Influence of ocean conditions on the timing of early life history events for blue rockfish (*Sebastes mystinus*) off California

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Abstract—Settled juvenile blue rockfish (*Sebastes mystinus*) were collected from two kelp beds approximately 335 km apart off Mendocino in northern California and Monterey in central California. A total of 112 rockfish were collected from both sites over 5 years (1993, 1994, 2001, 2002, and 2003). Total age, settlement date, age at settlement, and birth date were determined from otolith microstructure. Fish off Mendocino settled mostly in June and fish off Monterey settled mostly in May (average difference in settlement=23 days). Although the difference in the timing of settlement followed this same pattern for both areas over the five years, settlement occurred later in 2002 and 2003 than in the prior years of sampling. The difference in the timing of settlement was due primarily to differences in birth dates for the two areas. The time of settlement was positively related to upwelling and negatively related to sea level anomaly for most of the months before settlement. Knowledge of the timing of settlement has implications for design and placement of marine protected areas because protection of nursery grounds is frequently a major objective of these protected areas. The timing of settlement is also an important consideration in the planning of surveys of early recruits because mistimed surveys (caused by latitudinal differences in the timing of settlement) could produce biased estimates.

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Successful recruitment of fishes into adult populations can have a major influence on population biomass. Within a species, recruitment events can vary widely in magnitude both temporally and spatially (Doherty and Fowler, 1994; Ralston and Howard, 1995; Caley et al., 1996). Understanding this variability in recruitment strength is a critical goal in predicting adult population structure (Doherty and Fowler, 1994; Hidalgo et al., 2009). Knowledge of the spatial and temporal variability in recruitment of a population can lead to enhanced management of the species (e.g., to protection of important nursery areas) (Grorud-Colvert and Sponaugle, 2009).

Variation in recruitment strength is influenced by multiple biotic and abiotic factors, including the magnitude of spawning biomass, predation, available habitat, available prey, competition, temperature, upwelling, turbulence, water quality, and ocean currents (Peterman and Bradford, 1987; Ainley et al., 1993; Ralston and Howard, 1995; Hobson et al., 2001; Johnson et al., 2001; Sale et al., 2005; Hidalgo et al., 2009). Recruitment variability can occur from large-scale (e.g., El Niño or La Niña events, Pacific Decadal Oscillations) (Carr, 1991; Field and Ralston, 2005; Laidig et al., 2007) to small-scale processes (e.g., localized patchiness of suitable nursery habitats; fine-scale oceanographic events) (Sale et al., 2005; Johnson, 2006). Determining the relative influence of these processes on fish recruitment has been a goal for many studies (Peterman and Bradford, 1987; Yoklavich et al., 1996; Laidig et al., 2007).

Annual recruitment of rockfishes (*Sebastes* spp.) in the northeast Pacific can vary by orders of magnitudes between years (Ralston and Howard, 1995; Laidig et al., 2007). In addition to temporal variability in recruitment, latitudinal or spatial variability also has been observed for several rockfish species along the west coast (Sakuma et al., 2006). Variable recruitment leads to greater uncertainty in the prediction of year-class strength.

Rockfishes give birth to larvae (parturition) that survive in the plankton for several months before settling into nursery or adult habitats (Carr, 1991; Love et al., 2002; Ammann, 2004). For several rockfish species, it has been demonstrated that the strength of the year class is determined during this planktonic stage (Ralston and Howard, 1995; Laidig et al., 2007; Wilson et al., 2008) and that it can be affected further by postsettlement mortality from predation (Hobson et al., 2001).

In this study, the recruitment of juvenile blue rockfish (*S. mystinus*) from the pelagic environment to nearshore kelp beds was examined in two geographic regions along the California coast. Blue rockfish are an important commercial and recreational species in California ranging from at least British Columbia to northern Baja California (Love et al., 2002). Otolith microstructure was used to estimate

Table 1

Location, year, sampling date, number of samples collected, and size range of blue rockfish (*Sebastes mystinus*) examined for settlement marks in otoliths.

Location	Year	Sample date	Number of samples	Size range (mm standard length)
Mendocino	1993	2 Jun	11	37–48
Monterey	1993	3 Jun	11	38–48
Mendocino	1994	26 Jul	13	44–52
Monterey	1994	20 Jul	13	42–60
Mendocino	2001	11 Sep	10	48–70
Monterey	2001	5 Sep	10	53–68
Mendocino	2002	13 Aug	12	47–66
Monterey	2002	18 Jul	13	45–58
Mendocino	2003	4 Sep	10	58–73
Monterey	2003	1 Aug	9	47–59

the timing of settlement, birth dates, and length of the pelagic larval and juvenile stages of blue rockfish. Upwelling indices and sea level anomalies were used to evaluate the influence of oceanographic conditions on the timing of recruitment (settlement) for blue rockfish in the two regions.

Materials and methods

Juvenile blue rockfish were collected in two areas, approximately 335 km apart—one off northern California in Mendocino County (39°14′N lat., 123°46′W long.) and the other off central California along the southern edge of Monterey Bay in Monterey County (36°38′N lat., 121°55′W long.; Fig. 1). Each area is typified by large kelp beds that extend from shore to approximately 20 m depth. The Mendocino site is dominated by bull kelp (*Nereocystis luetkeana*) and the Monterey site by giant kelp (*Macrocystis pyrifera*). These kelp-bed areas comprise high-relief bedrock interspersed with low-relief cobble and sand areas. Both beds are exposed to open ocean conditions, although the Monterey site is slightly buffered from southerly seas by the tip of the Monterey Peninsula.

Fish were collected throughout the kelp beds by divers using small spears at depths of 5–20 m and were frozen for later analysis. Fish were collected during late spring and summer at both sites during five nonconsecutive years (1993, 1994, 2001–2003). Years for data analysis were selected on the basis of three criteria: 1) there were at least nine individuals collected from each area; 2) sampling dates at each study site in a particular year were reasonably close (approximately one month or less apart); and 3) samples were collected after 1 June to allow for complete settlement of the juveniles (Table 1).

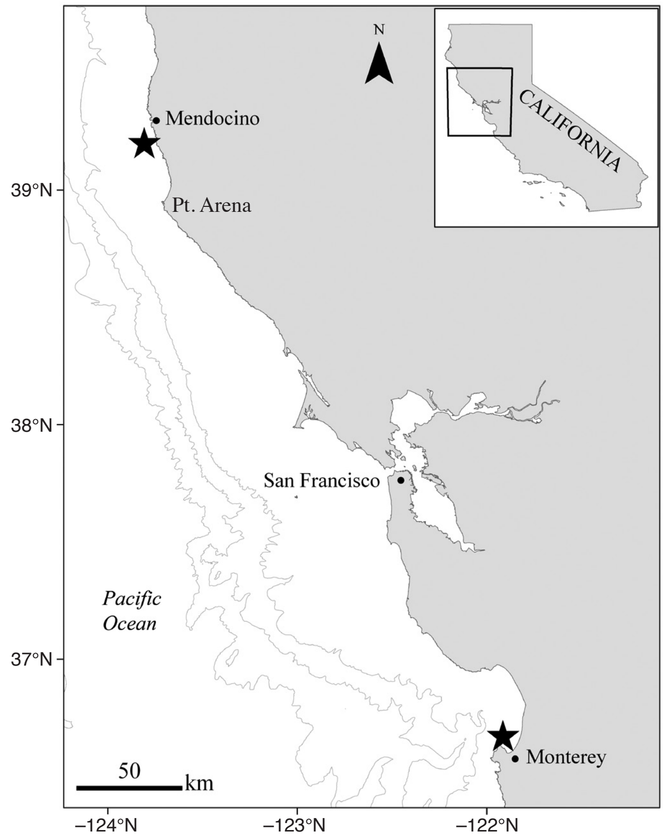

Figure 1

Map of the two study areas along the California coast. Black stars indicate areas where samples of blue rockfish (*Sebastes mystinus*) were collected for otolith analysis to determine the timing of early life history events.

Otolith data

Sagittal otoliths were removed and ages were determined visually by counting growth increments with a compound microscope at 1000× magnification (Laidig et al., 1991), beginning at the first increment after the extrusion check (a mark in the otolith formed when the larvae were released from their mother). No validation of the rate of deposition of these growth increments was performed during this study, and none was available from the literature. However, based on validation studies for other co-occurring rockfish species, such as shortbelly rockfish (*S. jordani* [Laidig et al., 1991]), bocaccio (*S. paucispinis*), chilipepper (*S. goodei*), widow rockfish (*S. entomelas*), and yellowtail rockfish (*S. flavidus* [Woodbury and Ralston, 1991]), increments were assumed to be deposited daily. Also, the calculated birth dates of the blue rockfish in this study occurred within the months of larval release for this species (Wyllie-Echeverria, 1987).

The duration of the pelagic larval and juvenile stages, age at settlement (the total duration of pelagic larval and juvenile stages), settlement date, and birth date were calculated by identifying specific marks in the otolith that indicate transitions from one life stage to the next. Transformation from the larval to the juvenile stage was ascertained by the occurrence of secondary growth primordia (areas of new increment growth that form away from the otolith core; Laidig et al., 1991). This transformation occurs during the planktonic stage before settlement. Duration of the pelagic juvenile stage was estimated as the number of increments occurring from the secondary growth primordia to the settlement mark. Settlement date was calculated by subtracting the number of increments formed after the settlement mark from the collection date, and birth date was determined by subtracting the total number of increments in the otolith from the collection date. The otolith increments deposited during the pelagic juvenile stage followed a regular pattern, increasing in width with fish age (Fig. 2). The settlement mark was the increment where a change in the depositional pattern of the increments was observed after the pelagic juvenile stage; typically the increment marking settlement is narrower than the preceding increments (Amdur, 1991). To be considered the settlement mark, this change in increment width had to be visible from the settlement mark to the outer edge of the otolith and not just in one section. Often the settlement mark was evident in the otolith as a dark ring of numerous closely spaced increments. After the settlement mark, increment widths followed no consistent growth pattern.

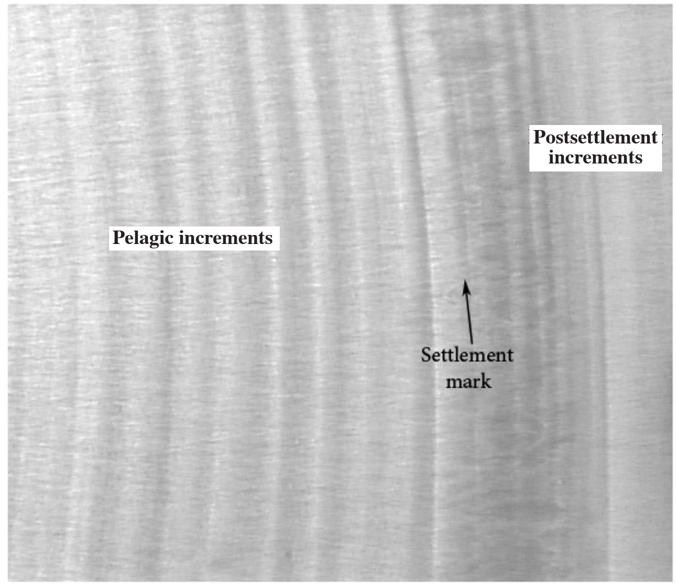

Figure 2

Growth increments in the otolith of a blue rockfish (*Sebastes mystinus*). The settlement mark and increments produced before (pelagic) and after (post) settlement are indicated.

Oceanographic data

Upwelling data were derived from monthly sea level pressure fields provided by the U.S. Navy Fleet Numerical Meteorology and Oceanography Center (data acquired from NMFS, Environmental Research Division, Southwest Fisheries Science Center at http://www.pfeg.noaa.gov, accessed July 2009) measured off Mendocino (39°11′N lat., 123°58′W long.) and Monterey (36°47′N lat., 122°24′W long.), California. Sea level anomaly data (adjusted for local atmospheric conditions) were collected from shore stations at Humboldt Bay (40°46′N lat., 124°13′W long.) and Monterey (36°36′N lat., 121°53′W long.), California, and monthly means were obtained from the University of Hawaii Sea Level Center. These data represent a measure of change in sea level height over time and reflect water movement a positive anomaly was associated with poleward flow and a negative anomaly was associated with equatorward flow.

Two-way analysis of variance was used to test the hypotheses that mean settlement date, mean birth date, mean duration of pelagic larval and juvenile stages, and mean settlement age did not differ significantly between the two study areas. Principal components analysis (PCA) was used to evaluate the relationship among the otolith data (settlement date, birth date, and settlement age) and the oceanographic variables (monthly average upwelling and sea level anomalies for January–June) for both areas. Canonical correlation analysis (CCA) of the oceanographic and otolith data was used to examine the possible causes of changes in interannual settlement dates.

Results

A total of 112 otoliths were examined (56 otoliths each from Mendocino and Monterey; Table 1). Sampling dates ranged from 2 June to 11 September each year, varying from 1 to 34 days between the two study areas in a particular year. Fish sizes ranged from 37 to 73 mm standard length (SL) for Mendocino and from 38 to 68 mm SL for Monterey.

Average birth dates varied annually, with a difference of 7–30 days between locations and an average of 19 days difference over all years (Fig. 3). Birth dates of Mendocino rockfish were always later in the year than those of rockfish from Monterey (significantly different in 1994, 2001, and 2002; $P<0.05$). Birth dates ranged from 4 January to 25 March for Mendocino fish (7 February average) and from 22 December to 9 March for Monterey fish (19 January average).

Average settlement dates were significantly different ($P<0.001$) each year between the two locations, with fish from Mendocino always settling later in the year than fish from Monterey (23 days average; Fig. 4). The difference in settlement between the two sites varied from an average of 17 to 29 days. The earliest date of settlement was 17 May 1993 for fish off Mendocino and 23 April (occurring in both 2001 and 1993) for fish from Monterey; the latest settlement date was 1 July 2002 for fish off Mendocino and 4 June 2002 for fish off Monterey. Settlement dates were later in 2002 and 2003 and earlier in 1993 than in the other years.

The duration of the larval and pelagic juvenile stages was not significantly different between the two areas in any particular year (Figs. 5 and 6). The average duration for the larval stage was 69 days (range=41–100 d) for fish off Mendocino and 68 days (range=47–90 d) for fish off Monterey. The average duration for the pelagic juvenile stage was 56 days (range=26–90 d) for fish off Mendocino and 52 days (range=14–81 d) for fish off Monterey. Duration of pelagic larval and juvenile stages generally was longer for fish born in the 2000s than for fish born in the 1990s. Fish settled at younger ages at both study sites in the 1990s than in the 2000s (Fig. 7). Age at settlement was significantly different ($P<0.05$) between the two locations only in 2003; fish from Mendocino settled at an older age than those from Monterey.

From the PCA, 56% of the variability in otolith data was explained by the first eigenvector for fish off Mendocino and Monterey. This vector was characterized by the inverse relationship of birth date and settlement age, i.e., the earlier the birth date, the older the settlement age. The second eigenvector explained 41% and 39% of the variability in otolith data for fish off Mendocino and Monterey, respectively; this vector was characterized by later settlement dates and birth dates. The first eigenvector for oceanographic data explained 60% of the variability from Mendocino and 61% of the variability in data from Monterey; this vector was associated with the inverse relationship of upwelling and sea level during the months of March through June off Mendocino and May and June off Monterey. The second eigenvector in the oceanographic data was related to the inverse relationship between upwelling and sea level in April at both sites and explained 30% and 28% of the variability in data from Mendocino and Monterey, respectively.

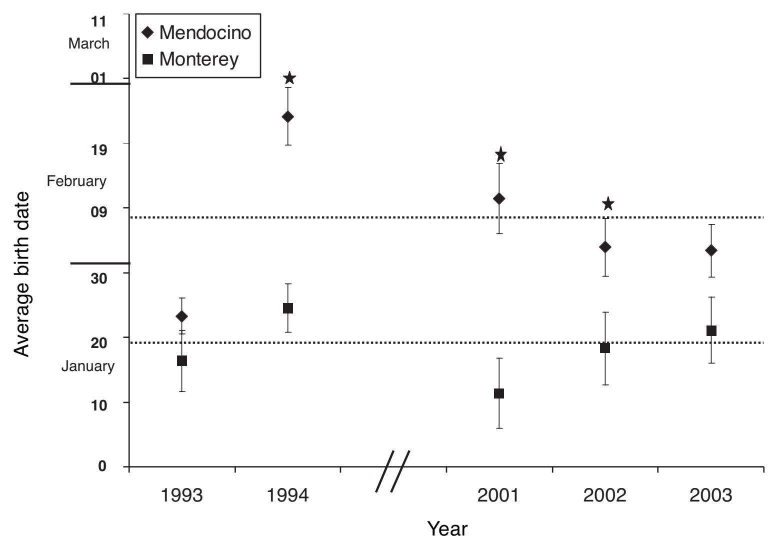

Figure 3

Average birth dates (in calendar days), back-calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas in California. Black stars indicate significant differences ($P<0.05$) between study areas for a particular year. Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error. Horizontal lines on the *y* axis separate months.

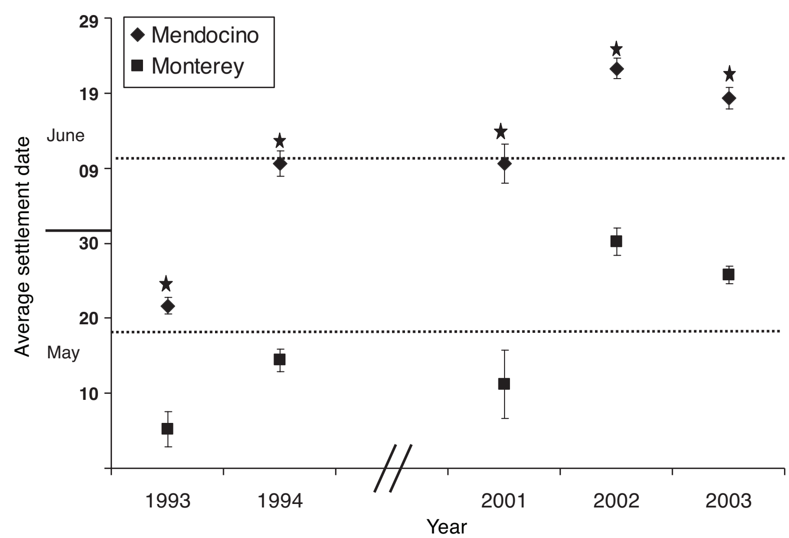

Figure 4

Average settlement dates (in calendar days), back-calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas in California. Black stars indicate significant differences ($P<0.001$). Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error. Horizontal lines on the *y* axis separate months.

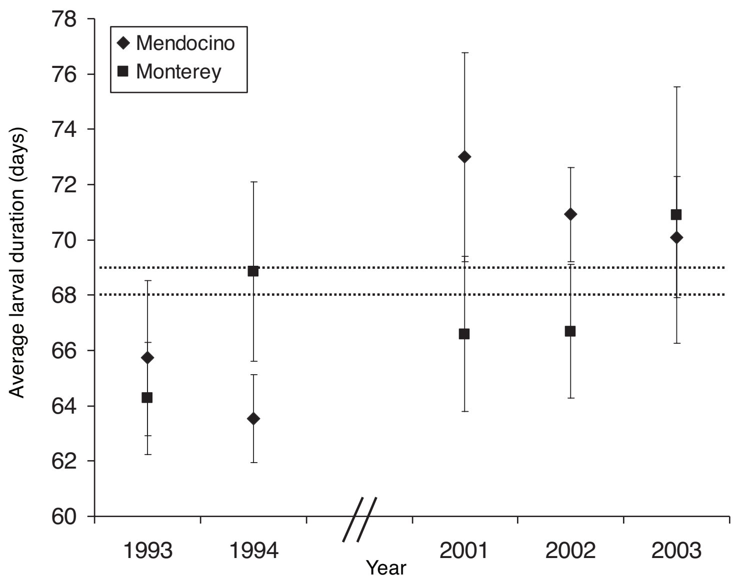

Figure 5

Average larval duration, calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas off California. Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error.

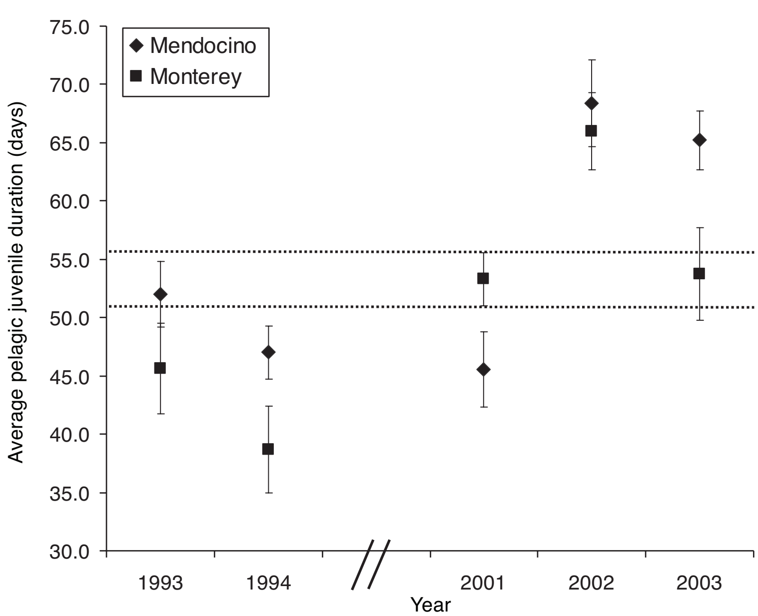

Figure 6

Average pelagic juvenile duration, calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas off California. Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error.

Results from the CCA were similar for data from both study areas (Fig. 8). For Mendocino, settlement dates later in the year (later than the average date for a particular year) were positively related to upwelling in February, May, and June, and inversely related to sea level anomalies in February, March, and May. For Monterey, later settlement dates were positively related to upwelling in all months, except April, and negatively related to sea level anomalies in all months, except April. There was an inverse relationship between birth date and settlement age for both sites, whereby an early birth date corresponded with an older settlement age.

Discussion

The timing of settlement of blue rockfish was related primarily to the timing of birth. Blue rockfish off Mendocino that settled on average three weeks later than fish off Monterey also were born, on average, about three weeks later than fish off Monterey. The age at settlement did not differ significantly between sites, nor did the duration of the larval or pelagic juvenile stages. Pasten et al. (2003) also attributed differences in settling date to time of parturition because early settlers of *Sebastes inermis* to seagrass beds in Japan were born earlier than late-settling fish. These researchers concluded that there was an ideal size for settlement and for active migration. Sogard et al. (2008) studied the maternal effects of rockfishes on their progeny and postulated that factors influencing the time of parturition also influenced recruitment success. It must be noted that parturition dates for blue rockfish in the present study were calculated from surviving juveniles. Those juveniles that did not survive may have been born at a different time and therefore would change the average parturition date (Woodbury and Ralston, 1991; Yoklavich et al., 1996). However, because no estimate of early larval or juvenile mortality exists for blue rockfish, I could not adjust for this effect.

Time of spawning and parturition of many fish species vary by latitude. Parturition dates for numerous eastern Pacific rockfish species occur later in northern study areas off Washington and Alaska than in areas off California

(Wyllie-Echeverria, 1987). Plaza et al. (2004) determined that parturition of *S. inermis* occurred later in the season at the more northerly sites in the western Pacific and suggested that this difference may be related to environmental cues. Vinagre et al. (2008a, 2008b) reported a latitudinal gradient in time of spawning for European sea bass (*Dicentrarchus labrax*) and common sole (*Solea solea*) off Portugal and that spawning onset occurs earlier in the south. These researchers suggested that warm water temperatures in winter at lower latitudes or differences in photoperiod may influence the onset of spawning.

The latitudinal difference in the timing of settlement and parturition in blue rockfish could be an adaptation by blue rockfish to oceanic conditions. Bograd et al. (2009) calculated the spring transition index (i.e., the beginning of the upwelling season) and found that upwelling began on average 20 days earlier off Monterey than off Mendocino. This difference is similar to the 23-day average difference in settlement timing between these two areas. It is possible that blue rockfish have adapted to this difference in the timing of upwelling.

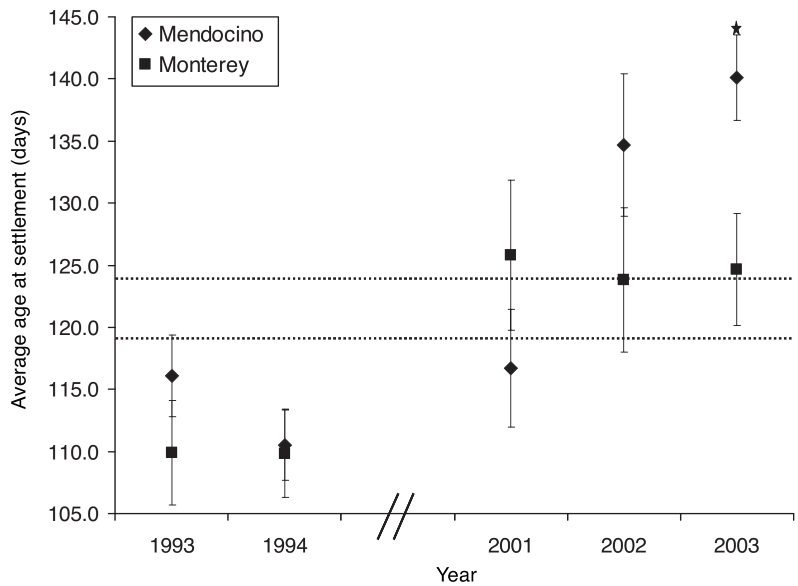

Figure 7

Average age at settlement, calculated from otolith data, for blue rockfish (*Sebastes mystinus*) from two study areas off California. Black stars indicate significant differences ($P<0.05$). Dashed lines represent the 5-year average for each site. Vertical bars represent one standard error.

Interannual variability in parturition dates has been noted by researchers, but specific causes for this variability are still unknown. Woodbury and Ralston (1991) observed variations in the timing of parturition for five species of rockfishes over six years. Early parturition dates have been related to increased maternal age and size for some rockfish species (Bobko and Berkeley, 2004; Plaza et al., 2004; Sogard et al., 2008). Plaza et al. (2004) proposed that the time of parturition could be influenced by effects of temperature on gestation times. Carr (1991) suggested that upwelling may influence the time of parturition. Interestingly, positive upwelling in January and February in this study was correlated with settlement date and this finding strengthens Carr's speculation.

Interannual variability in settlement date was related to upwelling and sea level height in this study. Settlement occurred later in years when upwelling was stronger and sea level anomaly was negative (i.e., there was an equatorward flow of cold water). Stronger upwelling may have transported juvenile rockfish farther offshore, making their return to the nearshore more difficult and causing successful recruitment to occur later in the season (Ainley et al., 1993; Larson et al., 1994; Sakuma et al., 2006; Wilson et al., 2008). Years with reduced or negative upwelling should result in onshore transport and thus earlier settlement to nearshore areas. Cold water produced by upwelling or flow from the north may result in slow growth of juvenile rockfishes (Boehlert and Yoklavich, 1983). These slow-growing individuals may migrate slowly to the nearshore environment. If prey are plentiful, the fish may remain in these food-rich waters longer or, if the quality of the prey items was low, the fish may exhibit reduced growth rates (Boldt and Rooper, 2009). Both of these factors could lead to later settlement of individuals.

Large-scale oceanographic processes (covering 100s of kilometers) can be important in determining recruitment strength over a broad area. Field and Ralston (2005) concluded that the synchrony in year-to-year recruitment for three rockfish species along the west coast of North America was caused by large-scale ocean processes (i.e., El Niño and Pacific Decadal Oscillation). Ralston and Howard (1995) reported similar recruitment strengths in blue and yellowtail rockfishes from two areas off California over a 10-year period and suggested large-scale ocean processes that affect sea surface temperatures (such as El Niño) are primarily responsible for the recruitment variation. Laidig et al. (2003) estimated similar ages and growth curves for adult blue rockfish from Mendocino and Monterey, which indicated that the fish from these areas are influenced by similar oceanographic conditions.

Understanding the causal relationship of biologic and oceanographic factors on recruitment dynamics has implications for fisheries management. For instance, the design and placement of marine protected areas can be augmented to include areas where juvenile rockfishes are recruited and grow, increasing the likelihood of sustained production for those rockfish species. Recruitment dynamics also need to be considered when conducting surveys of rockfish populations early in their life. These surveys can lead to enhanced recruitment predictions for the fishery. However, without information on the spatial and temporal occurrence of recruitment, surveys could be mistimed in a particular region and lead to biased estimates. Results of the present study indicate that coastwide recruitment surveys should be conducted from south to north to allow for later spawning times with increased latitude.

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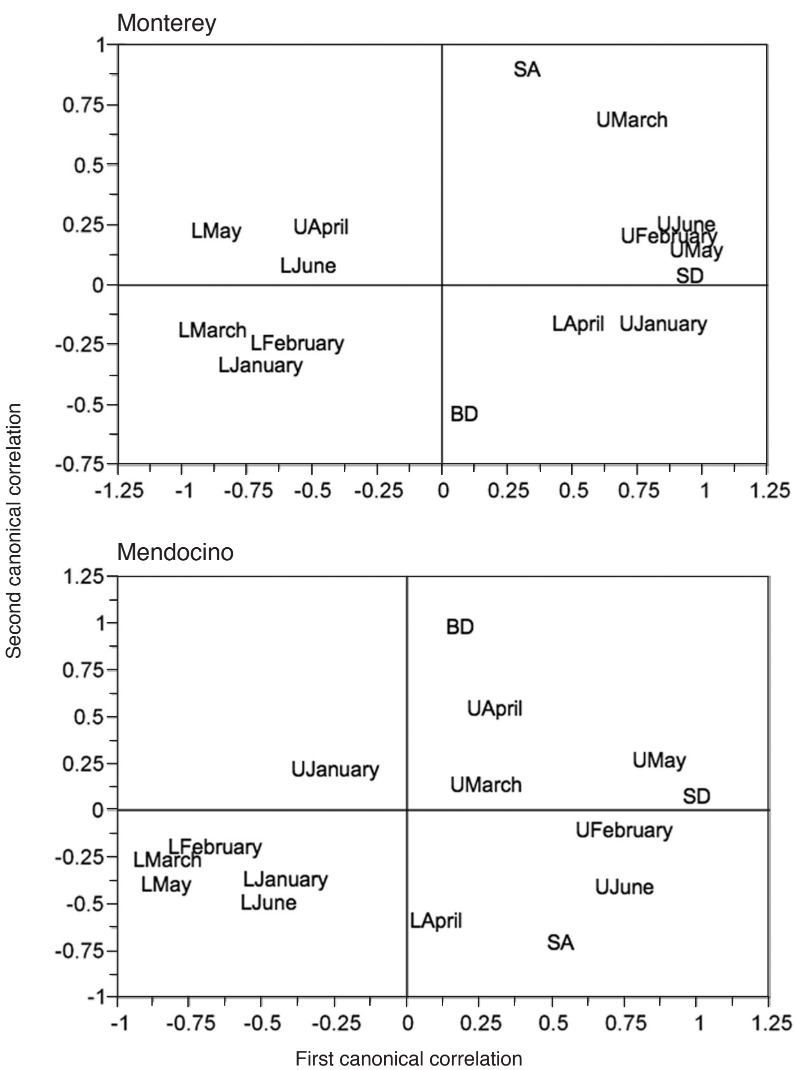

Figure 8

Comparison of first and second canonical correlation coefficients from oceanographic and otolith data at Monterey and Mendocino study sites. For each combined acronym, U=upwelling anomaly, L=sea level anomaly, and month is indicated. BD=birth date; SA=settlement age; SD=settlement date.

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