

**Abstract.**—We attempt to determine at what point in the early life history year-class strength is established in two species of rockfish, *Sebastes mystinus* and *Sebastes flavidus*. We compare abundance estimates of young-of-the-year rockfish before and after settlement to determine whether this life history transition alters relative year-class strength. Estimates of pelagic juvenile abundance obtained in midwater trawl surveys and indices derived from direct underwater observations of settled juveniles over a common 10-year period (1983–92) were in good agreement ( $r=0.58$ – $0.86$ ). Trends in rockfish year-class strength were similar, in spite of substantial spatial separation between the trawl and nearshore study areas (50–350 km) and differences in the timing of the surveys (2–4 months). Thus, settlement seems to have little effect on relative year-class strength. Estimates of stage-specific interannual cohort variability show that coefficients of variation (CV's) for five species of late-stage pelagic juvenile rockfish ranged from 0.96 to 2.25. Cohort variability measured at recruitment to the fishery (2–7 years) is much less (CV's=0.60–1.39), suggesting that year-class strength has been determined by the late pelagic juvenile phase. Because cohort variability declines from the recently settled juvenile stage to the age at recruitment to the fishery, some form of compensatory mortality may ameliorate interannual differences in reproductive success.

# On the development of year-class strength and cohort variability in two northern California rockfishes

Stephen Ralston

Daniel F. Howard

Southwest Fisheries Science Center  
National Marine Fisheries Service, NOAA  
3150 Paradise Drive, Tiburon, California 94920

Interannual fluctuations in reproductive success lead to substantial recruitment variability in fisheries. Understanding the causes of this variability is an important management issue. However, the problem has yet to be solved despite prolonged, intensive study (Cushing, 1973; Sissenwine, 1984; Rothschild, 1986). A number of investigators have argued that the greatest potential for regulation of year-class size occurs during the larval stage (e.g. Shepherd and Cushing, 1980; Houde, 1987). Likewise, Smith (1985) has shown that in northern anchovy, *Engraulis mordax*, dominant year classes arise only when larval mortality rates are low. Others have suggested that population regulation occurs later in the juvenile period (Beverton, 1984; Sissenwine, 1984; Sissenwine et al., 1984).

To identify at what point during the early life history of fish year-class strength is established, investigators have correlated young-of-the-year abundance measures with later stage recruitment indices. Dementjeva (1964) demonstrated a strong positive correlation between the catch rate (CPUE) of "one summer-old" Caspian bream, *Archosargus rhomboidalis*, in fishery-independent surveys and recruitment indices derived from virtual population analysis (VPA) of the catch. Peterman et al. (1988) tested Lasker's (1975) hypothesis that the annual

abundance of northern anchovy recruits is fixed at an early life history stage by comparing abundances of eggs, 4.5-day-old yolk-sac larvae, and 19-day-old larvae, with estimates of age-1 recruits derived from an age-structured analysis of the catch. They found very low correlations ( $r=-0.09$  to  $0.07$ ,  $n=13$ ) and concluded that year-class strength is determined at some point after age 19-day. Similarly, Bailey and Spring (1992) examined the relationship between survey estimates of walleye pollock, *Theragra chalcogramma*, larvae (15 mm SL) and young-of-the-year juveniles (50–130 mm FL) with the numbers of age-2 fish that had recruited to the fishery from a tuned VPA. They reported a good correlation between young-of-the-year juveniles and age-2 fish ( $r=0.69$ ), but the association between larval abundance and age-2 fish was not significant ( $r=0.36$ ). Like Smith (1985) they concluded that strong year classes are the result of good larval survival.

Bradford (1992) modeled early life history dynamics and the recruitment process using information assembled from the literature. Owing to poor correlations between the abundance of small larvae and subsequent recruitment, he concluded that year classes are fixed after the early larval period. He also showed that precise predictions of

year-class strength are feasible under a variety of scenarios, if abundance is indexed following juvenile metamorphosis.

The reproductive biology and early life history of *Sebastes* is distinctive (Boehlert and Yamada, 1991). All rockfishes are livebearers, displaying a primitive form of viviparity (Boehlert et al., 1987; Wourms, 1991). Along the west coast of North America, most commercial species of rockfish copulate around September, but fertilization may not occur until weeks, or even months, later (Wyllie Echeverria, 1987). Hatching occurs in the ovary after 25–35 days of embryonic development, and parturition occurs approximately five days later at about the time of yolk-sac absorption (Eldridge et al., 1991; Yamada and Kusakari, 1991). In the central and northern California region, parturition of most commercial species occurs in late fall, winter, and early spring but is most concentrated from January to March (Wyllie Echeverria, 1987; Moser and Boehlert, 1991).

Rockfish larvae typically are found in the upper mixed layer (Ahlstrom, 1961; Ralston et al.<sup>1</sup>), where they grow slowly until flexion is complete at an age of about 25 days (Laidig et al., 1991). Late larvae (10–20 mm SL) are distributed well offshore (Moser and Boehlert, 1991); at this stage growth rate increases. Late larvae then metamorphose into a pelagic juvenile stage characterized by attainment of mature meristics and pelagic coloration (Moser et al., 1977; Matarese et al., 1989; Moser and Boehlert, 1991). Growth of pelagic juveniles, which feed primarily on copepods and on both larval and juvenile stages of euphausiids (Reilly et al., 1992), can be quite rapid (0.3–0.6 mm·d<sup>-1</sup>) (Woodbury and Ralston, 1991). As pelagic juveniles approach sizes that are competent to settle (30–90 mm SL, depending on the species), they move deeper in the water column (Lenarz et al., 1991) and closer to shore (Larson et al., 1994). These changes in spatial distribution occur at a time of maximum offshore Ekman transport of the ocean's surface layer and onshore recirculation of subsurface waters (Mooers et al., 1978; Largier et al., 1993). Peak settlement to demersal nearshore habitats occurs during the upwelling season from May to July (Carr, 1983; Love et al., 1991), after the fish have spent from 3 to 6 months as plankton and micronekton. Settlement usually occurs in relatively shallow water and, after a period of several months to a year, many species begin to move into adult habitats located in deeper water (Love et al., 1991).

In this study, we attempt to determine at what point in the life history year-class strength becomes fixed in two species of rockfish, i.e. blue rockfish, *Sebastes mystinus*, and yellowtail rockfish, *Sebastes flavidus*. Of particular interest is the influence of settlement on interannual variations in reproductive success. We compare abundance estimates of young-of-the-year juvenile rockfish that were gathered before and after settlement to determine if this life history transition alters relative year-class strength. The comparison is based on two separate fishery-independent surveys conducted over a 10-year period (1983–92). In addition, we examine the relationship between sea-surface temperature (SST) during the larval period and estimates of year-class strength.

For the arguments developed here, we assume that during the study period variation in year-class strength of blue and yellowtail rockfish was due to interannual differences in reproductive success and not to fluctuations in spawning biomass. Given the generally weak relationship between recruitment and spawning stock (Cushing, 1973), this is not an unreasonable assumption, particularly since *Sebastes* are slow-growing species with low rates of natural mortality (Leaman and Beamish, 1984). Nonetheless, yellowtail rockfish have been the focus of a substantial commercial fishery for many years, even though the fishery operates primarily to the north of our study region (Tagart<sup>2</sup>).

## Materials and methods

### Midwater trawl surveys

Annual trawl surveys designed to estimate the distribution and abundance of pelagic juvenile rockfishes along the central California coast have been conducted aboard the RV *David Starr Jordan* since 1983 (Wyllie Echeverria et al., 1990). Cruises have been conducted during May and June when the pelagic juvenile-stage fish are most susceptible to capture by midwater trawling. These surveys use a modified 26 × 26 m Cobb midwater trawl, with a codend liner of 1.27-cm stretched mesh. Beginning in 1986, three spatially replicated “sweeps” of a series of standard stations were conducted in a study area bounded by Point Reyes and Cypress Point (Fig. 1); from 1983 to 1985 only one sweep was completed per year. As part of the survey design, the area was subdivided

<sup>1</sup> Ralston, S., J. R. Bence, M. B. Eldridge, and W. H. Lenarz. 1993. Estimating the spawning biomass of shortbelly rockfish (*Sebastes jordoni*) in the region of Pioneer and Ascension Canyons using a larval production method. Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Dr., Tiburon, CA 94920. Unpubl. manuscript.

<sup>2</sup> Tagart, J. V. 1993. Status of the yellowtail rockfish resource in 1993, Appendix E. In Appendices to the Status of the Pacific Coast groundfish fishery through 1993 and recommended acceptable biological catches for 1994. Pacific Fishery Management Council, 2000 SW First Ave., Suite 420, Portland, OR.

into seven geographical strata, with five to six standard stations located within each stratum. At each station a 15-minute nighttime trawl sample was taken at standard depth (30 m where possible, 10 m at shallow stations). Following the cruise, identification of rockfish specimens was confirmed in the laboratory, standard lengths were measured, and a subsample of otoliths were collected.

Abundance indices for pelagic juvenile rockfish were adjusted to account for interannual differences in the size structure of the catch. After truncating the data to include only the fully vulnerable portion of the catch (i.e. SL  $\geq$  25 mm; Woodbury<sup>3</sup>), additional adjustments were performed in a two-step process. Individual fish ages were predicted from standard length [SL] measurements by using linear inverse growth curves (age =  $f$ [SL]) that were estimated for each species during the 10-year period from 1983 to 1992. Specifically, the predicted age of species  $s$  in year  $y$  at standard length  $l$  is  $\hat{\tau}_{syl} = \alpha_{sy} + \beta_{sy}l$ , where the  $\alpha_{sy}$  and  $\beta_{sy}$  were estimated by least-squares regressions of age-length data gathered from microscopic examination of otolith daily increments (see Laidig et al., 1991; and Woodbury and Ralston, 1991). If otolith data were unavailable in a particular year, growth parameters were estimated from an analysis of covariance of all the yearly data, by assuming a common slope (days  $\cdot$  mm<sup>-1</sup>) and the mean of interannual intercepts.

For each haul conducted and each species sampled (subscripts not included), abundances of fish of different ages were then adjusted to a common age by using an exponential model with a constant mortality rate ( $Z$ ), i.e.

$$N_l^* = N_l \exp[-Z(\tau^* - \hat{\tau}_{syl})],$$

where  $N_l^*$  is the adjusted number of individuals of length  $l$ ,  $N_l$  is the unadjusted number, and  $\tau^*$  is the common age to which abundances were adjusted. In all calculations  $\tau^*$  was set equal to 100 d, which is generally representative of pelagic juvenile rockfish ages during May–June (Woodbury and Ralston, 1991), and  $Z$  was fixed at 0.04 d<sup>-1</sup>. This latter figure was based on combined estimates of mortality rate for 1) larval shortbelly rockfish, *S. jordani* (Ralston et al.<sup>1</sup>); 2) settled juvenile blue rockfish (Adams and Howard<sup>4</sup>); 3) pelagic juvenile Pacific cod, *Gadus macrocephalus*, and northern anchovy (Bradford,

1992); and 4) pelagic juvenile Pacific whiting, *Merluccius productus* (Hollowed, 1992). The  $N_l^*$  were then summed over all lengths occurring within a haul, yielding a haul-specific catch of each rockfish species sampled that was adjusted for variability in length composition.

Final calculation of abundance statistics from our midwater trawl surveys was based upon simple logarithmic transformation of the data, i.e.  $y_{jk} = \log_e[x_{jk} + 0.1]$ , where  $x_{jk}$  is the length-adjusted catch taken in haul  $j$  located in stratum  $k = 1$  to 7. We estimated the individual stratum means, variances, and standard errors for each sweep using conventional procedures appropriate to a stratified sampling design (Cochran, 1977). The equally weighted stratified mean was then used as a sweep-specific index of pelagic juvenile abundance. Lastly, because the availability of pelagic juveniles to midwater trawling shows marked seasonal change, the maximum value of the stratified mean (among sweeps completed in a year) was used to estimate relative annual abundance, i.e. year-class strength.

### Direct underwater observation surveys

Nearshore assessments were made by underwater observers by using SCUBA at four locations on the northern California coast (Fig. 1). Two of the study sites, Dark Gulch (lat. 39°14'N; long. 123°46'W) and Salmon Point (lat. 39°12'N; long. 123°46'W) in Mendocino County, were monitored since 1983. In 1984, nearshore assessments were initiated at Horseshoe Point (lat. 38°36'N; long. 123°22'W) and at Fisk Mill Cove (lat. 38°35'N; long. 123°21'W) in Sonoma County, 100 km to the south.

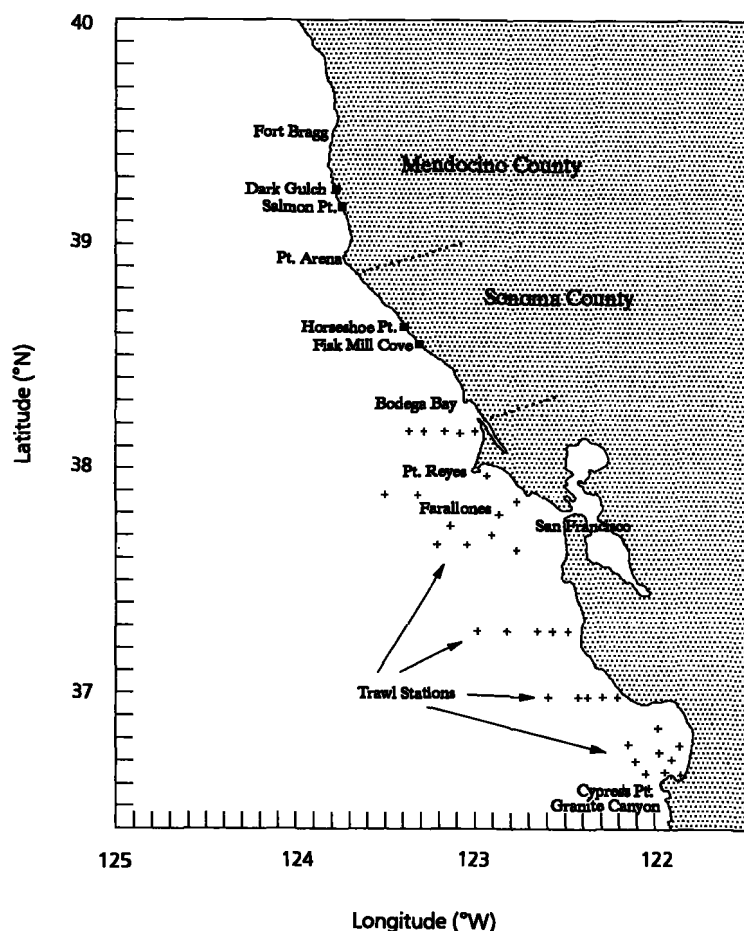
Each study site covers approximately 0.5 ha and consists of high-relief rocky reefs surrounded by lower reefs and boulders, interspersed by occasional sand patches. Vertical water clarity was measured from the boat with a white, plastic Secchi disk 20 cm in diameter. Horizontal water clarity at a bottom depth of 10 m was determined by estimating the distance at which rock surfaces could be clearly observed. Counts were not made when conditions were turbulent, nor when visibility was less than 4 m.

Observations for estimating year-class strength began in late July, when settlement of pelagic juveniles was essentially complete, and continued through the end of September. Young-of-the-year fish were distinguished from older cohorts by their size (40–50 mm SL in July), and from other species by characteristic pigment patterns.

Strip-transect counts were made between the hours of 1000 and 1400 by observers using SCUBA over bottom depths of 5–22 m. At each study site,

<sup>3</sup> Woodbury, D. 1993. Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Dr., Tiburon, CA 94920. Unpubl. data.

<sup>4</sup> Adams, P. B., and D. F. Howard. Natural mortality of blue rockfish (*Sebastes mystinus*) during their first year in nearshore benthic habitats. Manuscript submitted to Fishery Bulletin.



**Figure 1**

Map of the study area showing the location of trawl stations and diving sites where direct underwater observations of settled juvenile rockfish were made in Mendocino and Sonoma counties (1983–92). Temperature data were collected daily at Bodega Bay, the Farallon Islands, and Granite Canyon.

the abundance of young-of-the-year juveniles was assessed along haphazard transects by a series of timed 1-minute counts that covered approximately 20 m. Observers maintained a constant swimming speed, gazing ahead at all times during the counts. Transects started on the outside edge of the kelp bed and followed a series of arbitrary compass headings covering the offshore portion of the study site. After completing counts in deeper habitats, observers progressed into shallower water.

Species and number of juveniles observed each minute were recorded on a plastic slate with the aid of a watch fastened in the upper corner to monitor time. Observers swam 2 m off the bottom and counted young-of-the-year rockfishes within 3 m in any for-

ward direction during the transect. After 1–3 counts the observer made right-angle changes in direction, which resulted in thorough coverage of the study area. The number of daily counts at a site ranged from 10 to 35 ( $\bar{x}=18.8$ ).

Counts were excluded from data analyses when it was obvious that the distribution of juveniles was influenced by unusual conditions. For example, sampling sometimes coincided with a period of convergence when food-rich oceanic waters moved into nearshore surface layers. The distribution of juveniles was very different at these times, as they ascended into the upper 2 m of the water column to feed.

Annual indices of settled juvenile abundance were calculated separately for blue and yellowtail rockfish in Mendocino and Sonoma counties. Because variances increased with the means, individual strip-transect counts were first log-transformed to stabilize the variance. The annual index was then simply calculated as the mean of all counts, e.g.

$$I_{sct} = \frac{1}{n} \sum_{i=1}^n \log_e [C_{isct} + 1],$$

where  $I_{sct}$  is the index for species  $s$  in county  $c$  in year  $t$ , and  $n$  is the number of counts ( $C_{isct}$ ) conducted; the sampling precision of the index is given by the standard error of the mean.

### Interannual variability in year-class strength

As in many other species, recruitment in rockfish is highly variable and is described well by the log-normal distribution (Bence et al., 1993; Fogarty, 1993). An accepted way to portray relative levels of variation among different sets of data is through use of the coefficient of variation (CV). The CV of the log-normal distribution is unusual, being independent of the mean and equal to  $[\exp(\sigma^2) - 1]^{1/2}$ , where  $\sigma^2$  is the variance of logarithms of the log-normally distributed variable (Johnson and Kotz, 1970).

To compare and contrast levels of variation in rockfish year-class strength at specific life history stages, CV's of annual time series were calculated. Because individual annual abundance statistics were usually

estimated with some error, given by the standard error of the mean, and because variance terms are additive, this measurement error was subtracted from the total interannual variance in year-class strength prior to calculation of the CV, i.e.

$$\sigma_{CV}^2 = \sigma_{TOT}^2 - \sigma_\varepsilon^2$$

$$CV = \sqrt{(e^{\sigma_{CV}^2} - 1)}.$$

An estimate of measurement error ( $\sigma_\varepsilon^2$ ) was obtained as the mean of the squared standard error estimates ( $s_{It}^2$ ) of the annual index  $I$ , averaged over the  $k$  years that data were available,

$$\hat{\sigma}_\varepsilon^2 = \frac{1}{k} \cdot \sum_{t=1}^k s_{It}^2.$$

Likewise, the total variance in the index ( $\sigma_{TOT}^2$ ) was estimated simply as the sample variance of the index ( $I_t$ ),

$$\hat{\sigma}_{TOT}^2 = \frac{1}{k-1} \cdot \sum_{t=1}^k (I_t - \bar{I})^2$$

$$\bar{I} = \frac{1}{k} \cdot \sum_{t=1}^k I_t.$$

For small sample sizes ( $k < 50$ ) and large CV's ( $> 2.0$ ), there is a positive bias in this estimator (Finney, 1941). We determined the magnitude of the bias by Monte Carlo simulation (Naylor et al., 1966), and we applied a bias correction term to each CV estimated.

### Shore station sea-surface temperature

Sea-surface temperature (SST) and salinity are recorded daily at the University of California Bodega Bay Marine Laboratory (BB), the Point Reyes Bird Observatory facility on Southeast Farallon Island (FI), and at the California Department of Fish and Game Laboratory at Granite Canyon (GC) (Walker et al., 1993). SST data from all three sites are generally indicative of hydrographic conditions offshore over the continental shelf (Fig. 1).

Interannual fluctuations in SST within the central California study region were estimated by using an analysis of variance (ANOVA) model applied to the shore station data, i.e.

$$SST_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \varepsilon_{ijk},$$

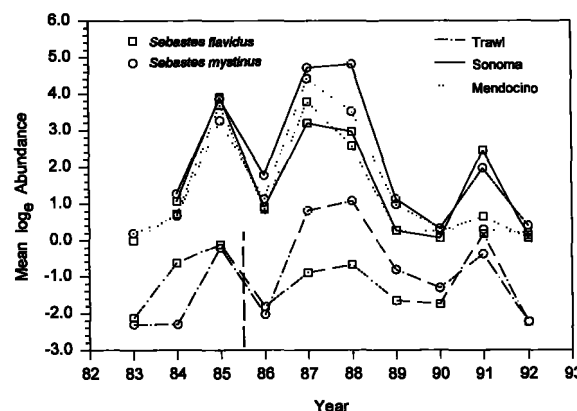
where  $SST_{ijk}$  is the sea-surface temperature recorded at shore station  $i$  ( $i = \text{BB, FI, or GC}$ ) on calendar date

$j$  ( $j = 1, \dots, 90$ ) in year  $k$  ( $k = 1980, \dots, 1992$ ),  $\mu$  is the population mean SST, and  $\varepsilon_{ijk}$  is a normally distributed error term. Only the first 90 days of the calendar year were included in the analysis because blue and yellowtail rockfish are winter-spawning species (Wyllie Echeverria, 1987) and a measure of the average SST prevailing from birth to completion of the late larval stage was desired. Year effects ( $\gamma_k$ ) in the model were obtained by calculating population marginal means (i.e. least-square means), providing year-specific estimates of SST at average levels of the  $\alpha_i$  and  $\beta_j$  (see Searle et al. [1980] for further discussion).

### Results

Annual abundance indices of pelagic juvenile blue and yellowtail rockfishes captured by midwater trawl were quite variable (Table 1; Fig. 2). The CV's of these abundance indices were 1.98 and 1.19, respectively, over the 10-year period from 1983 to 1992. Years of high abundance for both species were 1985, 1987, 1988, and 1991, whereas years of low abundance were 1983, 1986, and 1992.

A similar pattern was evident in the data collected by direct underwater observations of recently settled rockfish juveniles in Mendocino and Sonoma Counties (Table 1; Fig. 2), although levels of interannual variation in abundance for these species was somewhat greater. Specifically, estimated CV's ranged



**Figure 2**

Interannual trends in the abundance of blue (*Sebastes mystinus*) and yellowtail (*Sebastes flavidus*) rockfishes based on trawl surveys of pelagic juveniles and direct underwater observations of settled young-of-the-year fish (1983–92). The dashed vertical line shows when the trawl survey was changed from one to three sweeps. (see Methods section).

**Table 1**

Coefficients of variation in rockfish year-class strength at selected life history stages. All pelagic and settled juvenile results are based on this study. Within-year measurement error ( $\sigma_e^2$ ) removed for egg, pelagic juvenile, and settled juvenile life history stages (see Methods section).

Species	Young-of-the-year			Entry to fishery
	Egg	Pelagic juvenile	Settled juvenile	
<i>Sebastes mystinus</i>	—	1.98	3.06–3.68	—
<i>Sebastes flavidus</i>	0.10 <sup>1</sup>	1.19	2.59–2.69	0.60–0.87 <sup>2</sup>
<i>Sebastes entomelas</i>	—	2.25	—	0.82 <sup>3</sup>
<i>Sebastes goodei</i>	—	1.49	—	1.39 <sup>4</sup>
<i>Sebastes paucispinis</i>	—	0.96	—	0.72 <sup>5</sup>

<sup>1</sup> Eldridge and Jarvis (1995).

<sup>2</sup> Tagart (Footnote 2 in the text).

<sup>3</sup> Rogers and Lenarz. 1993. Status of the widow rockfish stock in 1993, Appendix B. In Appendices to the status of the Pacific Coast groundfish fishery through 1993 and recommended acceptable biological catches for 1994. Pacific Fishery Management Council, 2000 SW First Ave., Suite 420, Portland, OR.

<sup>4</sup> Rogers and Bence. 1993. Status of the chilipepper rockfish stock in 1993, Appendix D. In Appendices to the status of the Pacific Coast groundfish fishery through 1993 and recommended acceptable biological catches for 1994. Pacific Fishery Management Council, 2000 SW First Ave., Suite 420, Portland, OR.

<sup>5</sup> Bence and Rogers. 1992. Status of bocaccio in the Conception/Monterey/Eureka INPFC areas in 1992 and recommendations for management in 1993, Appendix B. In Appendices to the status of the Pacific Coast groundfish fishery through 1992 and recommended acceptable biological catches for 1993. Pacific Fishery Management Council, 2000 SW First Ave., Suite 420, Portland, OR.

from 3.06 to 3.68 for blue rockfish and from 2.59 to 2.69 for yellowtail rockfish. The observational data also indicated that 1985, 1987, 1988, and perhaps 1991, were relatively strong years, whereas 1983, 1992, and to some extent 1986, were weak years.

There were highly significant correlations between direct observation counts of settled juvenile rockfish at Mendocino and Sonoma Counties. For blue rockfish the correlation was 0.925 ( $P < 0.005$ ) and for yellowtail rockfish it was 0.887 ( $P < 0.005$ ). The greatest disparity in abundance between these localities occurred in 1991, when counts of the two species at Mendocino County were low, both in comparison with observations at Sonoma County and with catches in the trawl survey.

The time series of midwater trawl and direct observational data were also well correlated (Fig. 3). For example, results for blue rockfish, *Sebastes mystinus*, showed highly significant ( $P < 0.005$ ) positive correlations in excess of 0.80 at both the Mendocino and Sonoma sites. Similarly, the correlation between trawl survey estimates of yellowtail rockfish, *Sebastes flavidus*, abundance and direct

counts of this species at Sonoma County ( $r = 0.799$ ) was significant ( $P < 0.01$ ). The comparison between the trawl data and Mendocino County counts ( $r = 0.577$ ) was marginally insignificant ( $0.10 \leq P \leq 0.05$ ). Results were similar when comparisons were restricted to the time period 1986–92, i.e. when three repetitive sweeps of the trawl survey area were completed each year.

Not only were trends in the abundance of individual species at different study sites well correlated; so too were the interspecific abundance patterns of blue and yellowtail rockfish at each of the three specific study sites. For example, the time series of blue rockfish abundance at the Mendocino study site was highly correlated with the yellowtail rockfish series at the same site ( $r = 0.961$ ,  $P < 0.001$ ). At Sonoma, variations in the abundance of these two species was also closely linked ( $r = 0.906$ ,  $P < 0.001$ ), substantially more so than in the trawl data ( $r = 0.589$ ,  $P = 0.073$ ).

The substantial positive correlations among the data for each species (Figs. 2 and 3) suggest that principal component analysis (Green, 1978) would be effective in extracting the primary interannual signal jointly evident in all three time series (i.e. trawl, Mendocino, and Sonoma). Indeed, results for blue rockfish show that

the first principal component alone accounted for 89% of the variation present in the three data series. Likewise, for yellowtail rockfish the first component accounted for 87% of the total variation.

Winter SST's along the central California coast, from Bodega Bay to Granite Canyon (Fig. 1), varied greatly during the period 1983–92. Population marginal means for the year factor ( $\gamma_k$ ) in the ANOVA temperature model ranged from a low of 10.6°C in 1989 to a high of 13.5°C in 1983, an El Niño year. Typical winter SST's in the study region were 11.5–12.0°C. For the two other factors in the model, the shore station effect ( $\alpha_i$ ) showed that SST's at Bodega Bay were ~1.0°C cooler than at Southeast Farallon Island and at Granite Canyon, which were quite similar to one another. Likewise, the calendar date effect ( $\beta_j$ ) showed clearly the onset of spring transition to upwelling conditions (Strub et al., 1987), evidenced by an abrupt cooling trend that started in mid-March.

Interannual variability in January–March SST's appeared to be related to observed differences in the abundance of pelagic juveniles captured by midwater trawl during May–June and of settled juveniles ob-

served in nearshore habitats in August–September (Fig. 4). For blue rockfish and yellowtail rockfish, it is apparent that the abundance of young-of-the-year juveniles was lowest when winter SST's were highest, as for example in 1983 and 1992. Both years were distinguished by strong El Niño events (Wooster and Fluharty, 1985; Hayward, 1993). There was also the suggestion that cold winter SST's may have adversely impacted survival of these rockfish to the juvenile stage, as evidenced by the data for 1989 and 1990. Conversely, increased numbers of juveniles occurred in years when SST was intermediate, especially in 1987 and 1988. Overall, these findings are consistent with a dome-shaped relationship between larval survival and winter temperature.

## Discussion

### Biological synchrony and oceanographic scale

Our results show a broad spatial coherence in the temporal abundance patterns of young-of-the-year juvenile rockfish. The trawl study area is separated from Sonoma and Mendocino Counties by distances of 50–350 km (Fig. 1); yet interannual fluctuations in the abundance of blue and yellowtail rockfish at these sites are closely linked (Figs. 2 and 3). Even so, had there been closer spatial overlap between the trawl and nearshore study areas, the correlations probably would have been even higher. For example, our highest correlations between the annual abundance indices of pelagic and settled juveniles (0.861 and 0.799, Fig. 3) were for Sonoma County, the closer of the two nearshore sites to the trawl survey area.

Not only was there broad spatial agreement in the trends of blue and yellowtail rockfish, abundances of these species were highly correlated with one another. Strong and weak years closely mirrored each other over the 10-year study period (Fig. 2). Other studies have shown marked interannual synchrony among species of pelagic juvenile rockfish, in terms of growth rates and birthdate distributions (Woodbury and Ralston, 1991) as well as shifts in dietary composition (Reilly et al., 1992). These findings indicate that large-scale oceanographic processes are primarily responsible for the extensive interannual fluctuations in the abundance of young-of-the-year juvenile rockfishes.

This conclusion is in agreement with results from Hollowed et al. (1987), who showed extensive inter-

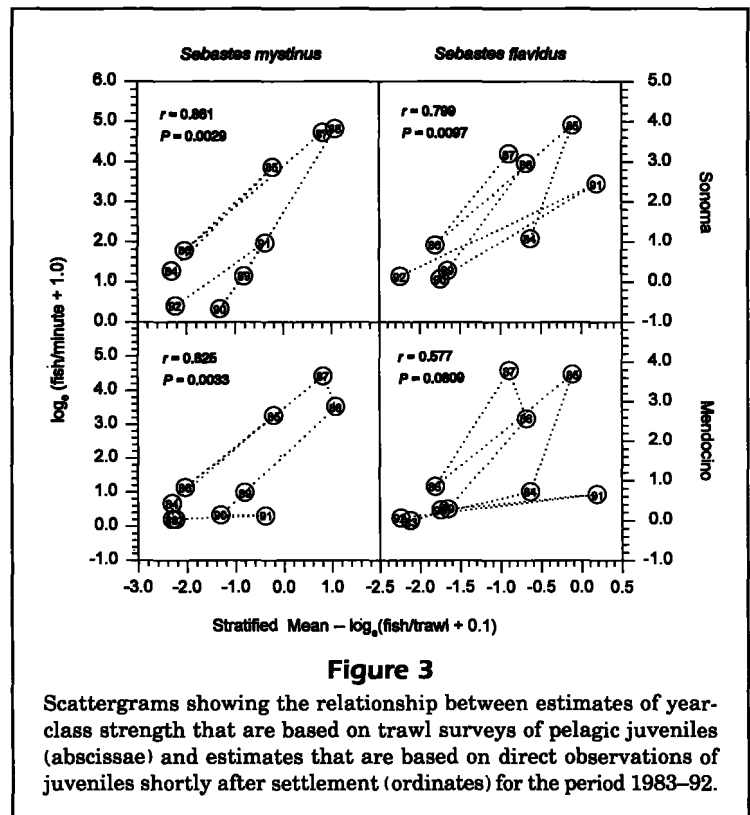


Figure 3

Scattergrams showing the relationship between estimates of year-class strength that are based on trawl surveys of pelagic juveniles (abscissae) and estimates that are based on direct observations of juveniles shortly after settlement (ordinates) for the period 1983–92.

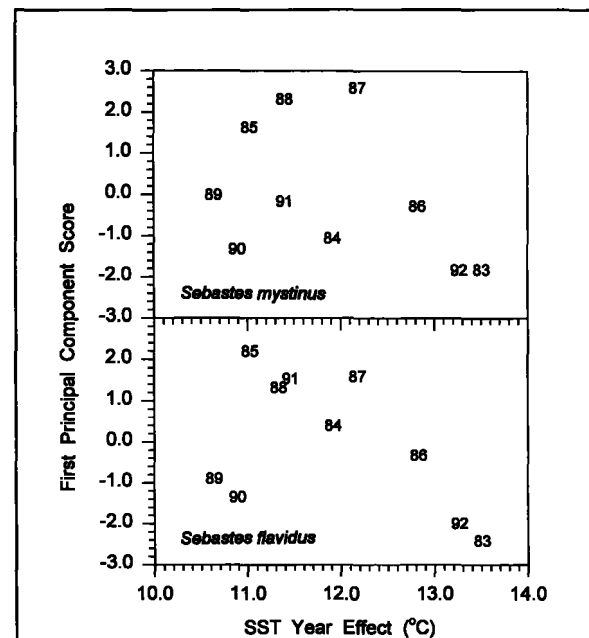


Figure 4

The relationship between interannual variability in sea surface temperature (SST) during the larval period (January to March) and combined estimates of year-class strength for blue (*Sebastes mystinus*) and yellowtail (*Sebastes flavidus*) rockfishes, 1983–92.

specific synchrony in the recruitment patterns of commercially harvested stocks on the west coast of North America, particularly on spatial scales similar to ours. Similar findings had been previously reported from commercial stocks in the northwest Atlantic (Koslow, 1984).

Although there is striking broad-scale synchrony in our data (Fig. 2), there is also reason to believe that in some years mesoscale differences in environmental conditions may strongly influence abundance patterns. For example, results from 1991 seemed to show an uncoupling of the abundance trends of blue and yellowtail rockfish at Mendocino County with those at Sonoma County, as well as with the trawl survey data (Fig. 2). That year was distinctive because northerly distributed species (e.g. *Sebastes emphaeus*, *Sebastes melanops*, and *Sebastes pinniger*) were relatively common in the trawl catches.

### Ontogeny and year-class strength

Year-class strength in blue and yellowtail rockfish is apparently established prior to the late pelagic juvenile stage. The strong correspondence between estimates of year-class strength obtained from trawl surveys of pelagic juveniles collected during May–June and from direct observations of settled juveniles in nearshore habitats three months later indicates that reproductive success is governed primarily by events that occur earlier in the life history, presumably during the larval stage (Houde, 1987; Myers and Cadigan, 1993).

This is not to suggest that substantial mortality does not occur after the pelagic juvenile stage. Indeed, over the same time period (1983–92), the among-year variation in nearshore settled juveniles was much greater than that for offshore pelagic juveniles (CV's are presented in Table 1). However, because cohorts maintained their rank in year-class strength through the settlement transition to nearshore habitats (Figs. 2 and 3), the increased variability evident in the Mendocino and Sonoma data is not associated with a reordered strength of year classes.

A possible reason for the greater CV's of recently settled rockfish is that the data collected nearshore are more strongly affected by spatial patchiness in the distribution of young-of-the-year juveniles. Owing to the inherently broader spatial scale of the trawl survey (i.e. each tow covered ~1 km and the survey area extended 200 km in a north-south direction), this latter sampling method would have integrated spatial patchiness on the scale of  $10^3$ – $10^5$  m. This hypothesis predicts a weakening of the correlation between pelagic and settled juvenile abundances with an increase in the difference in CV's. However, blue

rockfish from Sonoma showed the greatest increase in CV through the settlement transition (1.98 to 3.68) and yet had the highest correlation with pelagic juvenile numbers (0.86).

A competing hypothesis to explain the apparent increase in CV's is that of compensatory mortality during settlement. This type of mechanism could further deplete already weak year classes, while having virtually no effect on strong ones. The result would be an increase in interannual variability in abundance without altering relative year-class strength. A logical source of compensatory mortality at settlement is predation by a predator assemblage, which takes a fixed number of settling fish each year. However, Hallacher and Roberts (1985) showed that many kelp-dwelling fishes prey heavily on blue rockfish at the time of settlement but not during the rest of the year (see below). Similarly, recent work by Hobson et al.<sup>5</sup> has shown that three kelp-forest inhabitants that are not highly piscivorous, i.e. *Hexagrammus decagrammus*, *Sebastes melanops*, and *Sebastes mystinus*, feed heavily on recently settled juvenile blue rockfish in years when settlement is strong. These studies indicate that compensation during settlement is more likely than is depensation.

Whatever the cause of the greater CV's of settled juveniles, the strong correspondence between trawl and diver estimates of year-class strength in blue and yellowtail rockfish indicates that reproductive success has been established by the end of the pelagic juvenile stage (see also Myers and Cadigan, 1993). By estimating levels of variability in fecundity, one can infer at a much earlier stage that interannual differences in spawning output are too small to account for fluctuations in recruitment to the fishery (Table 1; see also Shepherd and Cushing, 1980). A seven-year study of weight-specific fecundity in yellowtail rockfish (Eldridge and Jarvis, 1995) yielded an among-year CV of 0.10, after within-year measurement error was removed (see Methods section). This amount of variation is insufficient to account for fluctuations observed at the time rockfish cohorts recruit to the fishery.

Levels of variability at the young-of-the-year juvenile stage, however, are more than adequate. In fact, it would seem that rockfish go through a phase of compensatory mortality, from the settled juvenile stage to the time a cohort enters the fishery (i.e. ages 3–4 in rockfishes). Note that for a log-normal distribution, the CV of year classes recruiting to rockfish fisheries, based on recruitments estimated from

<sup>5</sup> Hobson, E. S., J. R. Chess, and D. F. Howard. 1995. Interannual variations in predation on juvenile *Sebastes* spp. by three northern California predators. Unpubl. manuscript.



catch-at-age analysis in which the stock-synthesis model and other age-structured methods are employed, is typically less than 1.00 ( $\bar{x}=0.84$ ; Table 1). The "Entry to fishery" CV's presented in Table 1 were based on time series of recruitments ranging from 10 (*Sebastes goodei* and *Sebastes paucispinis*) to 25 years (*Sebastes flavidus*), although they did not all span the same time period.

A compensatory mortality source acting from postsettlement until recruitment to the fishery would tend to ameliorate year-class differences observed in the pelagic and recently settled juvenile stages. Two possible agents of compensatory mortality at this stage in life are 1) intraspecific competition for food (Shepherd and Cushing, 1980) or 2) a type-III functional response (sensu Holling, 1959) by predators (i.e. predator switching). Likewise, a rapid numerical response by predators could also lead to compensatory mortality.

There are other data to support this interpretation. Adams and Howard<sup>4</sup> provide data showing that blue rockfish experience compensatory mortality from the time they settle (August–September) until the following spring. They attributed the increased mortality rate experienced by strong year classes to predator switching. Hobson et al.<sup>5</sup> also describe predation on recently settled blue rockfish by *Hexagrammus decagrammus*, *Sebastes melanops*, and *Sebastes mystinus* (i.e. cannibalism), but only in years when settlement was particularly strong (see above). Likewise, Hallacher and Roberts (1985) showed low dietary overlap during the nonupwelling season among a kelp-forest assemblage of six *Sebastes* spp. However, when newly settled young-of-the-year rockfish became abundant during the upwelling season, these species fed heavily on the juveniles, and dietary overlap indices rose sharply. In addition, these authors observed other kelp-forest predator species feeding heavily on juvenile rockfish (*Ophiodon elongatus*, *Anarrhichthys ocellatus*, and *Scorpaenichthys marmoratus*). That a broad suite of predators capable of switching onto juvenile rockfish has been described provides a plausible compensatory mortality mechanism. Similar conclusions regarding the importance of compensatory mortality in recently settled plaice, *Pleuronectes platessa*, living in the North and Wadden Seas have been drawn by Lockwood (1980), Zijlstra et al. (1982), and van der Veer (1986).

It is a widely held precept that stage-specific mortality rates generally decrease with ontogeny, while stage duration increases concomitantly (Miller et al., 1988; Bradford, 1992). Because the total stage mortality is the product of the instantaneous mortality rate and the stage duration ( $M \cdot t$ ), an increase in du-

ration may more than offset a decrease in rate (Shepherd and Cushing, 1980). This has led some to suggest that population regulation may occur during the juvenile phase of the life history (Beverton, 1984; Sissenwine, 1984; Sissenwine et al., 1984). Our findings indicate that rockfish year-class strength is probably determined at some point in the larval phase, which lasts at least 50 days in *Sebastes jordani* (Laidig et al., 1991). Upon completion of the larval stage, however, compensatory density dependence in the settled juvenile phase seems to reduce cohort variability.

We have argued that recruitment success in these species of rockfish is governed by large-scale oceanographic processes (see also Mearns et al., 1980). There is evidence that year-class strength depends on the thermal environment at the time of spawning (Fig. 4), although we use SST only as a simple proxy for some complex set of covarying physical variables. However, the association between these variables is nonlinear; apparent year-class failures occur at the extremes of the continuum. This conclusion is supported by the findings of Ainley et al. (1993), who showed that the early summer occurrence of pelagic juvenile rockfish in the diet of a seabird (common murre, *Uria aalge*) was parabolically related to upwelling in January and February. Too little or too much upwelling during the rockfish spawning season had a negative impact on the availability of pelagic juvenile rockfish six months later. Notably, upwelling and SST in that study were inversely correlated. Cury and Roy (1989) have also argued that recruitment success of pelagic fish stocks in upwelling systems is greatest at an intermediate point along the environmental continuum, although they argued that wind speed is the forcing mechanism.

## Summary

We argue that events occurring in the larval period are primarily responsible for determining the success or failure of rockfish year classes in central California. Moreover, on the basis of a consideration of intra- and interspecific synchrony and oceanographic scale, physical factors seem to have the greatest impact on larval survival. Consequently, to the extent that recruitment limits stock size in rockfish, population regulation is based on larval dynamics. However, compensatory mortality in the juvenile phase may ultimately limit population growth. Like Myers and Cadigan (1993), we believe that the interplay between stochasticity in the larval period and compensation in the juvenile phase plays a seminal role in structuring rockfish population dynamics.

## Acknowledgments

The research reported here is based on over a decade of field work to which scores of people have contributed. Although it would be impossible to credit each person individually, we would like to acknowledge the crew of the RV *David Starr Jordan* and all Tiburon Laboratory staff members who helped further this research program since its inception in 1983. A few people, however, deserve mention for the significant contributions they made to the completion of this work. In particular, we would like to thank P. B. Adams, J. R. Bence, J. R. Chess, E. S. Hobson, W. H. Lenarz, and D. P. Woodbury. To all the unnamed others go our sincere gratitude and appreciation.

## Literature cited

- Ahlstrom, E. H.**  
1961. Distribution and relative abundance of rockfish (*Sebastes* spp.) larvae off California and Baja California. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 150:169–176.
- Ainley, D. G., R. H. Parrish, W. H. Lenarz, and W. J. Sydeman.**  
1993. Oceanic factors influencing distribution of young rockfish (*Sebastes*) in central California: a predator's perspective. Calif. Coop. Oceanic Fish. Invest. Rep. 34:133–139.
- Bailey, K. M., and S. M. Spring.**  
1992. Comparison of larval, age-0 juvenile and age-2 recruit abundance indices of walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska. ICES J. Mar. Sci. 49:297–304.
- Bence, J. R., A. Gordoa, and J. E. Hightower.**  
1993. Influence of age-selective surveys on the reliability of stock synthesis assessments. Can. J. Fish. Aquat. Sci. 50:827–840.
- Beverton, R. J. H. (ed.).**  
1984. Dynamics of single species—group report. In R. M. May (ed.), Exploitation of marine communities, p. 13–58. Springer-Verlag, Berlin.
- Boehlert, G. W., and J. Yamada (eds.).**  
1991. Rockfishes of the genus *Sebastes*: their reproduction and early life history. Environ. Biol. Fishes 30(1–2), 280 p.
- Boehlert, G. W., M. Kusakari, and J. Yamada.**  
1987. Reproductive mode and energy costs of reproduction in the genus *Sebastes*. In Proceedings of the international rockfish symposium; Oct. 1986, Anchorage, Alaska, p. 143–152. Alaska Sea Grant Rep. 87-2, Univ. Alaska, Fairbanks, AK.
- Bradford, M. J.**  
1992. Precision of recruitment predictions from early life stages of marine fishes. Fish. Bull. 90:439–453.
- Carr, M. H.**  
1983. Spatial and temporal patterns of recruitment of young-of-the-year rockfishes (genus *Sebastes*) into a central California kelp forest. M.S. thesis, San Francisco State Univ., San Francisco, CA, 102 p.
- Cochran, W. G.**  
1977. Sampling techniques, 3rd ed. John Wiley & Sons, New York, NY, 428 p.
- Cury, P., and C. Roy.**  
1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46:670–680.
- Cushing, D. H.**  
1973. Recruitment and parent stock in fishes. Washington Sea Grant Publ. WSG 73-1, Univ. Washington Press, Seattle, WA, 197 p.
- Dementjeva, T. F.**  
1964. Correlations between indices of relative abundance of young fish, recruitment size and maturity rate as a basis for annual prediction. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 155:183–187.
- Eldridge, M. B., J. A. Whipple, M. J. Bowers, B. M. Jarvis, and J. Gold.**  
1991. Reproductive performance of yellowtail rockfish, *Sebastes flavidus*. Environ. Biol. Fishes 30:91–102.
- Eldridge, M. B., and B. M. Jarvis.**  
1995. Temporal and spatial variation in fecundity of yellowtail rockfish. Trans. Am. Fish. Soc. 124:16–25.
- Finney, D. J.**  
1941. On the distribution of a variate whose logarithm is normally distributed. J. R. Statistical Soc. (Series B) 7:155–161.
- Fogarty, M. J.**  
1993. Recruitment in randomly varying environments. ICES J. Mar. Sci. 50:247–260.
- Green, P. E.**  
1978. Analyzing multivariate data. Dryden Press, Hinsdale, IL, 519 p.
- Hallacher, L. E., and D. A. Roberts.**  
1985. Differential utilization of space and food by the inshore rockfishes (Scorpaenidae) of Carmel Bay, California. Environ. Biol. Fishes 12(2):91–110.
- Hayward, T. L.**  
1993. Preliminary observations of the 1991–1992 El Niño in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 34:21–29.
- Holling, C. S.**  
1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. 91:293–320.
- Hollowed, A. B.**  
1992. Spatial and temporal distributions of Pacific hake, *Merluccius productus*, larvae and estimates of survival during early life stages. Calif. Coop. Oceanic Fish. Invest. Rep. 33:100–123.
- Hollowed, A. B., K. M. Bailey, and W. S. Wooster.**  
1987. Patterns in recruitment of marine fishes in the northeast Pacific Ocean. Biol. Oceanogr. 5:91–131.
- Houde, E. D.**  
1987. Fish early life dynamics and recruitment variability. Am. Fish. Soc. Symposium 2:17–29.
- Johnson, N. L., and S. Kotz.**  
1970. Distributions in statistics, continuous univariate distributions—1. John Wiley & Sons, New York, NY, 300 p.
- Koslow, J. A.**  
1984. Recruitment patterns in northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci. 41:1722–1729.
- Laidig, T. E., S. Ralston, and J. R. Bence.**  
1991. Dynamics of growth in the early life history of shortbelly rockfish *Sebastes jordani*. Fish. Bull. 89:611–621.
- Largier, J. L., B. A. Magnell, and C. D. Winant.**  
1993. Subtidal circulation over the northern California shelf. J. Geophys. Res. 98(C10):18147–18179.

- 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.
- Lasker, R.**  
1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. 73:453-462.
- Leaman, B. M., and R. J. Beamish.**  
1984. Ecological and management implications of longevity in some northeast Pacific groundfishes. Int. North Pac. Fish. Comm. Bull. 42:85-97.
- 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.
- Lockwood, S. J.**  
1980. Density-dependent mortality in 0-group plaice (*Pleuronectes platessa* L.) populations. J. Cons. Cons. Int. Explor. Mer 39(2):148-153.
- Love, M. S., M. H. Carr, and L. J. Haldorson.**  
1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. Environ. Biol. Fishes 30:225-243.
- Matarese, A. C., A. W. Kendall Jr., D. M. Blood, and B. M. Vinter.**  
1989. Laboratory guide to early life history stages of north-east Pacific fishes. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 80, 651 p.
- Mearns, A. J., M. J. Allen, M. D. Moore, and M. J. Sherwood.**  
1980. Distribution, abundance, and recruitment of soft-bottomed rockfishes (Scorpaenidae: *Sebastes*) on the southern California mainland shelf. Calif. Coop. Oceanic Fish. Invest. Rep. 21:180-190.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall.**  
1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45:1657-1670.
- Mooers, C. N. K., C. N. Flagg, and W. C. Boicourt.**  
1978. Prograde and retrograde fronts. In M. J. Bowman and W. E. Esaias (eds.), Oceanic fronts in coastal processes, p. 43-58. Springer-Verlag, Berlin.
- Moser, H. G., and G. W. Boehlert.**  
1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. Environ. Biol. Fishes 30:203-224.
- Moser, H. G., E. H. Ahlstrom, and E. M. Sandknop.**  
1977. Guide to the identification of scorpionfish larvae (family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 402, 71 p.
- Myers, R. A., and N. G. Cadigan.**  
1993. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. 50:1576-1590.
- Naylor, T. H., J. L. Balintfy, D. S. Burdick, and K. Chu.**  
1966. Computer simulation techniques. John Wiley & Sons, New York, NY, 352 p.
- Peterman, R. M., M. J. Bradford, N. C. H. Lo, and R. D. Methot.**  
1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45:8-16.
- Reilly, C. A., T. W. 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.
- Rothschild, B. J.**  
1986. Dynamics of marine fish populations. Harvard Univ. Press, Cambridge, 277 p.
- Searle, S. R., F. M. Speed, and G. A. Milliken.**  
1980. Population marginal means in the linear model: an alternative to least-square means. Am. Statistician 34(4):216-221.
- Shepherd, J. G., and D. H. Cushing.**  
1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. J. Cons. Cons. Int. Explor. Mer 39(2):160-167.
- Sissenwine, M. P.**  
1984. Why do fish populations vary? In R. M. May (ed.), Exploitation of marine communities, p. 59-94. Springer-Verlag, Berlin.
- Sissenwine, M. P., E. B. Cohen, and M. D. Grosslein.**  
1984. Structure of the Georges Bank ecosystem. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 183:243-254.
- Smith, P. E.**  
1985. Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42 (Suppl. 1):69-82.
- Strub, P. T., J. S. Allen, A. Huyer, and R. L. Smith.**  
1987. Large-scale structure of the spring transition in the coastal ocean off western North America. J. Geophys. Res. 92(C2):1527-1544.
- van der Veer, H. W.**  
1986. Immigration, settlement, and density-dependent mortality of a larval and early postlarval 0-group plaice (*Pleuronectes platessa*) population in the western Wadden Sea. Mar. Ecol. Prog. Ser. 29:223-236.
- Walker, P. W., D. M. Newton, and A. W. Mantyla.**  
1993. Surface water temperatures, salinities, and densities at shore stations, United States West Coast, 1992. Scripps Institution of Oceanography, Univ. California, La Jolla, CA, SIO Reference 93-18, 46 p.
- Woodbury, D. P., and S. Ralston.**  
1991. Interannual variation in growth rates and back-calculated birthdate distributions of pelagic juvenile rockfish (*Sebastes* spp.) off the central California coast. Fish. Bull. 89:523-533.
- Wooster, W. S., and D. L. Fluharty (eds.).**  
1985. El Niño North: Niño effects in the Eastern Subarctic Pacific Ocean. Washington Sea Grant Program, Univ. Washington, Seattle, WA, 312 p.
- Wourms, J. P.**  
1991. Reproduction and development of *Sebastes* in the context of the evolution of piscine viviparity. Environ. Biol. Fishes 30:111-126.
- Wyllie Echeverria, T.**  
1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. Fish. Bull. 85:229-250.
- Wyllie Echeverria, T., W. H. Lenarz, and C. A. Reilly.**  
1990. Survey of the abundance and distribution of pelagic young-of-the-year rockfishes, *Sebastes*, off central California. U. S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC 147, 125 p.
- Yamada, J., and M. Kusakari.**  
1991. Staging and the time course of embryonic development in kurosoi, *Sebastes schlegeli*. Environ. Biol. Fishes 30:103-110.
- Zijlstra, J. J., Dapper, R., and J. J. Witte.**  
1982. Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. Neth. J. Sea Res. 15:250-272.