## INFLUENCE OF WATER COLUMN STRATIFICATION ON THE DEPTH DISTRIBUTIONS OF PELAGIC JUVENILE ROCKFISHES OFF CENTRAL CALIFORNIA

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## ABSTRACT

We examined the vertical distribution of pelagic juveniles in 15 species of rockfishes off central California. In depth-stratified midwater trawls made at night, pelagic juveniles of most species were equally distributed throughout the water column. Notable exceptions were Sebastes paucispinis, which was significantly more abundant in 10 m and 30 m tows, and S. melanops, S. entomelas, and S. mystinus, which were common in 100 m tows though not significantly so. All species were collected mainly below the thermocline, but thermocline depth was a poor predictor of the vertical distribution of pelagic juveniles. Increased stratification of the water column, however, led to a tendency for deeper centers of density for most species (13 of 15), and smaller rockfishes (≤25 mm standard length) occurred primarily below the thermocline. In the presence of weak or gradual thermoclines, Simpson's (1981) parameter of water column stratification may be a better measure of overall water column characteristics than thermocline depth alone, and it may be a better indicator of the effects of water column characteristics on the distribution of pelagic juvenile rockfishes. The patterns indicated by our data suggest that it would be worthwhile to further examine the effects of ontogeny and hydrography on the vertical distributions of pelagic juvenile rockfishes.

## INTRODUCTION

While the effects of coastal oceanographic features and the horizontal distributions of the early life stages of fishes have been studied extensively (Kingsford and Choat 1986; Grimes and Finucane 1991; Cowen et al. 1993; Sabatés and Olivar 1996), comparatively little attention has focused on their influence on vertical distributions. Knowledge of vertical distribution of early life stages, however, is essential to understanding the interactions between oceanographic and biological processes. For example, pelagic early life stages of fishes may exhibit behavioral strategies that help them either to remain in, or

[Manuscript received 2 October 2002.]

to be transported to, favorable areas. A combination of vertical migration and vertically structured ocean processes may provide a mechanism for avoidance of passive larval drift, resulting in increased larval retention, survival, and recruitment (Sinclair 1988; Bakun 1996).

Interactions between active vertical migration (Parrish et al. 1981; Moser and Boehlert 1991), stage of development (Larson et al. 1994; Sakuma and Larson 1995), and physical transport mechanisms may affect the onshore/offshore distributions of the pelagic early life stages of fishes in the upwelling regions of the California Current system. Studies of vertical distribution in these upwelling areas suggest that the depth distributions of rockfish larvae in particular are directly related to water column stratification, with the lower depth limit of larvae being bound by either the depth of the thermocline (Ahlstrom 1959; Moser and Boehlert 1991) or the pycnocline (Sakuma et al. 1999). Lenarz et al. (1991) found no evidence of a relationship between thermocline depth and the vertical distributions of pelagic juvenile rockfishes off central California. However, the data of Shenker (1988) and Doyle (1992) indicate that pelagic juvenile stages may occur shallower in the water column than larvae, suggesting that responses to depth and to the thermocline may vary with ontogeny.

This article employs a long-term data set collected by the National Marine Fisheries Service, during May-June cruises from 1987 to 1998 to investigate the depth distributions of pelagic juvenile rockfishes in relation to hydrography. Specifically, we describe the vertical distributions of pelagic juvenile stages of fifteen *Sebastes* species relative to the stratification of the water column.

#### **METHODS**

The California Current system off central California is strongly influenced by seasonal, wind-driven upwelling (Hickey 1979) and associated filaments and eddies (Mooers and Robinson 1984). A strong upwelling center occurs at Point Reyes and a weaker one at Davenport, north of Monterey Bay (Schwing et al. 1991). Filaments from these centers carry upwelled water far offshore and to the south, forming frontal boundaries with warmer, less saline water masses (Mooers and Robinson 1984;

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Schwing et al. 1991). Filaments intermingled with synoptic mesoscale eddies may provide significant cross-shelf transport of heat, nutrients, and biota (Mooers and Robinson 1984).

## **Data Collection**

The National Marine Fisheries Service conducts annual May-June midwater-trawl surveys of pelagic juvenile fishes between Cypress Point (36°35'N) and Point Reves (38°10'N). A set of stations is sampled during tennight sweeps of the survey area using a modified Cobb midwater trawl with a nominally square 14 m by 14 m mouth and a 9.5 mm stretched mesh cod-end liner (Wyllie Echeverria et al. 1990). Three replicate sweeps are typically completed from mid-May to mid-June of each year. We used data from trawls at the four most consistently sampled depth-stratified stations to investigate species' depth preferences (see fig. 1). Because target depths varied over the years, catches were divided into three depth categories, 10 m (6 and 8 m target depth tows), 30 m (30 and 32 m target depth tows), and 100 m (80 and 110 m target depth tows). Since 1993, a Vemco TDR (time-depth recorder) was attached to the upper bridle of the net and recorded the depth of each tow. The net was lowered to the target depth and towed at a ship speed of approximately 5 km/hr for 15 min, as described by Lenarz et al. (1991).

Conductivity-temperature-depth (CTD) casts were made using a Sea-Bird Electronics SEA-CAT-SBE-19 profiler at each trawl station to obtain temperature, salinity, and density information at depth.

Pelagic juvenile *Sebastes* were collected, identified, counted, and frozen at  $-80^{\circ}$ C aboard the research vessel. In the laboratory, standard length (SL) was measured to the nearest mm for either all individuals of each species or a subsample of 100 fish per tow of each species.

## **Data Analysis**

Acoustic measurements indicate that the mouth width of the Cobb midwater trawl changes with depth. Width varies from 8 m at a depth of 10 m, to 11 m at 30 m depth, and 13.5 m at 100 m depth (Lenarz at al. 1991). We adjusted catch abundances for mouth width prior to analysis by multiplying the 10 m depth trawls by 1.375 (11/8) and 100 m depth trawls by 0.8148 (11/13.5); we did not adjust 30 m depth trawls. We log transformed adjusted species abundances (abundance +1) to normalize the data and equalize variances. Because of high variability of towed net sampling, we present data results at both the 0.05 and 0.10 significance levels.

We examined within-station differences in species' abundances due to year, depth, and year\*depth interactions using a two-factor, repeated-measures analysis of variance (ANOVA). For this analysis, catches for each



Figure 1. Location of four stations with depth-stratified tows sampled during May–June cruises, 1987–98, and included in the repeated measures analysis of variance.

species were averaged within depth categories for each station and year because not all depths at a station were sampled in each sweep and we needed a complete data matrix to perform the statistical analysis. As a result, the average catch at each station and depth, while typically based on three data points, was sometimes based on one or two data points. We considered year and depth as experimental treatments. We performed all *F*-tests under the assumption of multivariate normality and adjusted probability values for violations of the assumption of compound symmetry using the Huynh-Feldt epsilon (O'Brien and Kaiser 1985; Athey and Connor 1989).

We compared the vertical distribution of each species to the depth of the thermocline by subtracting the mean depth of catch from the depth of the thermocline at each of the four stations (Sakuma et al. 1999). We refer to this as the *depth of catch relative to the thermocline* (DCRT). We carried out this analysis for stations at which all three depth strata were sampled and at which the species was captured in at least one depth stratum. We calculated the mean depth of each species as the center of density:

$$Z = \sum_{i=1}^{n} P_i Z_i,$$

where  $Z_i$  is the depth of the *i*th sample, and  $P_i$  is the proportion of pelagic juveniles at depth *i* (Fortier and Leggett 1983).

Species	10 m tows			30 m tows			100 m tows		
	Catch	Length range	Length mode	Catch	Length range	Length mode	Catch	Length range	Length mode
Sebastes auriculatus	369	12-34	16	89	16-39	17	10	14-32	19
S. crameri	38	12-53	ND	15	18-52	ND	3	19-41	41
S. entomelas	356	27-81	62	529	20-73	34	320	25-66	53
S. flavidus	96	16-52	15-83	60	26-50	ND	36	31-50	ND
S. goodei	3,280	15-83	60	2,526	10-80	57	56	14-69	50
S. hopkinsi	707	17-64	50	1,076	16-62	53	87	19-59	48
S. jordani	46,925	8-81	73	111,251	9-82	67	2,831	9-83	68
S. levis	17	22-57	50	7	15-62	ND	1		48
S. melanops	10	31-46	ND	23	23-44	41	12	21-44	38
S. mystinus	239	39-63	48	196	23-55	43	239	29-60	49
S. paucispinis	352	13-110	48	134	14-107	47	19	23-83	24
S. pinniger	202	16-38	34	200	15-39	33	178	14-39	33
S. rufus	105	34-56	51	10	39-60	52, 54	3	46-53	51
S. saxicola	293	21-45	35	191	23-52	34	23	22-44	34, 37
S. wilsoni	59	27-36	32	44	14–38	30	14	28-36	34
Overall	53,048	8-110	73	116,358	9-107	67	3,832	9-83	68

TABLE 1 Standardized Catches and Lengths (mm SL) of Pelagic Juvenile Rockfishes Collected at Depth-Stratified Stations off Central California During May–June Cruises, 1987–98

Note: Catches adjusted for net width at depth. ND denotes no discernable mode.

We defined station thermocline depth as the depth of maximum change in temperature ( $\Delta$ T). We addressed the question of whether this represented a "true" thermocline by comparing a measure of water column stratification,  $\phi$  (Simpson 1981), to our estimated thermocline depths. A highly significant Spearman rank correlation between  $\Delta$ T and  $\phi$  supports our definition ( $r_s = 0.513$ , p = 0.000, n = 120). We calculated the stratification parameter,  $\phi$ , the amount of work per unit volume (J/m<sup>3</sup>) required to bring about vertical redistribution of the mass in complete mixing, as

$$\begin{split} \varphi &= 1/h \int_{-h}^{0} (\overline{\rho} - \rho) gz dz, \\ \text{where} \\ \overline{\rho} &= 1/h \int_{-h}^{0} \rho z dz, \end{split}$$

h = depth of CTD cast (m),

- $\rho = \text{density (kg/m^3)},$
- g = -9.8 (m/s<sup>2</sup>), and

$$z = depth (m),$$

using the density data over the depth of the CTD cast or 150 m, whichever was the least.

To determine if the depth of the thermocline had a direct influence on vertical distribution, we calculated the mean depth of catch relative to a fixed depth of 20 m (DCR20) and compared the variances with those of the DCRT (Sakuma et al. 1999).

We investigated the role of thermocline strength in determining species' depth distributions by regressing the mean depth of catch against water column stratification,  $\phi$ , at the same station. We assume that the stratification parameter is a good proxy for the strength of the thermocline (pycnocline and thermocline depths were highly correlated,  $r_s = 0.816$ , p = 0.000, n = 120).

## RESULTS

Over 173,000 pelagic juvenile rockfishes were collected in the midwater trawls, and catches were dominated by *Sebastes jordani* (tab. 1). Specimens ranged in size from 8 to 110 mm SL, with a mode of 73 mm SL in shallow tows, 67 mm SL in mid-depth tows, and 68 mm SL in deep tows. A small proportion of the individuals were either late larval or early juvenile stages 10–20 mm in SL, but most were larger juveniles of a size believed competent to settle (30–90 mm SL, depending on species) (Anderson 1983; Ralston and Howard 1995). Fish smaller than 25 mm SL, however, are not fully vulnerable to the midwater trawl gear, so they are underestimated in the catches (D. Woodbury, National Marine Fisheries Service, Southwest Region Field Office, pers. comm.).

A wide range of water column conditions was observed during the 12 years of the study (fig. 2). As these examples illustrate, the thermocline was relatively sharp at some stations, stepped at others, and quite gradual at others. Mean thermocline depth, computed from all CTD profiles, was 24.5 m (standard error = 1.3, n = 120) with a minimum depth of 4 m and a maximum depth of 89 m. Water column stratification ranged from 36 to 308 J/m<sup>3</sup>, with a mean of 141.1 J/m<sup>3</sup> (SE = 5.7, n = 120).

Pelagic juvenile rockfishes of most species were more or less evenly distributed among the three depth cate-



Figure 2. Examples of individual CTD cast profiles with strength of water column stratification,  $\phi$ , shown in density plot. For station locations, see fig. 1.

Target Haul Depth (m)

0.03 0 0.05 0.1 0 0.025 0.05 0 0.1 0.2 0 0.06 0. 0 0. 20. 20  $20 \cdot$  $20 \cdot$ 40 40. 40-40-60. 60. 60 60 80 80. 80 80 100. 100-100 100 120. 120-120 120 Sebastes auriculatus S. entomelas S. flavidus S. crameri  $F_{2,6} = 1.095; P = 0.393$  $F_{1,3} = 5.657; P = 0.087$  $F_{2,6} = 1.642; P = 0.270$  $F_{1,4} = 1.820; P = 0.255$ 0.2 0.2 0 0 0.5 0.01 0.02 0.10 0. 0 0 0 20 20-20. 20 40 40 40 40 60. 60 60 60. 80 80 80 80 100 100 100 100 120-120-120 -120 -S. goodei  $F_{1,5} = 1.732; P = 0.260$ *S. jordani*  $F_{2,6} = 1.561; P = 0.284$ S. hopkinsi S. levis  $F_{1,3} = 3.199; P = 0.158$  $F_{1,3} = 0.929; P = 0.413$ -0.02 0.02 0.04 0.1 0.2 0.2 0 0 0 0.1 0.05 0.1 0-0 0 0--e 20. 20  $20 \cdot$ 20 40. 40. 40 40 60. 60-60 60. 80-80 80. 80 100 -100-100. 100 120-120 -120 120 *S. mystinus*  $F_{2,6} = 3.266; P = 0.110$ S. pinniger  $F_{2,6} = 0.753; P = 0.511$ S. paucispinis S. melanops  $F_{2,6} = 2.154; P = 0.197$  $F_{1,4} = 9.552; P = 0.030$ 0 0.02 0.04 0 0.04 0.08 -0.01 0.01 0.03 0. 0. 20 20-20  $40 \cdot$ 40 40 60. 60 60 80-80 80 100. 100 100 120 120. 120 *S. rufus*  $F_{2,6} = 1.756; P = 0.251$ S. saxicola S. wilsoni  $F_{2,6} = 0.588; P = 0.585$  $F_{2,6} = 0.393; P = 0.691$ 

# Log (abundance +1)

Figure 3. Estimated mean abundances and standard errors showing the vertical distributions of pelagic juvenile rockfishes off central California during May–June cruises, 1987–98. *F*-test degrees of freedom adjusted and rounded to the next lowest integer using the Huynh-Feldt epsilon (O'Brien and Kaiser 1985). *X*-axis scales vary with species.



Figure 4. Mean depth of catch relative to the thermocline (DCRT) for pelagic juvenile rockfishes off central California during May–June cruises, 1987–98. Diamonds denote depth of thermocline minus mean depth of catch, horizontal lines denote standard error, and numbers in parentheses are number of positive stations.

gories (fig. 3). Juvenile *S. paucispinis* and *S. crameri* were most abundant in 10 m and 30 m tows, significantly so for *S. paucispinis* at the 0.05 level ( $F_{1,4} = 9.552$ , p =0.030), and for *S. crameri* at the 0.10 level ( $F_{1,3} = 5.657$ , p = 0.087) (fig. 3). In contrast, juvenile *S. melanops*, *S. entomelas*, and *S. mystinus* were more commonly taken in the 100 m tows, but not significantly so (fig. 3). We found no significant interactions between year and depth for any species.

The mean nighttime center of density for pelagic juvenile rockfishes occurred either in or below the thermocline in all species examined (fig. 4). Vertical distributions of shallow species—*S. levis, S. paucispinis,* and *S. crameri*—were centered closer to the thermocline than those of deep species—*S. entomelas, S. melanops,* and *S. mystinus.* Some individuals of each species, however, were found above the thermocline in these night-time samples.

Variances of the DCR20 were lower than those of the DCRT for just over half the species (8 of 15; see tab. 2). This suggests that these species orient to depth per se rather than to the thermocline. This is further suggested in a plot of mean depth of catch versus thermocline depth, which shows that pelagic juveniles of most species are widely scattered in the water column, leading to the observed high variances (fig. 5). However, linear regression analysis indicates that most species (11 of 15) tended to have deeper mean centers of density as a result of increasing thermocline depth, significantly

TABLE 2Variance of Mean Depth of Catch Relative tothe Thermocline (DCRT) and the Depth of CatchRelative to a Fixed Depth of 20 m (DCR20) forPelagic Juvenile Rockfishes off Central California,May-June Cruises, 1987–98

	Variance				
Species	DCRT	DCR20			
Sebastes levis (cowcod)	227.7	209.0			
S. paucispinis (bocaccio)	543.2	233.7			
S. crameri (darkblotched rockfish)	939.1	669.2			
S. pinniger (canary rockfish)	372.2	591.7			
S. auriculatus (brown rockfish)	967.0	1,117.3			
S. hopkinsi (squarespot rockfish)	1,416.8	1,336.6			
S. flavidus (yellowtail rockfish)	1,476.1	1,544.3			
S. jordani (shortbelly rockfish)	465.2	405.5			
S. goodei (chilipepper)	1,050.2	984.6			
S. saxicola (stripetail rockfish)	1,019.5	1,215.6			
S. wilsoni (pygmy rockfish)	2,217.7	1,837.7			
S. rufus (bank rockfish)	1,972.7	2,253.5			
S. entomelas (widow rockfish)	1,353.3	1,489.0			
S. melanops (black rockfish)	1,402.4	1,272.9			
S. mystinus (blue rockfish)	1,281.3	1,328.6			

so for *S. pinniger* (p = 0.002) and *S. jordani* (p = 0.034) at a level of 0.05, and for *S. rufus* at a level of 0.10 (p = 0.054) (fig. 5).

Mean depth of catch for rockfishes  $\leq 25 \text{ mm SL}$  occurred primarily beneath the thermocline (fig. 6). Mean depth of catch occurred below the thermocline slightly more frequently (80 of 88 stations, 91%) at stations with an overall species' mean SL of  $\leq 25 \text{ mm}$  than at stations with a mean species' SL of  $\geq 25 \text{ mm}$  (207 of 250, 83%) (chi-square = 3.341, df = 1, p = 0.068), suggesting that ontogeny may have influenced the depth distributions relative to the thermocline.

To further evaluate the effects of water column stratification on the depth distributions of pelagic juvenile rockfishes, we regressed mean depth of catch against the water column stratification coefficient (fig. 7). Most species (13 of 15) exhibited a deeper mean depth of catch with increasing stratification of the water column (as indicated by a negative slope), although the slope was significantly different from zero at the 0.05 level only for S. saxicola (p = 0.004, n = 21), and for S. entomelas and S. flavidus at the 0.10 level (fig. 7). Those species with greater mean depth of catch were affected by water column stratification more than shallow species, suggesting that the response to stratification depended on mean depth (fig. 8). We found a stronger relationship when we excluded S. levis and S. rufus, species with less than ten estimates of mean depth, from the regression analysis (Adj.  $r^2 = 0.151$ , p = 0.104, n = 13).



# Depth of Thermocline (m)

Figure 5. Influence of nighttime thermocline depth on mean depth of catch for pelagic juvenile rockfishes at positive depth-stratified stations off central California during May–June cruises, 1987–98. X-axis scales vary with species.



Figure 6. Depth distribution of rockfishes ≤25 mm standard length at night off central California during May–June cruises, 1987–98. Diagonal line indicates that mean depth of catch and depth of thermocline are equal.

## DISCUSSION

We attempted through this study to expand on the work of Lenarz et al. (1991), employing an additional eight years of sampling information. Despite the additional data, however, many of the relationships we present are not statistically significant. Perhaps the true patterns in nature are no stronger than those we report here, but much of the additional data came from years in which recruitment of rockfishes, and their abundance in midwater tows, was low, particularly 1992-98 (Ross 2001; S. Ralston, National Marine Fisheries Service, Southwest Fisheries Science Center, pers. comm.). The low catches in midwater tows reduced the opportunity for comparisons of depth distributions. We discuss our results fully recognizing the exploratory nature of the study but in the belief that trends and patterns documented are of enough interest to warrant future investigation.

The nighttime vertical distributions of pelagic juvenile rockfishes we observed in the coastal waters off central California were similar to those described by Lenarz et al. (1991). Our results agree qualitatively with those of Lenarz et al. (1991), who, based on fewer years of data, also found that *S. paucispinis* occurred at shallower depths and that *S. entomelas* and *S. mystinus* were most abundant at the deeper depths.

We found conflicting results on the influence of water column characteristics on the vertical distribution of pelagic juvenile rockfishes. Our data suggest that station thermocline depth is a poor predictor of the vertical distribution of pelagic juveniles. Gray (1996) and Sakuma

et al. (1999) also found that thermocline depth poorly predicts vertical distributions. However, Gray (1996) suggested that the occurrence of weak, gradual thermoclines (extending over 20-30 meters of depth) might have made it difficult to find such an association in the coastal waters off Australia. Weak or gradual thermoclines were also common in our data. Although we made no attempt at classification, we observed a wide range of water column conditions during the 12 years of sampling. Because of this variability in the nature of the thermocline, the water column stratification parameter might better indicate the effects of water column characteristics on the distributions of juvenile fishes. In addition, it appears that the response of species to water column stratification may depend on their mean depth in the water column, with deeper-living species showing a slightly greater response to stratification than shallow species.

The thermocline (Ahlstrom 1959; Boehlert et al. 1985; Moser and Boehlert 1991; Larson et al. 1994) and the pycnocline (Sakuma et al. 1999) have been reported as representing lower boundaries to the vertical distribution of larval rockfishes, but this does not appear to be the case for pelagic juvenile rockfishes. Our finding that juvenile rockfishes occur primarily below the thermocline, in contrast to the documented occurrence of larval stages above the thermocline or pycnocline (Ahlstrom 1959; Boehlert et al. 1985; Moser and Boehlert 1991; Larson et al. 1994; Sakuma et al. 1999), suggests a change in rockfish depth distributions with ontogeny. Larval and transforming prejuvenile fishes may need to undergo varying periods of acclimation to decreasing temperatures while descending through the thermocline (Steiner and Olla 1985). Micronektonic S. diploproa, splitnose rockfish, have a physiological predisposition for colder conditions (Boehlert 1978, 1981) but do not migrate directly from surface waters to the deeper adult habitat. Instead they have a midwater transition period lasting as long as several months (Boehlert 1977). Similarly, prejuvenile red hake (Urophycis chuss) do not descend immediately below the thermocline at transformation but remain above it in warmer waters (Steiner and Olla 1985). Juvenile walleye pollock (Theragra chalcogramma) in the laboratory have been observed to alter their vertical position in the water column in response to a thermocline, moving above it but making brief exploratory movements down into or along it (Olla and Davis 1990).

Our results also suggest that the depth distributions of pelagic juvenile rockfishes might be related to ontogeny, in that smaller fish ( $\leq 25 \text{ mm SL}$ ) occurred below the thermocline slightly more consistently than larger fish. The presence of smaller pelagic juvenile rockfishes ( $\leq 25 \text{ mm SL}$ ) beneath the thermocline is consistent with the hypothesis of Lenarz et al. (1991); they found that Mean Depth of Catch (m)

#### 75 150 225 300 150 225 300 150 225 300 150 225 300 وہ 0 0 000 B.B ഗ്ലാ ହତ യ ° 0 120-ω P = 0.967P = 0.391P = 0.090P = 0.057Sebastes auriculatus S. entomelas S. flavidus S. crameri 150 225 300 150 225 150 225 300 හි Ø О ò o<sup>o</sup> C O 00 00 = 0.170= 0.533 P = 0.671P P = 0.418S. hopkinsi S. jordani S. levis S. goodei 150 225 300 150 225 300 150 225 300 150 225 300 C 0 00 ρ රි Ω õ ၀ လည်ာ ၀ P = 0.188P = 0.252P = 0.535P = 0.565S. melanops S. mystinus S. paucispinis S. pinniger 150 225 300 150 225 150 225 300 -0 000 ૺૡૢૼૼ૾ૼૢ ωo = 0.004P = 0.410P = 0.446S. rufus S. saxicola S. wilsoni

# Water-column Stratification (J/m<sup>3</sup>)

Figure 7. Mean depth of catch as a function of water column stratification at night for pelagic juvenile rockfishes at positive depth-stratified stations off central California during May–June cruises, 1987–98.



Figure 8. Relationship between the rate of change in mean depth of catch due to water column stratification (see fig. 7) and the mean depth of the species in the water column. Solid dots are data points for *Sebastes levis* and *S. rufus*.

smaller pelagic juveniles of *S. jordani* (which they regarded as those less than 50 mm in SL, because they are small for fully transformed juveniles in this species) might be adapted to avoid shallower waters, in order to reduce the possibility of offshore advection during the May-June period of intense upwelling activity off central California. If the sensory and locomotory abilities of pelagic juvenile rockfishes  $\leq 25$  mm SL allow them to make similar adjustments in their depth distributions, this may represent a behavioral response to reduce the impact of upwelling on onshore/offshore distributions and possibly increase recruitment success (Parrish et al. 1981; Larson et al. 1994; Sakuma et al. 1999).

A suite of behavioral responses involving interactions between water temperature, prey availability, ontogenetic stage, and thermoclines, however, may influence the vertical distributions of early life stages of fish (Steiner and Olla 1985; Olla and Davis 1990; Sogard and Olla 1996). Experimental studies indicate that when food is present below a thermocline, prejuvenile walleye pollock (will migrate transiently beneath it, thereby altering their vertical distributions, at least temporarily (Olla and Davis 1990). Food-deprived juveniles may use an energy-conserving behavioral response, descending beneath the thermocline to lower metabolic costs, whereas under conditions of increased food availability they tend to stay above the thermocline (Sogard and Olla 1996).

Lenarz et al. (1991) suggested that larger pelagic juvenile rockfish may be adapted to searching the water column for optimal feeding conditions. The lack of statistical significance in the vertical distributions of 14 of 15 species of pelagic juvenile rockfishes may reflect this feeding behavior. Pelagic juvenile rockfishes appear to be opportunistic feeders, specializing on intermittently abundant single prey items (Reilly et al. 1992). Major prey items are the various life stages of calanoid copepods and subadult euphausiids, including eggs, but diet is apparently unrelated to predator size (Reilly et al. 1992). Synoptic vertical sampling of pelagic juvenile rockfishes, zooplankton, and hydrography is required to determine the relationships, if any, among the depth distributions of predator, prey, and oceanographic features.

Onshore vertical distributions may differ from the offshore vertical distributions presented in the present study, particularly for nearshore species of pelagic juvenile rockfishes as they move onshore into adult habitats later in the season. Moser and Boehlert (1991) reported that larval abundances of rockfish at an onshore and offshore station varied markedly for the 20-30 m depth interval. Almost no larvae were found within this depth interval at the offshore station, whereas a large proportion of the total larvae were found within this depth interval at the onshore station. The difference between the two stations corresponded to the associated depth of the thermocline, which was 20-40 m at the shelf station and 30-50 m at the offshore station. Larson et al. (1994) noted evidence of juvenile rockfishes with an unusually shallow bathymetric distribution in southern Monterey Bay, during the period 2-12 June 1987. This vertical distribution coincided with the development of a sharp, shallow thermocline (approximate depth 15 m) during an upwelling relaxation event and the apparent onshore movement of several species of Sebastes. In contrast, during the same relaxation event smaller pelagic juvenile rockfishes remained offshore and deeper (Larson et al. 1994). These results, in combination with the potentially deeper distribution of smaller pelagic juvenile rockfishes seen in this study, and the observations by Shenker (1988) and Doyle (1992) of pelagic juvenile rockfishes in the neuston, suggest that depth distributions may change ontogenetically.

In conclusion, our results suggest that pelagic juveniles of different rockfish species tend to be most abundant at different depths in the water column, in agreement with previous studies. We found conflicting results regarding the effects of water column stratification on vertical distributions. Mean depth of catch was statistically unrelated to thermocline depth, but in most species mean depth of catch tended to be deeper when the water column stratification parameter was greater, and this effect may have been larger for deeper occurring species. Finally, we had indications that depth distributions may change ontogenetically. Despite 12 years of sampling, usually with three replicate sample sets per year, the effects of water column characteristics and ontogeny were poorly resolved in our data set. This may, in part, be the consequence of low abundances of most pelagic juvenile species for most years from 1987 to 1998. We believe that it remains worthwhile to pursue questions about the relationships of ontogeny and hydrography with the vertical distributions of pelagic juvenile rockfishes. Sampling programs more strongly focused on depth distributions per se will be required to evaluate trends suggested by our results.

#### ACKNOWLEDGMENTS

We thank the officers and crew of the NOAA research vessel *David Starr Jordan*. We also thank the fishery biologists from the National Marine Fisheries Service, especially David Woodbury (Southwest Region Field Office, Santa Rosa, California), Stephen Ralston, Dale Roberts, and Keith Sakuma (Southwest Fisheries Science Center, Santa Cruz, California). Edward Connor (San Francisco State University) suggested many of the statistical analyses we conducted for this article. Edward Connor, Stephen Ralston, and two anonymous reviewers offered valuable suggestions on various versions of the manuscript.

### LITERATURE CITED

- Ahlstrom, E. H. 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fish. Bull. 60:107–146.
- Anderson, T. W. 1983. Identification and development of nearshore juvenile rockfishes (genus *Sebastes*) in central California kelp forests. Master's thesis, California State University, Fresno. 216 p.
- Athey, L. A., and E. F. Connor. 1989. The relationship between foliar nitrogen content and feeding by *Odontota dorsalis* Thun. on *Robinia pseudoacacia* L. Oecologia 79:390–394.
- Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. La Jolla, Calif.: California Sea Grant College System, NOAA, in cooperation with Centro de Investigaciones Biológicas del Noroeste. 323 p.
- Boehlert, G. W. 1977. Timing of the surface-to-benthic migration in juvenile rockfish, *Sebastes diploproa*, off southern California. Fish. Bull. 75:887–890.
- . 1978. Changes in the oxygen consumption of prejuvenile rockfish, *Sebastes diploproa*, prior to migration from the surface to the deep water. Physiol. Zool. 51:56–67.
- . 1981. The role of temperature and photoperiod in the ontogenetic migration of prejuvenile *Sebastes diploproa* (Pisces: Scorpaenidae). Calif. Fish Game 67:164–175.
- Boehlert, G. W., D. M. Gadomski, and B. C. Mundy. 1985. Vertical distribution of ichthyoplankton off the Oregon coast in spring and summer months. Fish. Bull. 83:611–621.
- Cowen, R. K., J. A. Hare, and M. P. Fahay. 1993. Beyond hydrography: can physical processes explain larval fish assemblages within the Middle Atlantic Bight? Bull. Mar. Sci. 53(2):567–587.
- Doyle, M. 1992. Neustonic ichthyoplankton in the northern region of the California Current system. Calif. Coop. Oceanic Fish. Invest. Rep. 33:141–161.
- Fortier, L., and W. C. Leggett. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. Can. J. Fish. Aquat. Sci. 40:1543–1555.
- Gray, C. C. 1996. Do thermoclines explain the vertical distributions of larval fishes in the dynamic coastal waters of south-eastern Australia? Mar. and Freshwat. Res. 47:183–190.

- Grimes, C. G., and J. H. Finucane. 1991. Spatial distribution and abundance of larval and juvenile fish, chlorophyll, and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. Mar. Ecol. Prog. Ser. 75:109–119.
- Hickey, B. M. 1979. The California Current system—hypothesis and facts. Prog. Oceanogr. 81:191–279.
- Kingsford, M. J., and J. H. Choat. 1986. Influence of surface slicks on the distribution and onshore movements of small fish. Mar. Biol. 91:161–171.
- Larson, R. J., W. H. Lenarz, and S. Ralston. 1994. The distribution of pelagic juvenile rockfish of the genus *Sebastes* in the upwelling region off central California. Calif. Coop. Oceanic Fish. Invest. Rep. 35:175–221.
- Lenarz, W. H., R. J. Larson, and S. Ralston. 1991. Depth distributions of late larvae and pelagic juveniles of some fishes of the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 32:41–46.
- Mooers, C. N. K., and A. R. Robinson. 1984. Turbulent jets and eddies in the California Current and inferred cross-shore transports. Science 223:51–53.
- Moser, H. G., and G. W. Boehlert. 1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. Environ. Biol. Fishes 30:203–224.
- O'Brien, R. G., and M. K. Kaiser. 1985. MANOVA method for analyzing repeated measures designs: an extensive primer. Psychol. Bull. 97:316–333.
- Olla, B. L., and M. W. Davis. 1990. Behavioral responses of juvenile walleye pollock, *Theragra chalcogramma* Pallas, to light, thermoclines, and food: possible role in vertical distribution. J. Exp. Mar. Biol. Ecol. 135:59–68.
- Parrish, R. H., C. S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175–203.
- Ralston, S., and D. F. Howard. 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. Fish. Bull. 93:710–720.
- Reilly, C. A., T. Wyllie Echeverria, and S. Ralston. 1992. Interannual variation and overlap in the diets of pelagic juvenile rockfish (Genus: Sebastes) off central California. Fish. Bull. 90:505–515.
- Ross, J. R. McG. 2001. Factors influencing the vertical distributions of pelagic juvenile fishes off central California. Master's thesis, San Francisco State University. 269 p.
- Sabatés, A., and M. P. Olivar. 1996. Variation of larval fish distributions associated with variability in the location of a shelf-slope front. Mar. Ecol. Prog. Ser. 135:11–20.
- Sakuma, K. M., and R. J. Larson. 1995. Distribution of pelagic metamorphic-stage sanddabs *Citharichthys sordidus* and *C. stigmaeus* within areas of upwelling off central California. Fish. Bull. 93:516–529.
- Sakuma, K. M., S. Ralston, and D. A. Roberts. 1999. Diel vertical distribution of postflexion larval *Citharichthys* spp. and *Sebastes* spp. off central California. Fish. Oceanogr. 8:68–76.
- Schwing, F. B., D. M. Husby, N. Garfield, and D. E. Tracy. 1991. Mesoscale oceanic response to wind events off central California in spring 1989: CTD surveys and AVHRR imagery. Calif. Coop. Oceanic Fish. Invest. Rep. 32:47–62.
- Shenker, J. M. 1988. Oceanographic associations of neustonic larval and juvenile fishes and Dungeness crab megalopae off Oregon. Fish. Bull. 86:299–317.
- Simpson, J. H. 1981. The shelf-sea fronts: implications of their existence and behavior. R. Soc. Lond. Phil. Trans. Series A 302:531–546.
- Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. Seattle: University of Washington Press. 252 p.
- Sogard, S. M., and B. L. Olla. 1996. Food deprivation affects vertical distribution and activity of a marine fish in a thermal gradient: potential energyconserving mechanisms. Mar. Ecol. Prog. Ser. 133:43–55.
- Steiner, W. W., and B. L. Olla. 1985. Behavioral responses of prejuvenile red hake, *Urophycis chuss*, to experimental thermoclines. Environ. Biol. Fishes 14:167–173.
- Wyllie Echeverria, T., W. H. Lenarz, and C. A. Reilly. 1990. Survey of the abundance and distribution of pelagic young-of-the-year rockfish, *Sebastes*, off central California. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFSC-147, 125 p.