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.

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.), 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⁻¹) (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 (Moors 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 (Tagart²).

**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

---


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 ≥ 25 mm; Woodbury3), 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 \( \hat{\tau}_{sy} = \alpha_{sy} + \beta_{sy}l \), 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·mm\(^{-1}\)) 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.

\[
N^*_l = N_l \exp \left[ -Z(\tau^* - \hat{\tau}_{sy}) \right],
\]

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\(^{-1}\). This latter figure was based on combined estimates of mortality rate for 1) larval shortbelly rockfish, S. jordani (Ralston et al.1); 2) settled juvenile blue rockfish (Adams and Howard4); 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. \( y_{jk} = \log[x_{jk} + 0.1] \), 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 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 Horsehoe 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,
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 forward 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.

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

where $I_{act}$ is the index for species $s$ in county $c$ in year $t$, and $n$ is the number of counts ($C_{act}$) 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.

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

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

An estimate of measurement error ($\sigma_e^2$) 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,

$$\sigma_e^2 = \frac{1}{k} \sum_{t=1}^{k} s_{it}^2.$$  

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

$$\sigma_{TOT}^2 = \frac{1}{k-1} \sum_{t=1}^{k} (I_t - \bar{I}_t)^2$$

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

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.

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

where $SST_{ijk}$ is the sea-surface temperature recorded at shore station $i$ (i.e. BB, FI, or GC) on calendar date $j (j=1, \ldots, 90)$ in year $k$ (k=1980, ..., 1992), $\mu$ is the population mean SST, and $\epsilon_{ijk}$ 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](image-url)
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 ($\chi^2$) 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 ($\alpha_j$) 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-
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 and the increasing abundance of settled 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 depensatory 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 depensatory 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. has shown that three kelp-forest inhabitants that are not highly piscivorous, i.e. *Hexagrammus decagrammurus*, *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

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 (1984) 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. (1995) 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 ($M\times t$), an increase in duration 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 we give our sincere gratitude and appreciation.

Literature cited

Ahlstrom, E. H.


Bence, J. R., A. Gordoa, and J. E. Hightower.

Beverton, R. J. H. (ed.).

Boehlert, G. W., and J. Yamada (eds.).

Boehlert, G. W., M. Kusakari, and J. Yamada.

Bradford, M. J.

Carr, M. H.

Cochran, W. G.

Curry, P., and C. Roy.

Cushing, D. H.

Dementjeva, T. F.


Eldridge, M. B., and B. M. Jarvis.

Finney, D. J.

Fogarty, M. J.

Green, P. E.

Hallacher, L. E., and D. A. Roberts.

Hayward, T. L.

Holling, C. S.

Hollowed, A. B.

Hollowed, A. B., K. M. Bailey, and W. S. Wooster.

Houde, E. D.


Koslow, J. A.

Laidig, T. E., S. Ralston, and J. R. Bence.

Largier, J. L., B. A. Magnell, and C. D. Winant.
Rothschild, B. J.


Sissenwine, M. P.


Smith, P. E.


van der Veer, H. W.


Woodbury, D. P., and S. Ralston.

Wooster, W. S., and D. L. Fluharty (eds.).

Wourms, J. P.

Wyllie Echeverria, T.


Yamada, J., and M. Kusakari.