al. 1988), increased predation intensity by planktivores that aggregate at fronts (Taggart et al. 1989, Sims & Quayle 1998) can easily counteract any trophic benefits (Grimes & Kingsford 1996, Grimes 2001). Fronts can affect recruitment by retaining larval fishes in suitable nursery grounds (Kjørboe et al. 1988, Sabatés & Olivar 1996, Lochmann et al. 1997) or transporting larvae to such habitats (Shelton & Hutchings 1982, Kingsford & Suthers 1996a,b, Eggleston et al. 1998).

Upwelling fronts, which mark sharp transitions between denser (colder, saltier) upwelled water and lighter (warmer, fresher) oceanic water, might play a similar role in the ecology of rockfishes in coastal upwelling regions. Such fronts are ubiquitous, dynamic

features in the coastal ocean off central California, and typically exhibit a complex structure in response to temporal variability in upwelling-favorable winds, topographic steering of coastal winds, and bathymetric influences on coastal circulation (Brink 1983, Send et al. 1987, Batteen 1997). Upwelling fronts influence the distribution and recruitment of intertidal invertebrate larvae that rely on transport to nearshore habitats for successful settlement (Farrell et al. 1991, Roughgarden et al. 1991, Grantham 1997), and can directly or indirectly affect the distribution and transport of larval fishes (Richardson & Percy 1977, Shelton & Hutchings 1982, Graham & Largier 1997). Local productivity maxima and elevated densities of small zooplankters often occur at upwelling fronts (Peterson et al. 1979, Dengler 1985, Traganza et al. 1987, Grantham 1997).

The role of upwelling fronts in the larval ecology of rockfish larvae has not been investigated. Large-scale, coarse-resolution ichthyoplankton surveys indicate an extensive cross-shelf distribution of larval rockfishes, and rockfish larvae are often captured hundreds of km out to sea (Moser et al. 1993); however, the distribution of pelagic juveniles is typically more restricted, and juveniles often occur at higher densities at or near upwelling fronts than in nearby water masses (Lenarz et al. 1991, Larson et al. 1994, Wing et al. 1998, K. Sakuma & S. Ralston unpubl. data). Upwelling fronts might provide a suitable, perhaps even superior, habitat during the early life history of rockfishes, which invites speculation that upwelling fronts play a role in determining which larvae survive to recruitment. Not all fronts off central California are formed by coastal upwelling, particularly during the winter, yet such fronts also appear to affect distributions of rockfish larvae (Sakuma & Ralston 1995).

An initial step toward developing and evaluating hypotheses regarding the role of upwelling fronts in the larval ecology and recruitment of rockfishes is to establish whether nearshore upwelling fronts affect rockfishes during early life history stages that are critical to determining recruitment success. In this paper, we address this issue with data on the cross-shelf distribution of larval rockfishes across frontal zones collected during the late spring and summer off central California. We conducted our study in the coastal ocean off the Big Sur Coast south of Monterey, California, which is affected strongly by the upwelling center off Point Sur and, to a lesser degree, by the southern end of the upwelling plume extending from the Point Año Nuevo upwelling center (Traganza et al. 1981, Breaker & Broenkow 1989, Rosenfeld et al. 1994). The study region is in an area marked by a narrow continental shelf penetrated by large submarine canyons, and was negligibly affected by freshwater input during the years of our study. Upwelling dynamics and the

formation of fronts in the Point Sur and Point Año Nuevo upwelling centers are effectively simultaneous due to large-scale coherence in temporal variability of wind stress (Rosenfeld et al. 1994). The 2 upwelling plumes can and do interact; however, even during periods of the strongest upwelling-favorable winds, a minimum of 5 to 6 d is required for transport of water upwelled off Point Año Nuevo across Monterey Bay and along the Big Sur coast to our study region (Breaker & Broenkow 1989, Rosenfeld et al. 1994). In our analysis, we focus on the distribution of larval rockfishes during the very beginning of the planktonic phase in relation to the position of nearshore fronts and cross-shelf changes in the vertical structure of the water column associated with these fronts.

MATERIALS AND METHODS

Larval fishes were sampled along transects extending due west from Granite Canyon ($36^{\circ} 25.9' N$, $121^{\circ} 55.0' W$, approximately 150 km south of San Francisco, California) on 4 separate cruises aboard RV 'Point Sur' during the upwelling seasons of 1993 and 1994 (Fig. 1). We used hydrographic data collected during previous transect crossings and recently collected (often quasi-synoptic) satellite AVHRR (advanced very high resolution radiometry) images of sea surface temperature to identify and select fronts for further investigation. We designed transects immediately prior to the start of sampling according to the following rules: (1) sampling was to begin as close to the coast as possible without risk to the gear, (2) stations were to be spaced at approximately 3 km intervals, and (3) ideally, the last (offshore) station was to be placed at least a Rossby radius (a natural scale of horizontal oceanographic structure; approximately 10 km in this region; Rosenfeld et al. 1994) offshore of the outermost front to be sampled. Transects thus had variable numbers of sampling stations. On each transect, sampling for larval fishes began with the station nearest to the coast, and progressed in an offshore direction. Sampling generally began during the afternoon or evening and continued into the night. Depending on the number of stations (8 to 14) in a transect, sampling required approximately 7 to 12 h to complete.

Physical data. At each station, a CTD (Seabird 9/11 Plus) cast to 250 m depth (or as limited by bathymetry) directly preceded biological sampling. CTD data were processed as described in Rosenfeld et al. (1995) to generate temperature, salinity, and density data with 1 m vertical resolution beginning at a depth of 4 m. Near-surface (approximately 3 m depth) temperature and salinity were measured at 30 s intervals with the ship's flowthrough system. Temperature and salinity

data were converted to density according to the IES 80 equation for density with no correction for pressure (JPOTS 1991).

Hydrographic cross-sections were generated from CTD profiles using contouring functions in MATLAB (Version 6.0; available at: www.mathworks.com). Surface density along each transect was smoothed by fitting a locally weighted, robust linear function (the 'lowess' function from S-Plus 3.0; available at: www.mathsoft.com) over a moving window that spanned approximately 3 km; surface density gradients were calculated from the resulting smoothed curve. We identified fronts as locally strong gradients in surface density that were clearly associated with shoaling isopycnals. Surface density-gradient minima (large negative values) indicated fronts between colder, saltier water nearshore and warmer, fresher water offshore.

Satellite AVHRR images and wind data collected over the 3 to 6 wk preceding a cruise were used to characterize upwelling conditions leading up to sample collection. Hourly wind measurements (averaged over an 8 min period) were obtained from National Data Buoy Center (NDBC) Buoy 46042 located at $36^{\circ} 45' N$, $122^{\circ} 24' W$, approximately 70 km northwest of Granite Canyon (data available at <http://seaboard.ndbc.noaa.gov/data/dataindex.shtml>). During each cruise, observations of sea surface temperature from satellite-based AVHRR sensors aboard NOAA satellites (NOAA-11, -12, and -14) were obtained and processed remotely, and retrieved while at sea for use in planning transects.

Biological data. Larval fishes were captured with a Tucker trawl (1 m² mouth opening) with 3 opening-closing nets, each of which was fitted with 200 μm mesh, a rigid cod end with 96 μm mesh windows, and a General Oceanics 2030R flowmeter. At each station, we conducted a single tow of the net; we did not collect repeated samples at each station for 2 reasons: (1) repeated occupation of stations would have greatly extended the time necessary to complete a transect and further compromised our efforts to obtain a synoptic view of the distribution of larvae across frontal zones, and (2) repeated sampling at a given set of coordinates in a dynamic upwelling zone provides no guarantee of sampling the same water mass, and thus gives a false impression of replication. The trawl was towed obliquely from depth at approximately 1 to 1.5 m s⁻¹, and nets were opened and closed during each tow to obtain discrete samples from 2 depth strata (approximately 55–27 and 27–0 m for August 1993, June and August 1994; 75–37 and 35–0 m in May 1994); actual depths fished were estimated trigonometrically from cable length and angle. We compensated for occasional flowmeter failures by estimating filtered volume from the distance the net was towed and the mean ratio between towed distance and filtration from adja-

cent stations. Samples were preserved with 2 to 4 % buffered formalin in filtered seawater and transferred to 50 to 70 % ethanol upon return to the laboratory.

All larval fishes were removed from $3/4$ or $7/8$ portions of each sample and identified to the lowest possible taxonomic level according to Matarese et al. (1989); larval rockfishes were identified only to genus. Larvae were measured to the nearest 0.1 mm (standard or notochord length), and scored for developmental stage (pre-flexion, flexion or post-flexion: Kendall et al. 1984). No attempt was made to correct lengths for the

effects of preservation (Pepin et al. 1998). Counts of larval rockfishes were converted to density (ind. per 1000 m³) for comparison to front structure.

The data for distributions of larval rockfishes along each transect consist of point estimates of the density of larval rockfishes by size class and depth stratum at each station. We infer relations between distributions of larval fishes and hydrographic structure by comparing the location of peak densities of larval rockfishes to the location of surface fronts, and overlaying depth-stratified distributions on hydrographic sections to dis-

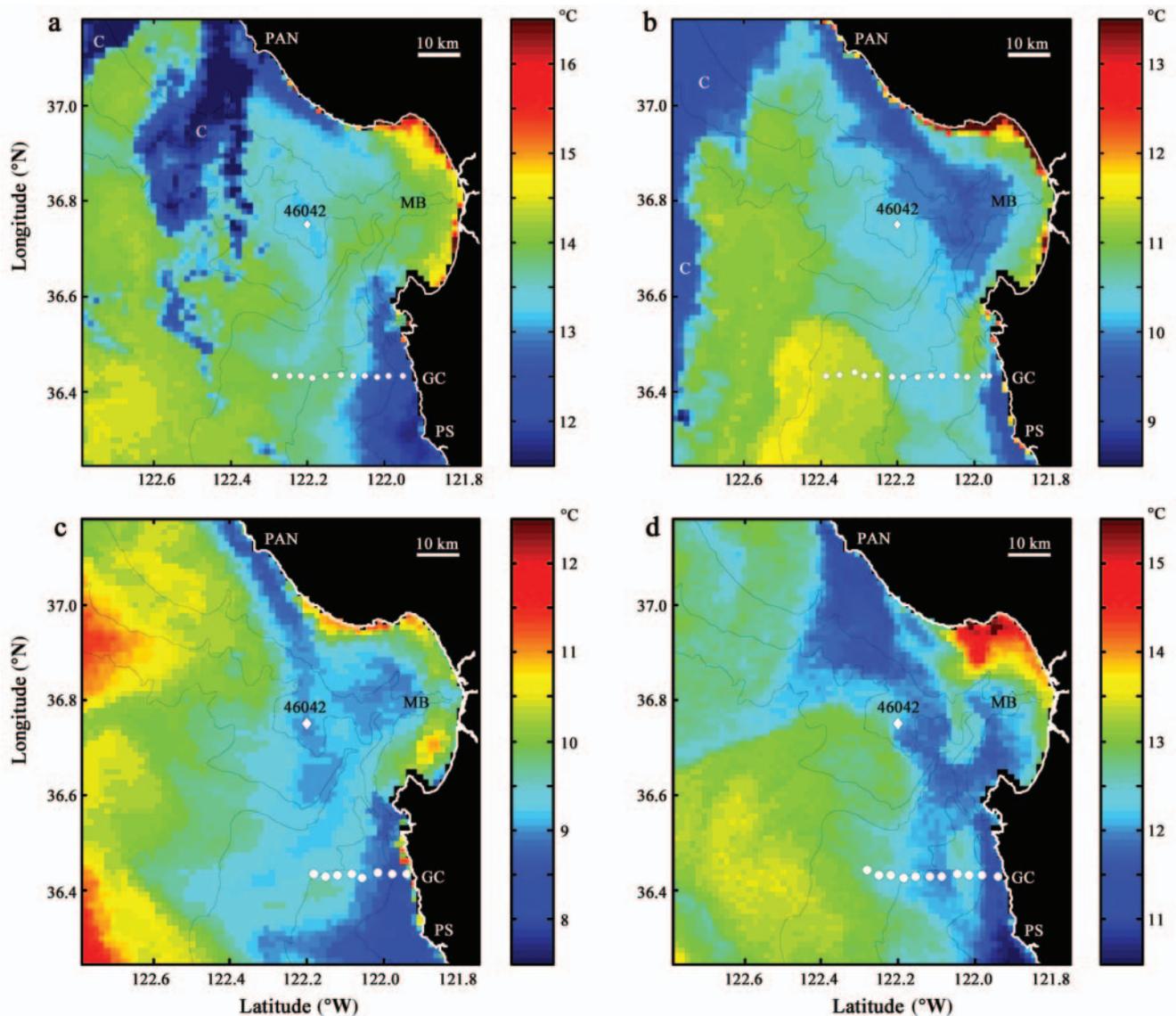


Fig. 1. Satellite AVHRR observations of sea surface temperature, and locations of sampling stations along transects off Granite Canyon, California. (a) Cruise I: 11–12 August 1993, image from approximately 16:00 h Pacific Daylight Time (PDT), 11 August 1993; (b) Cruise II: 4–5 May 1994, image from approximately 16:00 h PDT, 4 May 1994; (c) Cruise III: 26–27 June 1994, image from 06:00 h PDT, 26 June 1994; (d) Cruise IV: 4–5 August 1994, image from approximately 19:00 h PDT, 6 August 1994. Images are raw Channel 4 temperatures uncorrected for atmospheric moisture, and are intended to illustrate general structure of the coastal ocean rather than to represent accurately sea surface temperature. PAN: Point Año Nuevo; MB: Monterey Bay; GC: Granite Canyon; PS: Point Sur; C: areas masked by clouds. Contours indicate 200, 1000, and 2000 m isobaths. Note that temperature scales are unique to each map

cern how changes in the proportion of larval fishes captured in the deep and shallow nets were related to the location and slope of pycnoclines associated with surface fronts. In doing so, we assume that rockfish larvae occur in contiguous and smooth, although not necessarily unimodal, patches.

RESULTS

During the 4 cruises, 1923 larval and juvenile fishes were captured, 860 (44.7%) of which were rockfish *Sebastes* spp. Rockfishes were consistently abundant, comprising 33.5 to 76.8% of the catch for a given cruise. Other species were rare or inconsistently abundant across cruises (see Bjorkstedt 1998). Length data were obtained for 853 of the 860 rockfish larvae. Most rockfish larvae (83.6%) were small (≤ 6 mm) and exhibited little or no sign of flexion; a few (5%) were well developed (post-flexion) and exceeded 10 mm, almost all of which (41 of 43) were captured during Cruise IV. We found no difference between size distributions of larvae captured in shallow or deep nets; however, our ability to capture larvae > 8 mm long appears to have been greater during periods of darkness (data not shown). For this reason, we focus our analysis on the distributions of small (≤ 6 mm), pre-flexion larvae, and offer more cautious interpretations for larvae ranging in length from 6 to 8 mm.

Upwelling intensity varied substantially among cruises: conditions ranged from strong upwelling to rapid, complete relaxation from upwelling (Figs. 1 & 2). Such vari-

ation notwithstanding, several consistent, large-scale features are visible in satellite imagery coincident with each cruise: (1) cool water recently upwelled from the Point Sur upwelling center; (2) a plume of cool upwelled water extending south from the Point Año Nuevo upwelling center, across the mouth of Monterey Bay, and into the region sampled by our transect (partly obscured by clouds in Fig. 1a); (3) a tongue of warm water extending west and south of Monterey Bay which separated the 2 upwelling plumes; (4) warm oceanic water offshore influenced by coastal upwelling. The placement of our transects resulted in our sampling 3 different 'types' of upwelling fronts: (1) fronts lying near the coast on the northern side of the Point Sur upwelling center, (2) fronts on the oceanic (offshore) side of the distal end of the Point Año Nuevo upwelling plume, and (3) fronts on the coastal (inshore) side of the distal end of the Point Año Nuevo upwelling plume. Nearshore fronts associated with the Point Sur upwelling center were the only type encountered on each cruise; sampling of fronts associated with the Point Año Nuevo plume varied with the position of the plume and the length of the transect (Fig. 1). Particular characteristics of the fronts encountered differed among transects and are described below.

Cruise I: August 1993

Upwelling-favorable winds temporarily weakened prior to this cruise (Fig. 2a). A series of AVHRR images and independent remote measurements of currents (acoustic Doppler current profiler: Rosenfeld et al. 1995; high-frequency radar: Bjorkstedt 1998; data not shown) indicated poleward flow of cool, recently upwelled water along the coast during wind relaxation. This circulation pattern is typical during relaxation events (Send et al. 1987, Rosenfeld et al. 1994). Observations by both AVHRR and high-frequency radar (Bjorkstedt 1998; data not shown) indicate that upwelling resumed near Point Sur in response to renewed upwelling-favorable winds just prior to sampling.

The transect spanned a frontal region in which density fronts were defined almost entirely by temperature gradients (Fig. 3a–c). It spanned 2 fronts: (1) a front between upwelled water from Point Sur and warmer water just offshore (Figs. 1a & 3e; approximately 10 km offshore), and (2) a front on the

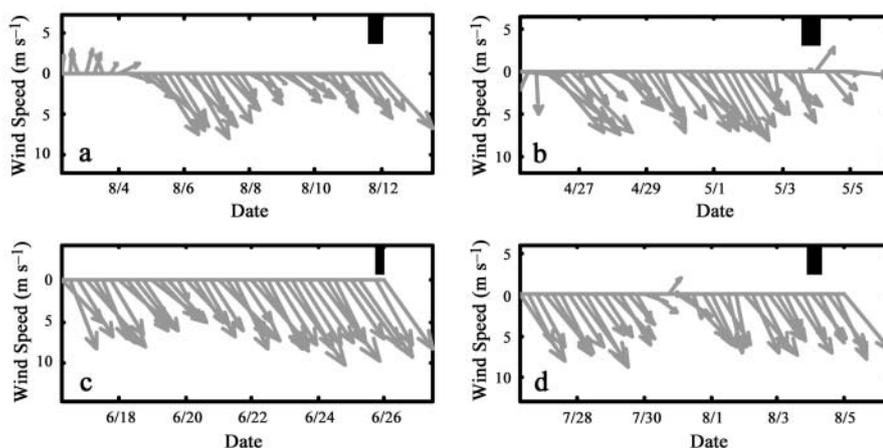


Fig. 2. Wind speeds measured at NDBC Buoy 46042 preceding and during (a) Cruise I, (b) Cruise II, (c) Cruise III, and (d) Cruise IV (dates presented as month/day). Vectors indicate speed and direction towards which the wind was blowing, winds from the northwest (indicated by vectors pointing southeast) are upwelling-favorable along the central California coast. Bar at top of each plot indicates plankton sampling period. For presentation, hourly data were subsampled for every sixth data point (such subsampling did not obscure patterns affecting upwelling dynamics)

coastal edge of the Point Año Nuevo upwelling plume (Figs. 1a & 3e; approximately 22 km offshore). The region between these 2 fronts exhibited complex surface density gradients that included weak frontal signatures at approximately 16 and 19 km offshore; however, the hydrographic sections do not indicate any fronts in this region (Fig. 3a–c, e).

The highest densities of larval rockfishes were captured in the shallow net near the inshore upwelling front. Larval rockfishes appear to be distributed in a contiguous patch along the slope of the pycnocline associated with this front (Fig. 3f). Relatively few fish were captured in the Point Año Nuevo upwelling

plume; however, the greatest concentration of larger, more developed larval rockfishes was observed at the front marking the coastal edge of this plume (Fig. 3e,f).

Cruise II: May 1994

Sampling along this transect began soon after the onset of a strong relaxation event, and weak and variable winds persisted throughout sampling (Fig. 2b). A series of quasi-synoptic observations of the frontal zone made during previous crossings of the transect suggests that (1) shoreward advection affected the

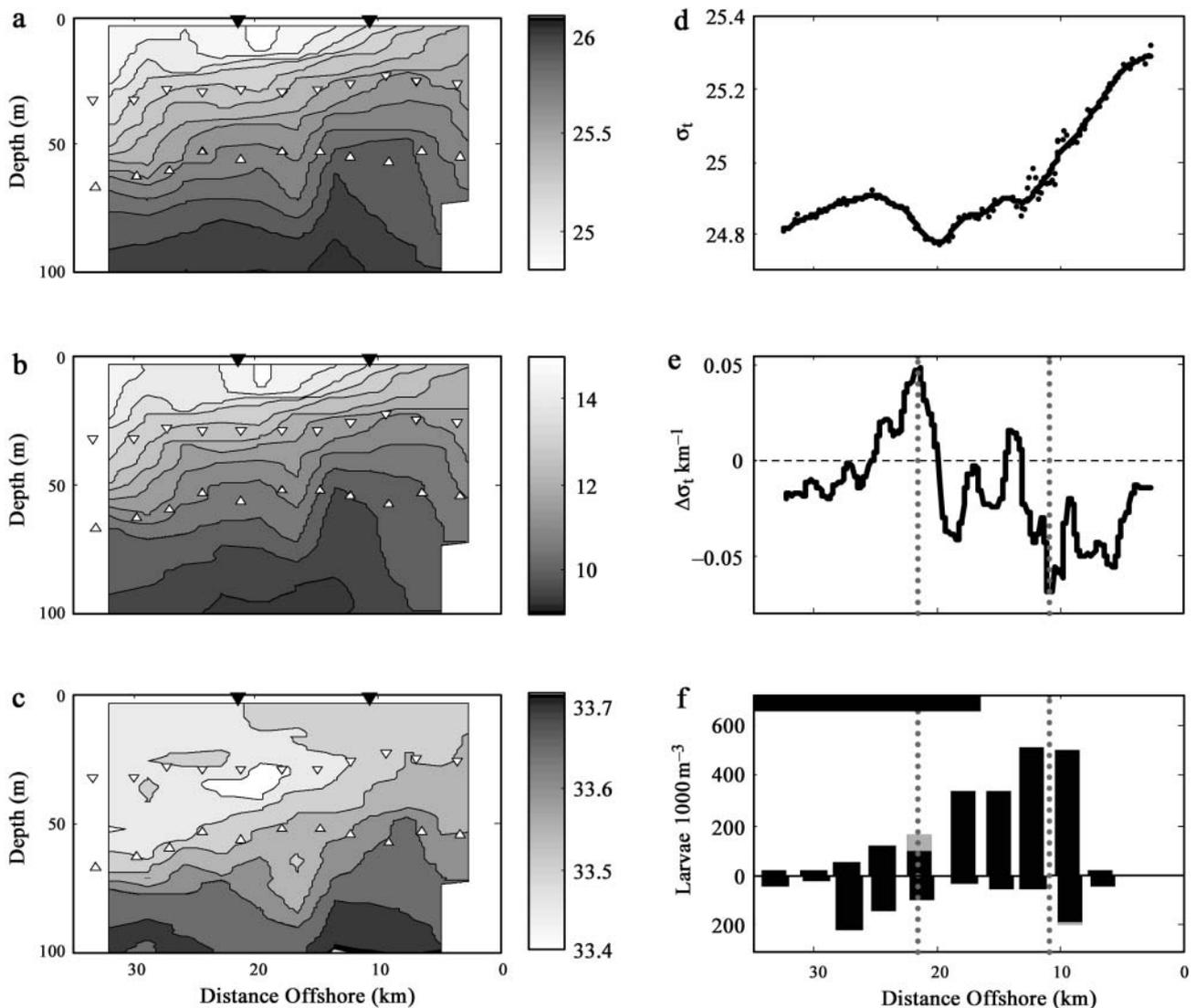


Fig. 3. Physical and biological data for Cruise I. (a) Density, (b) temperature, (c) salinity; open symbols indicate depths of deep (Δ) and shallow (∇) nets and filled symbols (\blacktriangledown) indicate the location of surface fronts. (d) Lowess-smoothed near-surface density. (e) Density gradients derived from smoothed curve in (d); negative gradients indicate effects of upwelling, vertical dotted lines indicate location of surface fronts. (f) Density of rockfish *Sebastes* spp. larvae of <6 mm (dark bars) and 6 to 8 mm (light bars); ascending bars represent larvae captured in the shallow net, descending bars represent larvae captured in the deep net; bar at the top of the plot identifies stations sampled during darkness, vertical dotted lines indicate location of surface fronts

upper 50 to 80 m of the water column, (2) onshore transport was especially rapid in the upper 20 m, and (3) downwelling occurred near the coast (Rosenfeld et al. 1995).

The transect crossed 2 fronts: (1) a strong, near-shore front associated with the Point Sur upwelling center (Figs. 1b & 4a–e; approximately 8 km offshore), and (2) a strong front between the upwelling plume from Point Año Nuevo and a poleward-flowing tongue of warm, oceanic water (Figs. 1b & 4a–e; approximately 27 km offshore). A weaker front on the coastal side of the Año Nuevo upwelling plume is apparent in the satellite image (Fig. 1b); however, the transect did not cross this front where it formed a clear feature, and appears instead to have skirted the southern edge of warmer water extending from Monterey Bay. Surface density in the region between the

2 strong fronts was highly variable (Fig. 4d), but this variability was not resolved in the hydrographic section (Fig. 4a), and appears to indicate shallow structure along the edge of the warm plume extending from Monterey Bay.

As on Cruise I, larval rockfishes were abundant near surface fronts associated with distinct subsurface structure, and the distribution at each front indicates a patch of larvae oriented along a frontal pycnocline (Fig. 4f). We observed elevated densities of small, preflexion larvae near the surface at both fronts. The highest densities of small larvae occurred near the surface at the nearshore front; larvae occurred in a compact patch that coincided with the steep pycnocline at this front (Fig. 4f). Larger (6 to 8 mm), more developed larvae were captured only at stations in the Point Año Nuevo upwelling plume, and occurred at higher densities near

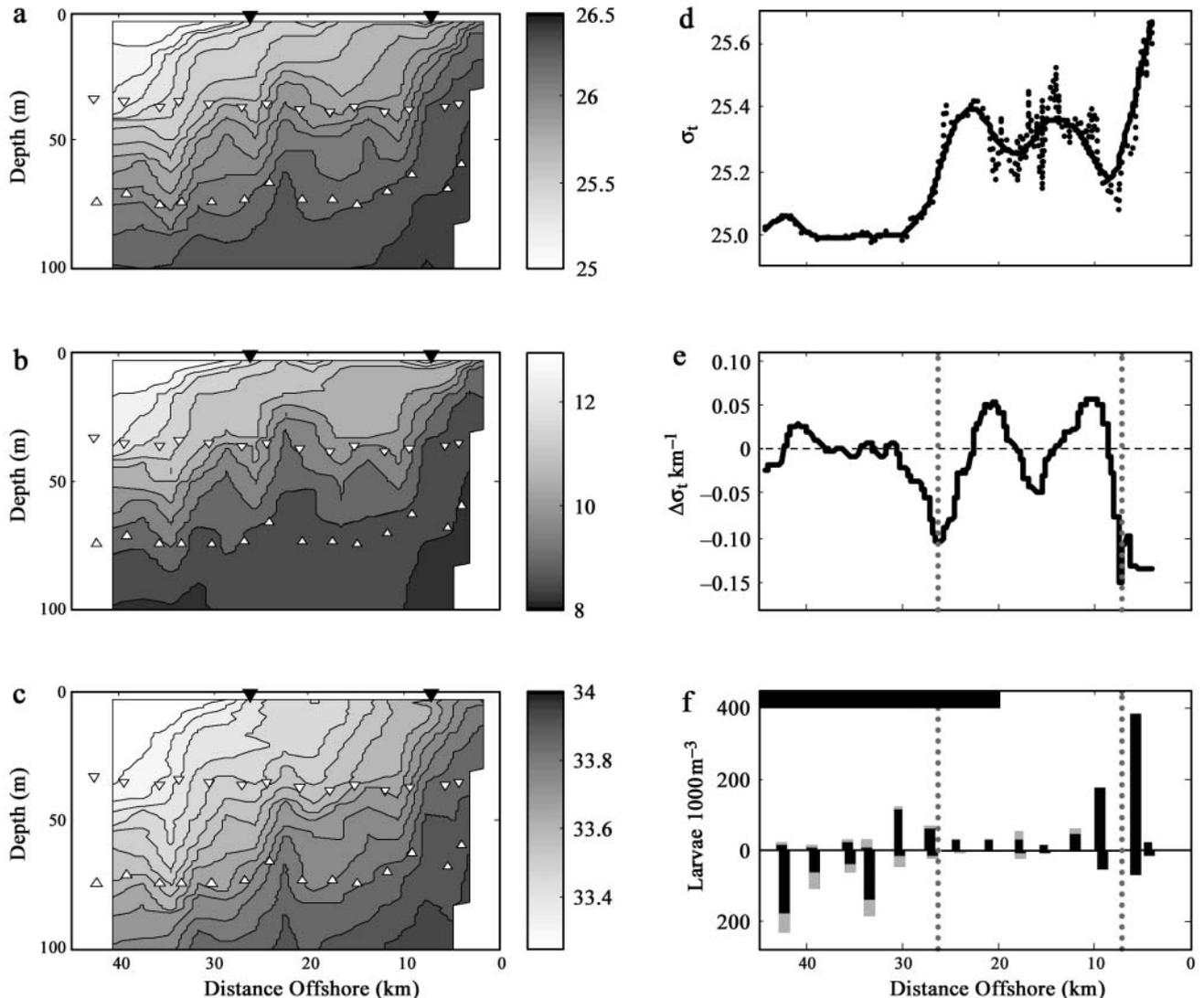


Fig. 4. Physical and biological data for Cruise II (4–5 May 1994). Details as in Fig. 3

the front on the oceanic side of the plume (Figs. 1b & 4f). The offshore displacement of the peak density of larval rockfishes relative to the surface front and the rapid shift in the vertical distribution of larval rockfishes between 30 and 33 km offshore match the structure of this front, i.e. the shallow slope and subsequent rapid increase in depth of the pycnocline offshore of the surface front (Fig. 4a,f). Rockfish larvae were largely absent from the region between the 2 fronts and in warm surface waters >30 km from shore (Fig. 4b,f), but occurred at relatively high density in the layer sampled by the deep net at stations >33 km offshore. The transect failed to span the entire offshore patch of rockfish larvae, and we lack hydrographic data that might provide a useful context for the relatively high larval density in the most offshore, deep sample (Fig. 4f).

Cruise III: June 1994

In contrast to the strong relaxation event observed during Cruise II, strong upwelling-favorable winds prevailed for 15 d prior to and throughout sampling on this transect (Fig. 2c). The transect crossed 2 fronts: (1) an upwelling front bounding the Point Sur upwelling center (Figs. 1c & 5a–e; approximately 8 km offshore), and (2) a front on the inshore side of the Point Año Nuevo upwelling plume, which extends completely across the mouth of Monterey Bay (Figs. 1c & 5a–e; approximately 15 km offshore). Complex structure in surface density gradients along the transect indicates a third front approximately 5 km offshore, but this feature does not exhibit substantial subsurface structure (Fig. 5a–e).

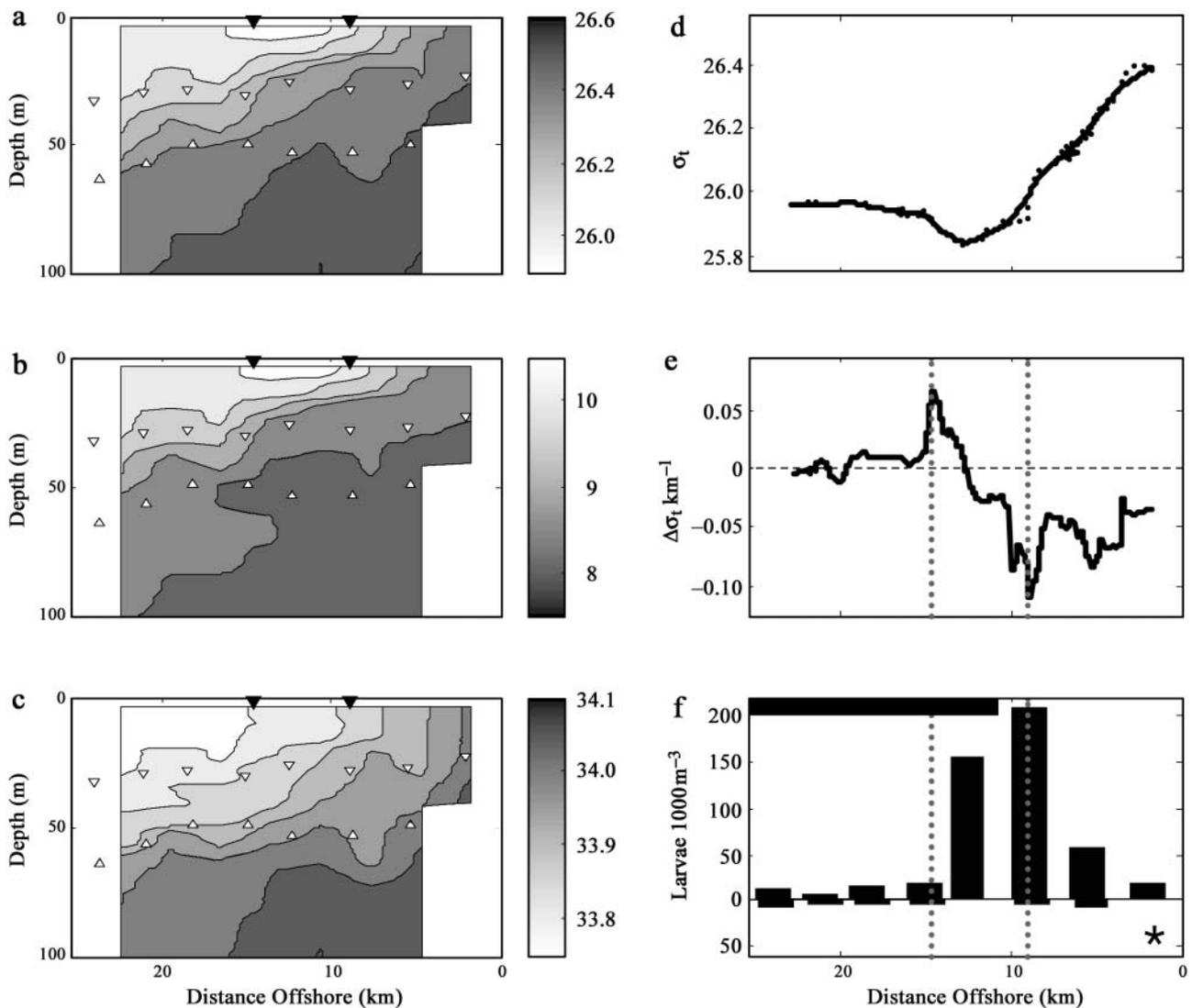


Fig. 5. Physical and biological data for Cruise III (25–26 June 1994). Details as in Fig. 3. ★ the deeper stratum was not sampled at the most inshore station

The highest density of larval rockfishes observed on this cruise occurred at the station coincident with the nearshore upwelling front, with substantial numbers of larvae captured at the stations immediately offshore and immediately inshore of that front (Fig. 5e,f). Almost all rockfish larvae captured were small, and only 1 of the larvae captured showed any sign of flexion. Note that the pycnocline associated with the surface front at 8 km offshore was sampled entirely by the shallow net, and thus our sampling was unable to determine whether the vertical distribution of larvae changed in response to the shallow slope of the pycnocline across the frontal zone (Fig. 5a,f). Very few larvae were captured at depths exceeding 25 to 30 m (Fig. 5f).

Cruise IV: August 1994

Upwelling favorable conditions preceded and continued through this cruise, save for a brief relaxation event approximately 3 d prior to sampling (Fig. 2d). This transect spanned 2 fronts: (1) a sharp upwelling front associated with the Point Sur upwelling center (Figs. 1d & 6a–c; approximately 5 km offshore); and (2) a front on the offshore side of the Point Año Nuevo upwelling plume (Figs. 1d & 6a–c; approximately 23 km offshore). The latter front occurred in a region marked by a deeper surface mixed layer and nearly vertical isopycnals, and exhibited a relatively deep, vertically oriented structure (Fig. 6a). Surface density gradients do not indicate a front on the inshore side of the Point

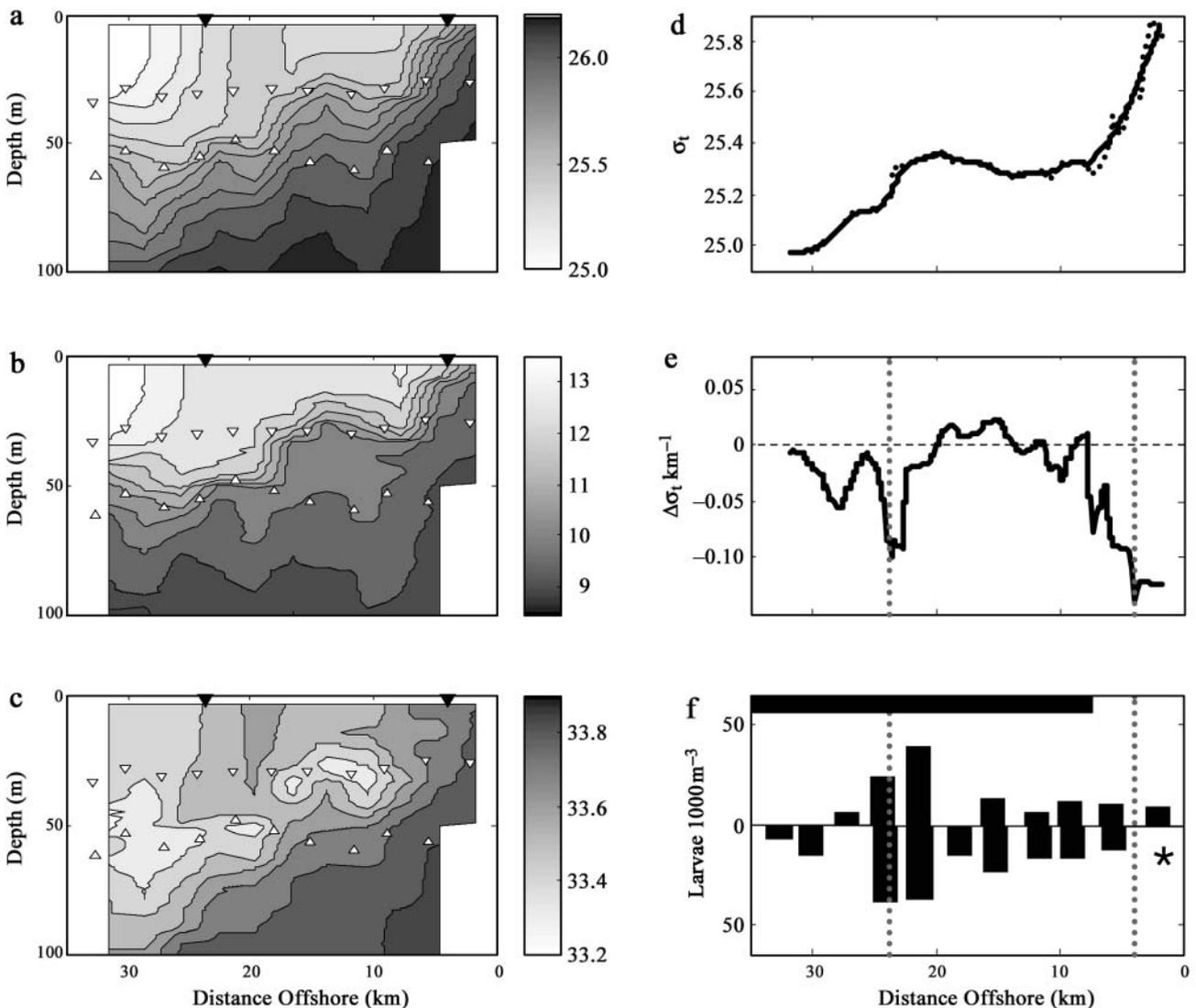


Fig. 6. Physical and biological data for Cruise IV (4–5 August 1994). Details as in Fig. 3. ★ the deeper stratum was not sampled at the most inshore station

Año Nuevo upwelling plume (Figs. 1d & 6e); this area is marked by unusual positive correlation between temperature and salinity (i.e. warmer, higher salinity water lying next to cooler, fresher water) in the area just offshore of the nearshore front.

Peak densities of small larval rockfishes were substantially lower on this cruise than densities observed on the previous cruises. Small, preflexion rockfish larvae were most abundant in both shallow and deep nets near the offshore front, and their cross-shelf distribution is truncated at this feature (Fig. 6f). In sharp contrast to previous cruises, a patch of larvae was not observed at the inshore front. As noted at the beginning of 'Results', larger larvae and small juveniles (ranging from 10.2 to 24 mm in length; data not shown) were far more common on this cruise than on the previous 3 cruises, but the inability of our gear to sample these individuals quantitatively precludes further analysis.

DISCUSSION

We present evidence, based on data collected under conditions ranging from intense upwelling to complete relaxation, that distributions of larval rockfishes *Sebastes* spp. are related to the location and cross-sectional structure of upwelling fronts off central California. The dataset consists of 4 temporally discrete transects, each of which provides a 2-dimensional 'snapshot' of the larval dynamics, which itself is the integration of larval production, transport, growth and mortality in the context of dynamic, 3-dimensional processes in the coastal ocean. Despite this limited perspective, the combination of our data with inferences on frontal history and the age and source of larvae captured in our samples supports the hypothesis that upwelling fronts affect distributions of early-stage larval rockfishes.

Distribution of larval rockfish in relation to upwelling fronts

Two general patterns emerge from comparisons between distributions of larval rockfishes and the location and structure of upwelling fronts. First, densities of rockfish larvae at or near upwelling fronts were higher than larval densities at stations away from such fronts. Elevated densities of larval rockfish were observed at 3 of 4 nearshore upwelling fronts (Cruises I–III; Figs. 3 to 5), and at 2 of 2 fronts on the oceanic side of the Point Año Nuevo upwelling plume (Cruises II and IV; Figs. 4 & 6). Second, changes in the vertical distribution of rockfish larvae, as indicated by changes in the propor-

tion of larvae captured in the shallow and deep nets, indicates a shift to deeper distributions at offshore stations that follows the slope of pycnoclines associated with upwelling fronts. Observations that suggest this relation range from larval patches that exhibit gradual increases in depth parallel to frontal pycnoclines (e.g. the inshore front of Cruise I [Fig. 3] and the offshore front of Cruise II [Fig. 4]) to more compact, vertically oriented patches at steeper fronts (e.g. the inshore front of Cruise II [Fig. 4], and the offshore front of Cruise IV [Fig. 6]). These patterns are similar to those reported from surveys of larval fish distributions in other frontal systems (e.g. Kiørboe et al. 1988, Grimes & Finucane 1991, Kingsford et al. 1991, Munk et al. 1995, Thorrold & McKinnon 1995, Lochmann et al. 1997).

Note that patches of larval rockfishes were not observed at all fronts; however, this is not surprising given the numerous conditions that must be satisfied for the generation and maintenance of a patch of larvae at a front. For example, low production or high mortality of larval rockfishes near the coast would fail to meet a necessary initial condition for formation of a patch of larvae and might account for the absence of a patch of larval rockfishes at the sharply defined front encountered near the coast during Cruise IV (Fig. 6). Note also that evidence that fronts on the coastal side of the Año Nuevo upwelling plume affect larval distributions was more equivocal than for other fronts encountered in this study. The capture of larger, more developed larvae at such a front during Cruise I (Fig. 3) suggests that such fronts can affect larval distributions, but no such concentration of larvae was observed at a similar front during Cruise III (Fig. 5). Without dismissing the importance of these exceptions, however, we note that we observed no cases in which a substantial patch of larval rockfishes occurred away from a front. Thus, our data support the hypothesis that fronts contribute to, but are not sufficient for the formation and maintenance of patches of larval rockfishes.

The preceding inferences appear to be robust for a number of reasons. First, from a statistical perspective, the generally smooth nature of changes in larval distributions along each transect suggests that within-station sampling variance is small relative to variation in density at the spatial scales of our study. Thus, in spite of the fact that our data consist of single estimates of larval density at each station, our sampling protocol appears to have been adequate to identify general associations of larval rockfishes and upwelling fronts. Second, since larval fishes exhibit behavioral responses to environmental cues and predator attacks, it is important to note that no potential artifact of our sampling program appears to confound our analysis. Correlation between illumination and front structure arising from the consistent practice of occupying

sampling stations in a day-tonight, onshore-to-offshore order, raises the possibility that changes in depth of larval rockfishes are related to changes in illumination rather than front structure. However, larval rockfishes do not exhibit typical diel vertical migrations, much less the atypical behavior of descending at night which would be required under this alternative hypothesis (Sakuma et al. 1999). The susceptibility of larval fishes, including larval rockfishes, to capture in plankton nets is also a function of illumination and is expected to increase during twilight and darkness (Morse 1989, McGurk 1992, Sakuma et al. 1999). The effect of increasing capture efficiency would, however, tend to mask the declines in abundance we observed at stations offshore of surface fronts.

Differences in the distribution of larval rockfishes of different sizes and developmental stages highlight the importance of considering the 3-dimensional dynamics of the coastal ocean in studies of larval ecology. In this study, all rockfish larvae captured at the near-shore fronts, save 1, were of the smaller, less developed, and presumably younger class. In contrast, almost all of the larger, more developed, presumably older larvae were captured at stations in the Año Nuevo upwelling plume. We lack direct estimates of age of larvae in our samples (e.g. otolith ring counts); however, rough estimates of larval age based on larval growth rates reported for *Sebastes saxicola*, *S. jordani*, and *S. goodei* suggest that the smaller larvae in our samples had undergone parturition 1 to 10 d prior to capture, while the larger larvae had been in the plankton for 5 to 25 d (Laidig et al. 1991, 1996, Sakuma & Laidig 1995, Ralston et al. 1996). While it is not known whether these growth dynamics adequately represent the growth of the larvae in our samples, the age classes estimated for larvae in our samples are consistent with the expected age of the fronts at which the larvae were captured.

Origins of patches of larval rockfishes at fronts

Species that undergo parturition primarily during the spring and summer, including some nearshore-demersal species and species of the subgenus *Sebastes* that occupy deeper benthic habitats on the inner shelf (Chen 1971, Love et al. 1991, Lenarz et al. 1995), are most likely to comprise the assemblage of larval rockfishes in our samples. Concentrations of larval rockfishes occurred at fronts well offshore of the distribution of adults of these species (which is restricted by the narrow continental shelf off the Big Sur coast) and thus apparently reflect the effects of transport following parturition. The general rarity of larval rockfishes in warmer waters surrounding the upwelling plumes, and differences in the size/developmental stage com-

position of larval populations in the Point Sur and Point Año Nuevo plumes support the hypothesis that larval rockfishes at a front originate from adults living in coastal habitats affected by the upwelling center bounded by the front, and not from other regions of the coast.

Our ability to discern conclusively the mechanism(s) that underlie observed distributions of larval rockfishes at upwelling fronts is limited by the 'snapshot' nature of the data at hand, yet our data do not contradict predictions from 2 plausible mechanisms: convergent accumulation and differential mortality. Distributions of larval rockfishes at upwelling fronts resemble general predictions from models of plankton accumulation and retention at fronts (Franks 1992), and are consistent with patterns reported for systems in which convergent accumulation of larval fishes has been demonstrated (e.g. Govoni & Grimes 1992, Lochmann et al. 1997). Modeling studies and field observations indicate that upwelling fronts exhibit convergent circulation in the upper water column (Federiuk & Allen 1995, Flament & Armi 2000); however, evidence that rockfish larvae actively maintain shallow depths—the other condition necessary for accumulation at a convergent surface front (Franks 1992)—is based only on reports that rockfish larvae and juveniles of some species reside in the upper part of the water column (Boehlert et al. 1985, Moser & Boehlert 1991, Lenarz et al. 1995, Yoklavich et al. 1996, Sakuma et al. 1999). Increased survival of larvae at fronts, presumably supported by convergent accumulation or increased production of suitable prey in frontal zones, might also generate and support elevated densities of larval (and pelagic juvenile) rockfishes at fronts. Whether sufficient time has elapsed since parturition for improved survival of larvae at fronts to generate spatial variation in abundance of larvae is not clear, particularly for the small, preflexion larvae. Differential survival, or perhaps active response to concentrated prey resources, is likely to have a greater influence on the distributions of larger larvae and pelagic juveniles at fronts than on the distributions of smaller larvae.

Implications for continued studies and management of *Sebastes* spp.

Our study differs substantially from previous investigations of early life history stages of rockfishes with respect to spatial extent and resolution, season, and species or life history stage of interest. Previous studies have investigated changes in the cross-shelf distribution of early-stage rockfishes in relation to variability in cross-shelf transport (Yoklavich et al. 1996), described the effects of (non-upwelling) oceanic fronts on

the distribution of larval rockfishes during the winter (Sakuma & Ralston 1995), and have documented higher densities of pelagic juvenile rockfishes at or near upwelling fronts (Lenarz et al. 1991, Larson et al. 1994, Wing et al. 1998). In contrast, our results demonstrate an association between larval rockfishes and upwelling fronts at a finer spatial scale (a few kilometers horizontally and tens of meters vertically) and at an earlier stage of the life history (the first few days to weeks following parturition) than had been previously documented. Importantly, our results apply to the life history stages that determine recruitment (Woodbury & Ralston 1991, Ralston & Howard 1995, Yoklavich et al. 1996). Thus, our results have important implications for future studies of mechanisms that generate variability in rockfish recruitment success.

Rockfish species vary substantially in the seasonality and ecology of their early life histories (Wyllie-Echevarria 1987, Love et al. 1990, Moser & Boehlert 1991, Lenarz et al. 1995). Results from a simple comparison, based on this diversity, among rockfish species with respect to patterns of larval survival and exposure of larvae to upwelling point out where our findings might have particular relevance. Recruits from species that undergo parturition during the winter and early spring are drawn from larvae born during discrete pulses of favorable conditions (Woodbury & Ralston 1991, Yoklavich et al. 1996). Interestingly, these species are exposed to variable, intermittent bursts of upwelling conditions and variation in the timing of the spring transition to sustained upwelling. Such variation is likely to affect the proportion of larval rockfishes that encounter an upwelling front. In contrast, birth-date distributions for the kelp rockfish *Sebastes atrovirens*, a species which undergoes parturition during the spring and summer, indicate that survivors are drawn from larvae born throughout the parturition season (Lenarz et al. 1995). Larvae of *S. atrovirens* and other species that undergo parturition during the upwelling season are more consistently exposed to upwelling fronts. In combination, these patterns identify upwelling fronts, or some correlated process, as a candidate mechanism to explain seasonal differences in patterns of larval survival among species of rockfishes and to translate intra-annual variability in upwelling dynamics into interannual recruitment variability.

Given the potential for upwelling fronts to influence the ecology of larval rockfish and the results presented here, analysis of frontal dynamics in relation to larval production might provide useful insight into processes that generate recruitment variability (Dixon et al. 1999). Understanding these mechanisms will also help us to understand how coastwide changes in upwelling associated with global climate change (Bakun 1990,

Schwing & Mendelssohn 1997) will affect recruitment and subsequent population dynamics of rockfishes. From a spatial perspective, understanding how upwelling fronts affect larval survival might contribute to development of spatially explicit models of recruit production which would provide information useful for delineating marine refugia (Allison et al. 1998, Morgan & Botsford 1998). Important issues remaining to be addressed to evaluate the role of upwelling fronts in rockfish recruitment include (1) whether feeding success, growth and survival (predation) differ between larval rockfish at upwelling fronts and larvae in water masses away from fronts in ways that generate differences in recruitment success, (2) whether fronts affect the distribution and transport of larvae continuously over the course of the pelagic life cycle, and (3) the generality (or the lack thereof) in how upwelling fronts affect larval ecology across species. Regardless of the particular species in the data reported here, the exposure of almost all rockfish species to at least intermittent upwelling during the larval phase suggests that our results have broader relevance and supports further study of the role of upwelling fronts in the early life history of rockfishes.

Acknowledgements. We thank C. Grimes, T. Laidig, R. Larson, S. Ralston, K. Sakuma, and M. Yoklavich for comments and criticism, and 3 anonymous reviewers for comments on an earlier version of the manuscript. We are grateful to S. Alexander, J. Paduan, F. Schwing, and G. Boehlert for discussions of coastal oceanography and the ecology of larval fishes; to T. Anderson and G. Hatcher for their efforts in obtaining and processing the hydrographic data; and to the captains and crew of the RV 'Point Sur' for ably assisting the sampling program. This research was funded under grants from the National Science Foundation to J.R. (OCE-9115876) and L.K.R. (OCE-9116408). E.P.B. gratefully acknowledges support from a National Science Foundation Graduate Research Fellowship and the Earth Systems Program at Stanford University.

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