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Interannual variation in pelagic juvenile rockfish (*Sebastes* spp.) abundance – going with the flow

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ABSTRACT

We report results from 28 yr of a midwater trawl survey of pelagic juvenile rockfish (*Sebastes* spp.) conducted off the central California coast. The fishery-independent survey is designed to provide pre-recruit indices of abundance for use in groundfish stock assessments. Standardized catch rate time series for 10 species were developed from delta-generalized linear models that include main effects for year, station, and calendar date. Results show that interannual fluctuations of all 10 species are strongly coherent but highly variable, demonstrating both high- and low-frequency components. A similarly coherent result is observed in the size composition of fish, with large fish associated with elevated catch rates. In contrast, spatial and seasonal patterns of abundance show greater species-specific differences. A comparison of the shared common trend in pelagic juvenile rockfish abundance, derived from principal components analysis, with recruitments from five rockfish stock assessments shows that the time series are significantly correlated. An examination of oceanographic factors associated with year-to-year variability indicates that a signature of upwelled water at the time of the survey is only weakly related to abundance. Likewise, basin-scale indices (the Multivariate El Niño-Southern Oscillation Index, the Pacific Decadal Oscillation, the North Pacific Gyre Oscillation, and the Northern Oscillation Index) are poorly correlated with abundance. In contrast, sea level anomalies in the months preceding the survey are well correlated with reproductive success. In particular, equatorward anomalies in the alongshore flow field following the spawning season are associated with elevated survival and poleward anomalies with poor survival.

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INTRODUCTION

Recruitment to the adult population of temperate and subarctic marine fish and invertebrate species typically varies greatly from year to year as a result of both density-dependent and density-independent factors. The most compelling hypotheses to date regarding density-independent processes are based on the impacts of physical forcing on the abiotic and biotic environments (Houde, 2008). It has been theorized that greater variability in recruitment of temperate and subarctic stocks is a consequence of slower growth rates, resulting in longer larval stage durations and increased variation in mortality rates (Houde, 1987; Bradford, 1992; Sogard, 1997). As recruitment variability contributes greatly to uncertainty in modeling exploited populations and translates directly into variation in fisheries productivity, the ability to forecast population productivity has long been a key goal of fisheries scientists and managers.

Along the U.S. west coast, rockfishes (genus *Sebastes*) are important components of marine ecosystems and represent a substantial fraction of the volume and value of commercial and recreational fisheries. No fewer than 72 species have been described, with still more being discovered (Love *et al.*, 2002; Hyde *et al.*, 2008). Like most marine fishes, they exhibit extreme year-to-year variation in annual reproductive success, as quantified in recruitment estimates obtained from stock assessment models. The types of information that typically inform such estimates are year-specific age and/or length compositional data. However, for many rockfish species these data sources suffer from considerable imprecision in resolving cohort strength, both because aging rockfish is challenging and because length tends to correlate poorly with age. In addition, these data are primarily derived from catch samples taken from fishery landings and offer no glimpse into what impending recruitment to the fishery might be in the near term. As an alternative, fishery-independent

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surveys offer an opportunity to estimate the abundance of a cohort well before it recruits to the exploitable portion of the population (Nash and Dickey-Collas, 2005; Field *et al.*, 2010a; Rogers-Bennett and White, 2010).

In this study we describe the findings of a pre-recruit survey for rockfish that was implemented with the goal of developing indices of age-0 abundance that could be incorporated into stock assessment models of rockfish in the California Current. The survey began in 1983, and we evaluate the relationship between pelagic juvenile rockfish abundance over the long term and ocean conditions, both at the time of the survey and in the months preceding it. Although this long-term data set is based on sampling only in the central California region, indices currently in use in stock assessments rely upon a coastwide survey effort initiated in 2004 (Sakuma *et al.*, 2006). Not only do such surveys offer the potential to directly measure the strength of a cohort at a very early age, they give a preview of the near-term productivity of a fishery, which can be of use to management when turnover rates are high and the fishing opportunities offered to an industrialized fleet are highly regulated (PFMC, 2008).

Rockfish biology

Rockfish display a primitive form of viviparity (Boehlert and Yoklavich, 1984) leading to parturition of larvae after a gestational period of 30–40 days (Bowers, 1992). The reproductive cycle of winter spawning rockfishes starts with copulation in the fall (September –October), although fertilization of oocytes typically does not occur for several months (Love *et al.*, 2002). Hatching occurs internally, and larvae at parturition have functional jaws and are capable of first-feeding on copepod nauplii (Sumida and Moser, 1984). Parturition in the winter-spawning species occurs primarily from December to March, peaking in January–February (Wyllie Echeverria, 1987). After release, larvae tend to occur within the mixed layer, showing conflicting evidence of vertical migration (Sakuma *et al.*, 1999; Auth *et al.*, 2007). Following the larval period, which lasts 30–60 days, fish transform into pelagic juveniles of 15–25 mm SL, a stage that lasts until fish settle into demersal habitats from April to June (Laidig, 2010).

As adults, the winter-spawning rockfishes reside largely on the continental shelf and slope and are responsible for the vast majority of commercial rockfish landings in the State of California. For example, from 1980 to 2007, five winter-spawning species (*Sebastes entomelas*, *Sebastes flavidus*, *Sebastes goodei*, *Sebastes paucispinis*, and *Sebastes pinniger*) accounted for two-thirds of all commercial rockfish landings in the State, even though at least 55 rockfishes were landed during that time. The winter-spawning species tend to form large aggregations in habitats near the continental shelf break (150–250 m depth). In contrast, many of the nearshore species, whose populations are too small to support large-scale fisheries, spawn during the spring and have a different early life history strategy.

METHODS

Sampling procedures

The National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) Southwest Fisheries Science Center has conducted an annual midwater trawl survey off the coast of central California since 1983 (Table 1), representing 28 yr of information. During this time the R/V *David Starr Jordan* was deployed during the first 26 yr of the survey, the R/V *Miller Freeman* in 2009, and the F/V *Frosti* in 2010. In the earliest years of the survey, two to three cruises were completed each year, but by 1991 the survey was consolidated into a single cruise. Over the entire time series, cruises started as early as 9 April and ended as late as 30 June, but the preponderance of sampling has occurred during the 6 weeks spanning May and the first half of June. The survey design is based on occupying a series of fixed sampling locations (Fig. 1), which have been modified over time to improve and optimize sampling effort. For example, four stations in the Gulf of the Farallones were dropped in 1997 due to frequent encounters with jellyfish (*Chrysaora fuscescens*), which often resulted in serious gear damage. In 2004, the survey area was expanded to encompass nearly all of California (Sakuma *et al.*, 2006). However, for this analysis we excluded all stations sampled outside of the 'core' area historically sampled from 1983 to 2003. The majority of these stations are typically occupied three times every year in an effort to account for short-term temporal variation in pelagic juvenile rockfish abundance (see below).

From its inception the survey has sampled with a standardized modified-Cobb midwater trawl, with a 26-m headrope and a 9.5-mm (3/8″) cod-end liner. Based on net mensuration, the height and width of the net are 12 m, resulting in a sampled swath of approximately 144 m^2; the fine-mesh liner retains epipelagic micronekton. Due to net avoidance, trawling operations are conducted at night, and the target depth for the trawl's headrope is 30 m, except at the few stations located in shallow water (<60 m), in which case the net is fished at 10 m. Time-depth recorders and, more

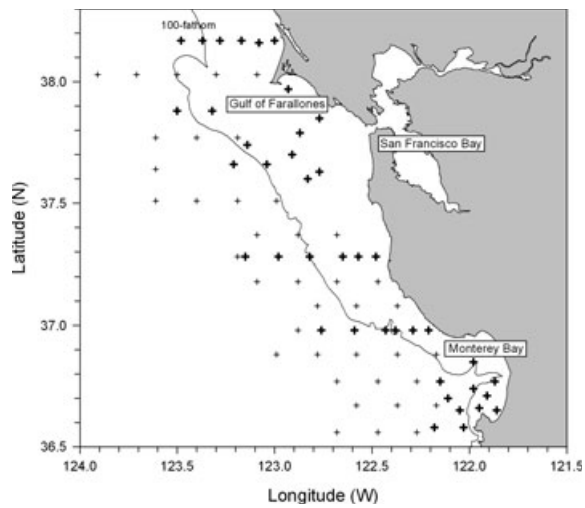
Table 1. Pelagic juvenile rockfish survey cruises, sampling dates, total trawling effort, and trawls at core central California standard stations.

Cruise	Year	Start–end dates	All trawls	Core trawls
DSJ-8302	1983	3–8 June	19	15
DSJ-8303	1983	8–23 June	38	22
DSJ-8405	1984	7–12 June	9	7
DSJ-8406	1984	12–27 June	55	26
DSJ-8503	1985	9–16 April	18	15
DSJ-8504	1985	31 May–4 June	13	11
DSJ-8505	1985	5–30 June	100	33
DSJ-8605	1986	13–22 April	22	19
DSJ-8607	1986	29 May–3 June	17	15
DSJ-8608	1986	3–25 June	102	90
DSJ-8703	1987	10–22 April	76	35
DSJ-8705	1987	23 May–21 June	180	106
DSJ-8804	1988	16–22 April	49	29
DSJ-8806	1988	22 May–18 June	195	105
DSJ-8904	1989	14 May–13 June	171	100
DSJ-9003	1990	28 March–6 April	59	37
DSJ-9005	1990	13 May–10 June	164	99
DSJ-9105	1991	14 May–10 June	159	120
DSJ-9206	1992	11 May–17 June	193	94
DSJ-9307	1993	13 May–13 June	168	101
DSJ-9406	1994	18 May–21 June	150	95
DSJ-9506	1995	17 May–15 June	129	94
DSJ-9606	1996	17 May–19 June	158	94
DSJ-9707	1997	14 May–16 June	149	85
DSJ-9807	1998	3 May–2 June	163	90
DSJ-9903	1999	9 May–3 June	117	90
DSJ-0002	2000	11 May–6 June	128	97
DSJ-0103	2001	11 May–8 June	123	92
DSJ-0205	2002	9 May–3 June	85	77
DSJ-0304	2003	14 May–11 June	118	100
DSJ-0403	2004	4 May–11 June	150	88
DSJ-0504	2005	1 May–11 June	155	83
DSJ-0603	2006	6 May–18 June	163	79
DSJ-0703	2007	5 May–17 June	182	95
DSJ-0803	2008	5 May–18 June	102	36
MF-0902	2009	20 May–24 June	137	83
FR-1002	2010	1 May–11 June	138	86

recently, SIMRAD acoustic sensors are attached to the net during each tow to ensure proper gear performance. The ship's speed is approximately 2.0 knots (3.7 km h^{-1}) and is adjusted while trawling to maintain a proper headrope depth. Tows are standardized by fishing the net for exactly 15 min at depth.

Upon completion of a trawl the contents of the cod end are immediately sorted. All fish, cephalopods, and select decapod crustaceans are enumerated, and several other key taxa (e.g., euphausiids, jellies) are either counted or estimated by expansion from a subsample.

Figure 1. Map of the study region showing the locations of the 40 midwater trawl stations included in the analysis (+). CTD casts are conducted at all trawl stations, as well as other sites (+).



Pelagic juvenile rockfish are identified to species, frozen, and returned to the laboratory. There, the identifications of the rockfish are confirmed and standard lengths (SL, mm) measured. For each species of rockfish captured during a survey, otoliths are extracted from a subsample of fish that spans the size range of juveniles captured and subsequently analyzed to estimate individuals' ages through enumeration of daily increments (Laidig *et al.*, 1991; Woodbury and Ralston, 1991).

Beginning in 1987, physical oceanographic conditions were monitored using conductivity-temperature-depth (CTD) sensors. CTD casts to a depth of 500 m are conducted at all trawl stations, with additional casts completed during daylight hours (Fig. 1). The data are post-processed following the cruise and stored in a database (see for example Baltz *et al.*, 2006).

Data analysis

Conductivity-temperature-depth (CTD) data were analyzed to characterize among-year variation in water type within the survey area. The data were first filtered to only include temperature, salinity, and density (σ_θ) observations in the headrope depth range (28–32 m). For each cast, mean values for each variable were calculated and three analyses of variance (ANOVAs) were conducted, employing year and station as main effects. For example, the temperature model was $T_{ijk} = Y_i + S_j + \varepsilon_{ijk}$, where T_{ijk} is the mean temperature at 30 m in the kth cast conducted in year Y_i $\{i \in 1987, 1988, \ldots, 2009\}$ at CTD station S_j and ε_{ijk} is a normal error term. Temperature year-effects were then

calculated from the ANOVA model by averaging over station effects (see LSMEAN option in PROC GLM; SAS, 1988). Similar analyses were conducted with salinity and density as the dependent variable.

The 9.5-mm cod-end liner in the trawl net is ineffective at retaining late larval fish (<20 mm SL; Ralston, 1993; Eldridge, 1994). Because of the size-selective bias we excluded fish smaller than 20 mm from further analysis. In addition, due to interannual variability in the size distribution of the pelagic juvenile rockfish collected during the survey, for comparative purposes it is essential to standardize fish to a common ontogenetic stage to support interannual comparisons (Ralston and Howard, 1995). The average age of pelagic juvenile rockfish sampled in the survey is approximately 90 days, and so we standardized our abundance data to a common age of 100 days to adjust for the natural mortality that occurs as fish grow. To do so, for each species × year combination (subscripts not included), we calculated linear regressions of age as a function of standard length (SL) using subsamples of aged fish. We then estimated the ages ($\hat{t}$) of fish from their lengths and calculated the number of 100-day-old equivalents (N^*) as:

$$N^*_{h,t} = N_{h,t} \exp[-\mathrm{M} \cdot (100 - \hat{t})]$$

where $N_{h,t}$ is the number of fish from haul h of estimated age t and M is the natural mortality rate of pelagic juvenile rockfish. In our application we used a value of 0.04 day^{-1} for M, which was obtained by interpolation of larval (Ralston *et al.*, 2003; Ralston and MacFarlane, 2010) and settled juvenile (Adams and Howard, 1996) rockfish natural mortality rates. Sensitivity analysis showed that the adjustment was relatively insensitive to the choice of M. Ontogenetically standardized abundances by haul were then obtained by summing over the age variable, i.e., $N^*_h = \sum N^*_{h,t}$.

To estimate year-specific annual abundances the standardized haul statistics of each species were fitted to a delta-generalized linear model (Δ-GLM) (Stefánsson, 1996; Dick, 2004; Maunder and Punt, 2004). With this approach the data are fitted separately to a binomial presence/absence model and a lognormal model with zero catches removed. Estimated effects from the two models were then combined multiplicatively. Aside from the dependent variables, link functions, and the error structure, both models were identically structured, including only main effects for year {1983, 1984, …, 2010}, station (see Fig. 1), and 'period'. The period variable accounts for seasonal variation in the availability of pelagic juvenile rockfish to the survey and was calculated by dividing the calendar date that a trawl occurred by 10 and taking the integer value of the quotient. For example, 15 May (calendar date 135) was assigned to period 13. Separate Δ-GLM models were fitted to the catch data associated with the 10 most abundant species of rockfish encountered by the survey. Year, station, and period effects were obtained from each of the models, which were then used to characterize the spatial distribution, as well as the annual and seasonal trends in abundance.

Adult distribution

In any particular year, the abundance of pelagic juvenile rockfish in the survey area is affected by the geographic distribution of spawning adults and ocean conditions. To quantify the adult latitudinal distribution of the rockfish included in our study, we analyzed catch statistics from the NOAA NMFS Triennial Trawl Survey (Gunderson and Sample, 1980; Weinberg *et al.*, 2002). This fishery-independent survey was conducted every third year, starting in 1977 and ending in 2001, representing nine separate surveys extending over a 25-yr period. The spatial distributions of rockfish species were estimated as the mean and standard deviation of haul (=sample) latitudes weighted by the density (kg ha^{-1}) of a species in a haul. This analysis produces positively biased statistics for rockfishes with southern distributions (e.g., *Sebastes jordani* and *S. paucispinis*) because the survey never passed south of Point Conception (34°25′N) and in some years was limited to north of Point Sur (36°20′N).

Rockfish stock assessments

A stock assessment is a comprehensive attempt to estimate the dynamics of an exploited fish population through statistical modeling of life history, fishery-dependent, and fishery-independent information (Hilborn and Walters, 1992). A time series of recruitments to the exploitable phase is a key output of an assessment in situations where informative age and/or length composition data are available. To compare midwater trawl survey estimates of pelagic juvenile rockfish abundance with information derived from stock assessments, we tabulated time series of recruitment estimates for species held in common between the two approaches. Of the 10 species that are well sampled in the survey (see below), seven have been assessed for the Pacific Fishery Management Council (PFMC) and time series of recruitments have been estimated. These include *Sebastes entomelas* (He *et al.*, 2011), *S. flavidus* (Wallace and Lai, 2004), *S. goodei* (Field, 2007), *S. jordani* (Field *et al.*, 2007), *Sebastes mystinus* (Key *et al.*, 2008), *S. paucispinis* (Field *et al.*, 2009), and *S. pinniger* (Stewart, 2009). Wallace and

Lai (2004), however, did not provide numerical recruitment estimates in their report, and Key *et al.* (2008) have disavowed the accuracy of the recruitment time series developed in their analysis [this was attributed to strong spatial and temporal patterns in growth rates and inadequate age data with which to parameterize growth, which led to low confidence that strong year classes could be correctly assigned to the appropriate year of recruitment (M. Key, A. MacCall, J. Field, and D. Pearson, personal communication)]. Those two studies were therefore excluded from further consideration. Recruitment estimates derived from the remaining five studies were then tabulated and analyzed by principal components analysis (PCA) to evaluate interrelationships and common trends in the recruitment data (Green and Carroll, 1978; SAS, 1988). Correlations, eigenvalues, eigenvectors, and component scores stemming from the analysis were considered in the evaluation.

Oceanographic indices

We evaluated correlations between several oceanographic indices and pelagic juvenile rockfish abundance. Specifically, the following indices were considered: (i) upwelling anomalies, (ii) sea level anomalies, (iii) the Northern Oscillation Index (NOI), (iv) the Multivariate El Niño-Southern Oscillation Index (MEI), (v) the North Pacific Gyre Oscillation (NPGO), and (vi) the Pacific Decadal Oscillation (PDO). A brief description of each follows, including the URL where the data were downloaded.

Upwelling anomalies (http://las.pfeg.noaa.gov/las6_5/servlets/dataset). The frictional stress of equatorward winds on the ocean's surface, in concert with the effect of the Earth's rotation, causes water in the surface layer to move away from the western coast of continental land masses (Bakun, 1973). This offshore moving water is replaced by water which 'upwells', or flows toward the surface from depths of 50–100 m and more. Upwelled water is cooler and saltier than surface water, and typically has much greater concentrations of nutrients such as nitrates, phosphates and silicates that are necessary to sustain the biological production cycle.

Upwelling anomalies are calculated and available at three-degree intervals along the U.S. west coast. We summarized data from 33°, 36°, 39°, and 42°N, which broadly encompasses the study region (Fig. 1). To evaluate and consolidate the common trends in the upwelling statistics from these sites we performed a PCA of the monthly upwelling anomalies for the period January 1946–February 2011 (N = 782). Principal component scores were extracted to obtain orthogonal monthly upwelling values for the central California region. Finally, to compare with juvenile rockfish abundance statistics, we defined the physical/biological year to extend from October to May and dropped records from June–September (see *Rockfish biology* above). Hence, we evaluated eight monthly upwelling PCA scores, from October of the prior year through May of a survey year, in comparisons with rockfish catch rates.

Sea level anomalies (http://uhslc.soest.hawaii.edu/). Variability in dynamic height and alongshore geostrophic flow is translated into sea level anomalies measured at tide gauge stations along the U.S. west coast (Reid and Mantyla, 1976). Positive seasonally adjusted sea level anomalies are proportional to poleward flows and negative anomalies with equatorward flows (Chelton *et al.*, 1982). Data from tide gauge stations, when coupled with satellite altimetry data, improve predictions of nearshore (25–50 km) geostrophic flow (Saraceno *et al.*, 2008).

Like upwelling statistics, sea level data are available from multiple sites along the U.S. west coast. Due to extensive time series of available observations (January 1950–December 2010), we analyzed data from three sites, San Diego (32°42.9′N, 117°10.4′W), San Francisco (37°48.4′N, 122°27.9′W), and Crescent City (41°44.7′N, 124°11.0′W) to characterize variability in alongshore flow in the central California survey region. Missing values (amounting to 3.2% of the observations) were estimated from a main effects ANOVA that incorporated year, month, and site as classification variables. The resulting time series (N = 732) were de-trended by linear regression, and sea level anomalies were calculated for each site using climatologies calculated from the monthly means. Finally, PCA was applied to the data to determine and extract common trends among the three locations in a manner similar to the analysis of upwelling statistics.

Northern Oscillation Index (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix.html). The NOI is an index of climate variability based on the difference in sea level pressure (SLP) anomalies at the North Pacific High in the northeast Pacific and a low pressure center near Darwin, Australia. Because of the role of these SLP centers in global atmospheric circulation patterns, the NOI reflects variability in equatorial and extratropical teleconnections (Schwing *et al.*, 2002).

Multivariate ENSO Index (http://www.esrl.noaa.gov/psd//people/klaus.wolter/MEI/). ENSO is the most important coupled ocean-atmosphere phenomenon to

cause global climate variability on interannual time scales. MEI is based upon the six main observed variables over the tropical Pacific: sea level pressure, zonal and meridional components of surface winds, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky (Wolter and Timlin, 1998).

North Pacific Gyre Oscillation (http://www.o3d.org/npgo/). North Pacific Gyre Oscillation (NPGO) is a climate pattern that emerges as the second dominant mode of sea surface height variability in the Northeast Pacific and is significantly correlated with fluctuations in salinity, nutrients, and chlorophyll *a* measured in long-term observations in the California Current and Gulf of Alaska. Its fluctuations reflect changes in the intensity of the central and eastern branches of the North Pacific gyre circulation, driven by regional and basin-scale variations in wind-driven upwelling and horizontal advection (Di Lorenzo *et al.*, 2008).

Pacific Decadal Oscillation (http://www.jisao.washington.edu/pdo/). Pacific Decadal Oscillation (PDO) is a low-frequency El Niño-like pattern of Pacific climate variability. While the two climate oscillations have similar spatial climate signatures, they have very different behavior in time. Two main characteristics distinguish the PDO from El Niño/Southern Oscillation: (i) PDO events persist for 20–30 yr, while typical ENSO events persist for 6–18 months, and (ii) the climatic record of the PDO is most visible in the North Pacific/North American sector with secondary signatures in the tropics; the opposite is true for ENSO (Mantua and Hare, 1997).

RESULTS

Forty stations in the core survey area (Fig. 1) were sampled at least 10 times from 1983–2010 (Fig. 1), amounting to 2543 valid trawl samples that resulted in a collection of 200 070 pelagic juvenile rockfish. These represent distinct 27 species, with an additional five subgeneric taxa collected that were not identifiable to species (e.g., the subgenus *Sebastomus*). Of the total catch, a single haul conducted in 1988 caught 99 000 *S. jordani*, amounting to almost half of the entire rockfish catch over the 28-yr time series. We exclude that haul when characterizing the species composition of rockfish. Even so, *S. jordani* is still by far the most commonly encountered species in the survey (Table 2). Presented in the table are the 10 most abundant pelagic juvenile rockfishes encountered, which collectively form the basis of our analysis.

Table 2. The 10 most commonly collected pelagic juvenile rockfish species that occur in the midwater trawl survey.

Scientific name	Common name	Code	Percent of catch (%)
Sebastes auriculatus	Brown rockfish	auri	2.7
Sebastes entomelas	Widow rockfish	ento	7.4
Sebastes flavidus	Yellowtail rockfish	flav	1.6
Sebastes goodei	Chilipepper	good	12.9
Sebastes hopkinsi	Squarespot rockfish	hopk	2.1
Sebastes jordani	Shortbelly rockfish	jord	62.9
Sebastes mystinus	Blue rockfish	myst	2.4
Sebastes paucispinis	Bocaccio	pauc	1.3
Sebastes pinniger	Canary rockfish	pinn	1.9
Sebastes saxicola	Stripetail rockfish	saxi	2.3

Δ-GLM year effects

Time series of ontogenetically standardized pelagic juvenile abundance for the 10 species are provided in Table 3, where 'year' effects from the Δ-GLM model are given. Because the distribution of fish recruitments is typically modeled as lognormal (Fogarty, 1993), we report these values as natural logarithms. Nonetheless, when exponentiated to the arithmetic scale, the time series exhibit extreme variability. For example, the ratio of the 75th percentile (P_{75}) of a species' distribution to its 25th percentile (P_{25}) can be used as a conservative measure of the relative extent of interannual variability in survey abundance (last row in table). Across these species, abundances have varied tremendously, ranging from a factor of ×12 (*S. flavidus*) to a factor of ×47 (*S. pinniger*). Typically, the ratio of P_{75}/P_{25} exceeds 20. These results are consistent with the conclusion that year-class strength has been established by the time the survey is conducted.

There is extensive positive covariation among the 10 time series, with correlation coefficients ranging from 0.27 to 0.93 (Table 4). Of the 45 possible pairwise correlations, all are positive and significant at the $P < 0.01$ level, except for those associated with *Sebastes auriculatus*. This result indicates that mortality factors that influence among-year variation in juvenile rockfish abundance operate quite similarly across this suite of species.

The 10 species-specific time series of log-abundance were transformed to standard scores with mean (μ) zero and unit standard deviation (σ), i.e., $Z = (X - \mu)/\sigma$. Plotting those statistics (Fig. 2) reveals several important findings. First, the highly synchronous pattern of covariability among the species is obvious. Secondly, there is extensive high-frequency variability in

Table 3. Estimated log-transformed year effects from the 10 Δ-GLMs fit to rockfish survey catch data (codes as in Table 2). Also shown are the first two scores (PC1 and PC2) from a principal components analysis of the data. As a measure of interannual variability, the last row of the table reports the ratio of the 75th percentile of the antilogged values to the 25th percentile.

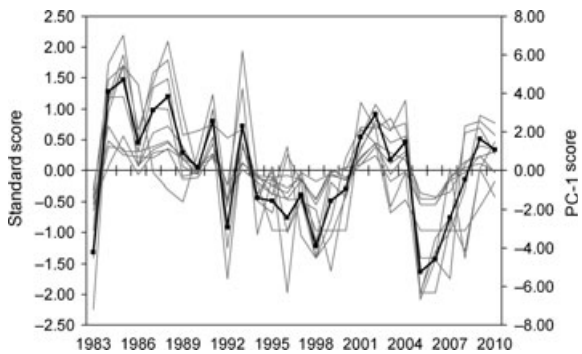
Year	auri	ento	flav	good	hopk	jord	myst	pauc	pinn	saxi	PC1	PC2
1983	−5.78	−3.26	−3.62	−6.73	−5.99	−1.53	−6.32	−8.11	−6.91	−5.78	−4.23	−0.23
1984	−1.17	1.27	0.23	1.85	0.27	2.73	−1.61	2.40	1.09	0.60	4.08	0.38
1985	0.30	3.22	0.68	1.91	1.34	4.12	2.19	−1.15	−0.86	0.46	4.72	0.85
1986	−0.29	−2.07	−2.63	−0.36	−2.55	1.68	−1.49	−1.15	−1.09	−2.18	1.45	0.90
1987	−3.09	0.97	−1.52	2.26	−0.09	3.23	0.46	−0.46	−1.22	0.05	3.15	0.57
1988	−3.61	0.91	−1.30	2.62	0.41	4.57	1.35	0.36	0.09	0.31	3.86	0.73
1989	−3.98	−2.58	−1.97	−0.95	−2.42	2.19	−0.42	−2.15	−1.32	−2.62	0.93	0.49
1990	−2.49	−2.37	−2.82	−1.28	−2.27	0.29	−1.72	−2.96	−3.55	−2.42	0.18	0.60
1991	−0.60	−0.52	−0.75	−0.04	−2.01	1.24	−0.56	−1.35	0.71	−0.15	2.55	−0.11
1992	−4.14	−7.82	−5.32	−1.72	−2.51	−0.64	−5.63	−5.60	−6.91	−5.07	−2.94	1.84
1993	0.78	−0.85	−1.89	2.19	−2.21	1.84	−1.33	−2.60	−2.84	0.58	2.32	0.64
1994	−3.15	−3.43	−3.76	−3.67	−4.23	−0.60	−2.83	−4.70	−4.66	−2.37	−1.37	0.13
1995	−3.77	−2.31	−2.64	−1.36	−5.99	−0.98	−3.09	−4.96	−6.21	−3.26	−1.55	−0.40
1996	−2.27	−8.52	−4.78	−2.27	−5.99	0.90	−2.83	−5.95	−6.91	−3.98	−2.42	1.41
1997	−5.07	−2.23	−3.75	−2.22	−4.54	0.04	−3.23	−4.70	−4.38	−1.93	−1.21	−0.29
1998	−5.78	−5.95	−4.03	−4.64	−5.99	−2.44	−6.32	−7.60	−6.91	−2.84	−3.87	−0.49
1999	−5.08	−2.33	−6.07	−1.60	−5.99	−1.18	−2.82	−3.93	−2.82	−2.03	−1.54	−0.69
2000	−3.79	−2.22	−3.37	−2.15	−5.99	0.79	−3.23	−3.29	−3.98	−2.73	−0.93	−0.17
2001	−0.84	−0.55	−2.08	−0.19	−2.20	1.79	−0.64	−2.88	−2.18	−0.34	1.76	0.40
2002	−1.70	1.15	−1.10	0.75	−2.74	1.76	1.28	−1.71	0.24	0.92	2.94	−0.64
2003	−1.37	−0.14	−1.48	0.00	−5.30	−0.77	0.05	−5.17	−2.05	−2.13	0.59	−0.95
2004	−2.27	0.19	−0.45	0.30	−4.83	0.30	−0.75	−3.84	−0.36	−0.17	1.51	−1.33
2005	−5.78	−8.52	−7.01	−6.03	−5.99	−3.63	−6.32	−8.11	−6.91	−3.97	−5.22	0.10
2006	−5.78	−8.52	−5.68	−4.36	−5.99	−1.81	−6.32	−8.11	−6.91	−4.32	−4.56	0.41
2007	−2.97	−5.12	−6.32	−3.53	−5.99	−1.12	−3.44	−4.65	−3.93	−3.86	−2.43	0.37
2008	−5.78	−0.32	−1.30	−1.83	−5.99	−2.23	−2.36	−3.31	−1.70	−1.19	−0.47	−2.18
2009	−2.96	−0.07	−1.15	1.13	−5.08	0.42	−0.34	−2.78	−1.13	0.71	1.62	−1.35
2010	−2.12	−1.37	−1.58	0.82	−4.17	−0.46	−2.47	−3.79	−0.38	0.31	1.08	−1.01
P_{75}/P_{25}	15	24	12	20	42	16	15	20	47	21	–	–

Table 4. Correlation coefficients (lower left) and significance probabilities (upper right) derived from comparisons of the time series of abundance of 10 pelagic juvenile rockfish species (1983–2010).

Species	auri	ento	flav	good	hopk	jord	myst	pauc	pinn	saxi
auri	1	0.1176	0.1939	0.0020	0.0322	0.0766	0.2127	0.0269	0.0191	0.0367
ento	0.34	1	0.0001	0.0001	0.0003	0.0003	0.0001	0.0002	0.0001	0.0001
flav	0.28	0.78	1	0.0033	0.0006	0.0099	0.0001	0.0039	0.0035	0.0001
good	0.61	0.72	0.55	1	0.0001	0.0001	0.0025	0.0001	0.0001	0.0001
hopk	0.51	0.76	0.73	0.81	1	0.0001	0.0002	0.0003	0.0329	0.0016
jord	0.38	0.67	0.50	0.70	0.79	1	0.0106	0.0001	0.0048	0.0012
myst	0.27	0.84	0.93	0.59	0.77	0.52	1	0.0033	0.0047	0.0001
pauc	0.46	0.68	0.56	0.75	0.75	0.89	0.57	1	0.0010	0.0008
pinn	0.51	0.81	0.60	0.74	0.52	0.59	0.58	0.65	1	0.0004
saxi	0.44	0.87	0.78	0.73	0.69	0.60	0.79	0.62	0.69	1

the data, as evidence by wide swings in log-abundance that occurred, for example, 1983–84, 1992–93, and 2004–2005. Thirdly, there is also a low-frequency component to variation, with elevated abundances of pelagic juvenile rockfish during the 1980s, reduced abundances during the mid-1990s, increased levels from 2001 to 2004, etc. Lastly, strong El Niño events (e.g., 1983, 1992, and 1998) typically lead to much

Figure 2. Time series of pelagic juvenile rockfish abundance sampled by the midwater trawl survey. The 10 light gray lines are the log-scale standard scores of species data presented in Table 4. The bold line represents the first principal component score (see text for further details).



reduced catches of rockfish, although very low catches also occur in non-El Niño years (2005).

Principal components analysis (PCA) of the standardized data shows that the first principal component (PC1) accounted for 77% of the combined variability in the 10 time series (Table 5; Survey Rockfish). Not surprisingly, all species had very similar positive loadings on PC1, representing the common temporal trend observed in juvenile abundance (Table 6; Survey Rockfish). Yearly scores for the first two principal components are reported in Table 3 and PC1 is plotted in Fig. 2, superimposed over the 10 individual standardized species-specific time series of abundance. Given the very strong positive covariation among these species, we use the PC1 score as a composite, integrated indicator of interannual variation in the abundance of pelagic juvenile rockfish sampled in the survey.

Even though the second principal component (PC2) only accounted for 8% of the total variance (Table 5), the latitudinal distribution of spawning adults seems to be responsible for that aspect of variation. Plotted in Fig. 3 are the species' loadings on PC2 against the average latitude of the adult catch from the fishery-independent triennial trawl survey (1977–2001). Note that species with distinctly southern distributions (e.g., *Sebastes hopkinsi* and *S. jordani*) had strong positive loadings on PC2, whereas northerly distributed species (*S. entomelas*, *S. flavidus*, and *S. pinniger*) had strong negative loadings; the

Table 5. Eigenvalues and variance terms obtained from principal component analysis of biological (survey pelagic juvenile rockfish and adult stock assessments) and physical variables (upwelling and sea level anomalies).

Analysis	Component number	Eigen-value	Proportion of variance	Cumulative variance
Survey rockfish	1	7.68	0.768	0.768
	2	0.78	0.078	0.846
	3	0.49	0.049	0.895
	4	0.30	0.030	0.925
	5	0.22	0.023	0.947
	6	0.20	0.020	0.967
	7	0.12	0.012	0.979
	8	0.09	0.009	0.988
	9	0.08	0.008	0.996
	10	0.04	0.004	1.000
Assessments	1	2.403	0.481	0.481
	2	1.129	0.226	0.707
	3	0.721	0.144	0.851
	4	0.395	0.079	0.930
	5	0.352	0.070	1.000
Upwelling	1	2.488	0.622	0.622
	2	1.111	0.278	0.900
	3	0.273	0.068	0.968
	4	0.128	0.032	1.000
Sea level	1	2.61	0.869	0.869
	2	0.28	0.095	0.964
	3	0.11	0.036	1.000

Table 6. Eigenvectors (loadings) from principal components analysis of biological (survey pelagic juvenile rockfish and adult stock assessments) and physical variables (upwelling and sea level anomalies).

Analysis	Variables	Prin1	Prin2
Survey rockfish	auri	0.269	0.290
	ento	0.320	−0.377
	flav	0.315	−0.284
	good	0.337	0.037
	hopk	0.289	0.532
	jord	0.312	0.458
	myst	0.334	−0.058
	pauc	0.333	0.114
	pinn	0.327	−0.289
	saxi	0.321	−0.316
Assessments	ento	0.255	0.699
	good	0.467	−0.494
	jord	0.493	0.190
	pauc	0.455	−0.397
	pinn	0.516	0.270
Upwelling	lat. 33°N	0.424	0.648
	lat. 36°N	0.557	0.343
	lat. 39°N	0.545	−0.375
	lat. 42°N	0.461	−0.567
Sea level*	SD	0.555	0.830
	SF	0.586	−0.432
	CC	0.590	−0.352

Rockfish abbreviations as in Table 2.
*SD, San Diego; SF, San Francisco; CC, Crescent City.

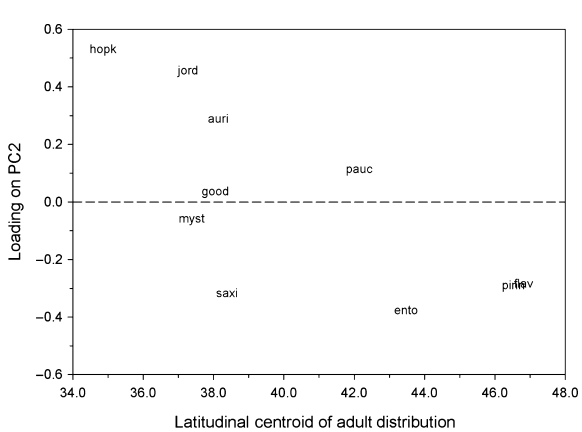
correlation between the two variables ($r = -0.710$) is significant ($P = 0.021$). We conclude that while the shared common trend (PC1) strongly dominates these time series of abundance, minor shifts in species composition in the study area arise annually that depend upon the geographic distribution of adults (PC2).

Recruitment time series from stock assessments

Time series of recruitment at age-0 obtained from rockfish stock assessments conducted for the PFMC are presented in Table 7. A PCA of the log-transformed data spanning 1980–2005 shows that recruitments of all five species tend to covary positively, with the 10 between-stock correlations ranging from −0.01 to 0.61 (median $P = 0.087$, range 0.001–0.978). PC1 explained half of the combined variation in assessment recruitments ($\lambda_1 = 2.403$; Table 5), and loadings on the first component (Table 6) were all positive, ranging from 0.255 (*S. entomelas*) to 0.516 (*S. pinniger*). The first component score (PC1; Table 7) captures the shared time series of log-recruitment variation among these species.

These results indicate that 1984, 1988, 1991, and 1999 were years of strong recruitment, whereas 1982, 1983, 1992, 1997, 1998, 2000, and 2005 were relatively weak. Note that *S. entomelas* deviates most from this generalization, as predicted by its weaker loading on PC1. The relationship between the common trend in survey rockfish abundance (Table 3) and the common trend in recruitment estimates from stock assessments (Table 7) is presented in Fig. 4. There is a significant positive correlation between these variables ($r = 0.622$, $P = 0.0015$), indicating that variation in pelagic juvenile rockfish abundance sampled in central California during the trawl survey tracks subsequent recruitments to rockfish stocks.

Figure 3. The relationship between a species' triennial trawl survey latitudinal distribution and its loading on the second principal component.



Δ-GLM station and calendar date effects

Station effects estimated in the Δ-GLM analysis are plotted for the 10 species in Fig. 5a,b. In the figure, circle diameters are linearly proportional to estimated station effects, with each species scaled to range over similar symbol sizes. While year effects for these species are highly correlated (Table 4), from a spatial perspective they tend to have unique distributions within the survey frame. For example, *S. entomelas* tends to be distributed near the continental shelf break in the northern portion of the study area. *Sebastes flavidus* tends to occur over the continental shelf, but still in the north, and *S. mystinus* is found in the nearshore region. Conversely, *S. paucispinis* has the most offshore distribution of the 10 species and *S. goodei* the most southerly distribution; *S. pinniger* is almost exclusively distributed north of Monterey Bay. These spatial differences in abundance among the species stand in contrast to the shared interannual trends in abundance (PC1).

Similar to station effects, there is considerable variation in the estimated calendar-date effects for the 10 species (Fig. 6). The availability of pelagic juveniles to the midwater trawl survey is shifted to March–April for some species (e.g., *S. goodei* and *Sebastes saxicola*), whereas others peak in their availability in late May or early June (e.g., *S. entomelas*, *S. flavidus*, *S. paucispinis*, and *S. pinniger*). It is interesting to note that the most northerly distributed species as adults (i.e., *S. entomelas*, *S. flavidus*, *S. paucispinis* and *S. pinniger*; see Fig. 3) are generally not well represented in the survey during March–April, which may be related to the observation that rockfish tend to spawn later in the year with increasing latitude, both on an intra- and interspecific basis (Love *et al.*, 1990, 2002; Laidig, 2010).

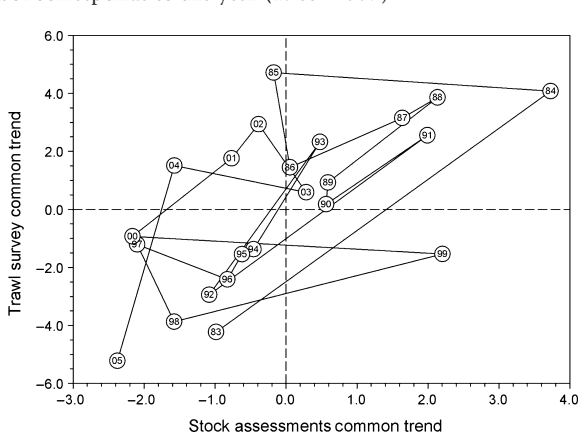
Size structure

In some years the survey encounters large pelagic juveniles, whereas in other years the fish are much smaller. The implication of this characteristic is that there is extensive positive covariation among species in the size of juveniles captured in the survey. For example, if one considers all possible correlations of mean size among the 10 species, calculated over the 28 yr of the survey, there are 45 possible pairwise combinations. Of these, 41 (91%) result in $r \geq 0.40$, with a median correlation coefficient of 0.64 ($r_{crit} = 0.37$ for $\alpha = 0.05$ and 26 df). For brevity we do not show all of the yearly species-specific length compositions. Instead, we

Table 7. Recruitment estimates (/1000) reported from five rockfish stock assessments conducted for the Pacific Fishery Management Council (references: He *et al.*, 2011[1]; Field, 2007[2]; Field *et al.*, 2007[3]; Field *et al.*, 2009[4]; Stewart, 2009[5]).

Year	*Sebastes entomelas*[1]	*Sebastes goodei*[2]	*Sebastes jordani*[3]	*Sebastes paucispinis*[4]	*Sebastes pinniger*[5]	PC1 score
1980	60 263	13 496	644	1994	1576	1.18
1981	72 447	8719	502	1041	3527	1.51
1982	27 625	3130	179	190	1622	−1.26
1983	30 792	3862	57	2092	1103	−0.99
1984	30 657	122750	594	14196	3972	3.73
1985	22 270	7999	525	1215	1043	−0.17
1986	9139	27210	197	1032	1558	0.06
1987	30 350	22 256	785	3318	1903	1.64
1988	16 520	32 477	805	9495	2122	2.13
1989	13 824	35 464	287	464	2342	0.59
1990	28 153	16 270	93	2708	1937	0.57
1991	37 388	27 574	1260	2395	2131	1.99
1992	9694	10 565	70	678	1382	−1.08
1993	18 881	39 139	166	1565	1355	0.48
1994	18 482	12 526	52	1147	1662	−0.46
1995	9269	15 080	250	608	1202	−0.62
1996	7239	6555	301	1080	1202	−0.83
1997	15 792	7584	67	227	787	−2.10
1998	31 276	12 569	9	1237	860	−1.58
1999	18 250	153 415	245	8067	1726	2.21
2000	24 765	3708	52	268	904	−2.16
2001	6805	15 148	128	318	1936	−0.77
2002	14 301	23 831	125	1250	1004	−0.39
2003	7107	14 082	591	3952	1148	0.28
2004	19 301	25 895	89	566	422	−1.57
2005	6587	7647	9	3642	594	−2.38
2006	7577	6645	–	433	1679	
2007	10 833	32 063	–	838	2276	
2008	12 194	–	–	850	1012	
2009	10 787	–	–	–	1886	
2010	21 124	–	–	–	–	

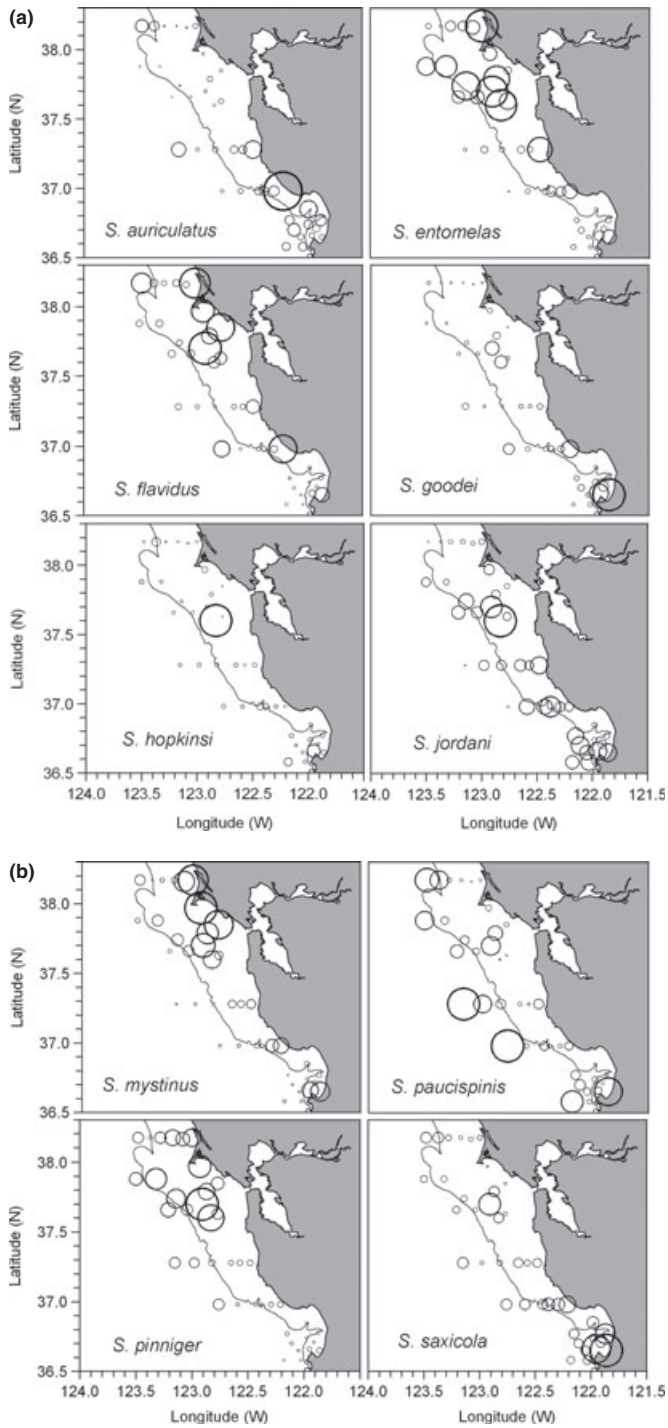
Figure 4. Relationship between the common trend (PC1) of recruitments estimated in five rockfish stock assessments and the common trend of 10 pelagic juvenile rockfish sampled in the midwater trawl survey. The number in each symbol corresponds to the year (1983–2005).



simply aggregated all of the length-frequency data of the pelagic juvenile rockfish sampled by year (Fig. 7). Note that the mean size of fish sampled during the survey has fluctuated over a threefold range, from 17.3 mm (2005) to 54.5 mm (1989), a result which aptly illustrates the need to standardize abundance statistics to a common ontogenetic stage (100-days). Similar to the abundance statistics discussed previously, both high- and low-frequency cycles are evident.

There is a positive correlation between the catch rate of pelagic juvenile rockfish (represented by PC1) and their average size ($r = 0.80$, $P < 0.0001$), which is illustrated in Fig. 8. In years where fish are numerous, they are large and vice versa. Consequently, the fundamental effect of standardizing catch rates to a common age is to amplify variability and increase contrast in the abundance time series.

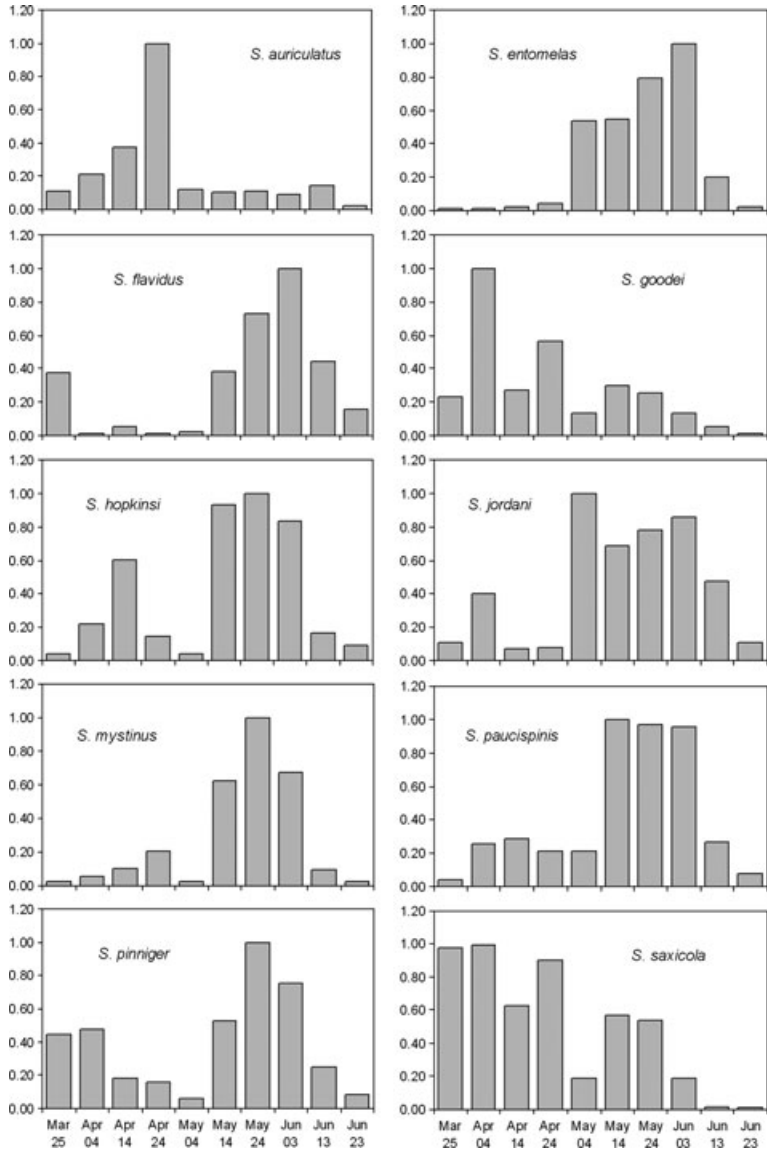
Figure 5. Station effects from Δ-GLM analysis of pelagic juvenile rockfish abundance for (a) *Sebastes auriculatus*, *Sebastes flavidus*, *Sebastes hopkinsi*, *Sebastes entomelas*, *Sebastes goodei and Sebastes jordani*; (b) *Sebastes mystinus*, *Sebastes pinniger*, *Sebastes paucispinus* and *Sebastes saxicola*.



Hydrographic conditions

Regional hydrographic conditions encountered during the survey may well influence annual catch rates. To examine this possibility we analyzed the temperature (T), salinity (S), and density (σ_θ) of seawater sampled during CTD casts at the trawl headrope depth (28–32 m). To spatially integrate the data and derive an

Figure 6. Calendar date effects from Δ-GLM analysis of pelagic juvenile rockfish abundance.



annually averaged statistic, we fit the CTD data to an ANOVA model that included year and CTD station location (Fig. 1) as independent class variables (SAS, 1988), with separate models fit to T, S, and σ_θ. Because CTD sampling began in 1987, the data set encompassed 23 yr, 97 stations, and represented 3975 individual CTD casts. In all three of the models, year and station were both highly significant, with r^2 values for the T, S, and σ_θ models equal to 0.615, 0.627, and 0.645, respectively. Least-square means (Searle *et al.*, 1980) for the year effect were calculated from the three ANOVA analyses to provide annual time series of hydrographic conditions within the core survey region.

Results of the analysis are shown in Fig. 9. The upper panel shows that the water types encountered during the survey generally fall along a primary axis of cold-salty and warm-fresh seawater, i.e., a signature of upwelled versus non-upwelled waters. The most extreme conditions occurred during the 1998 El Niño, when the average temperature at 30 m was 12.02°C and mean salinity was 33.02 ppt. Because the primary axis of hydrographic variability is an upwelling signature, seawater density at 30 m represents a useful index of interannual variability in water properties (lower panel).

As displayed in Fig. 10, there is a weak relationship between prevailing hydrographic conditions

Figure 7. Time series of length distributions of pelagic juvenile rockfish collected during the survey (solid line with closed circles = median; solid lines lacking symbols = 1st and 3rd quartiles; dotted lines = 5th and 95th percentiles).

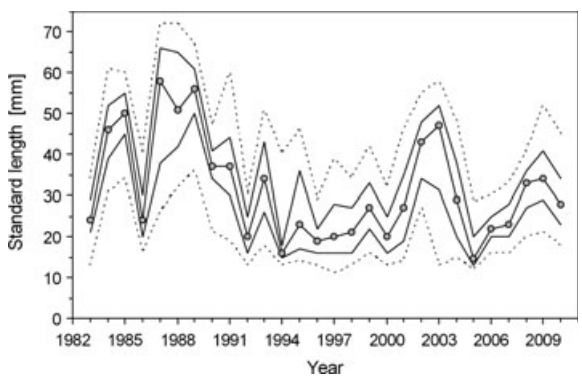
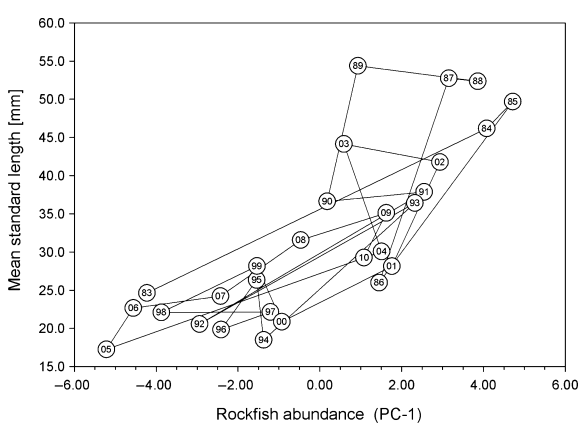


Figure 8. The relationship between pelagic juvenile rockfish abundance and average size. The number in each symbol corresponds to the year (1983–2010).



encountered during the survey and pelagic juvenile rockfish abundance, which plots the common trend (PC1) from the Δ-GLM analysis against σ_θ at 30 m depth. The two variables are weakly correlated and are borderline significant ($r = 0.38$, $P = 0.077$). Generally speaking, there is a tendency for pelagic juvenile rockfish abundance to be elevated (PC1 > 0) during years associated with moderate to strong upwelling ($\sigma_\theta > 25.8$) in May–June.

Oceanographic indices

On first principles, one would expect that environmental conditions during and immediately after the spawning season would regulate the establishment of year-class strength (Houde, 1987) and, as a consequence, the abundance of pelagic juvenile rockfish encountered by the survey. To test this hypothesis, we examined the correlation of the rockfish PC1 with six different environmental variables at various lags from the time of the survey. As described previously, the phenology of events surrounding the establishment of year-class strength for winter-spawning rockfish begins in the fall of the year preceding the survey when insemination occurs and the ocean is pre-conditioned for larval survival, and ends in May when the survey is conducted. Correlation coefficients were therefore calculated between PC1 in year t and oceanographic indices spanning October of year $t-1$ through May of year t. Correlations were also calculated between rockfish PC1 and a centered 3-month running mean of the oceanographic indices. The indices (see Methods) can be classified as either basin-scale (MEI, PDO, NPGO, and NOI) or regional in scale (upwelling and sea level anomalies off California).

The regional scale indices were developed from PCAs of upwelling and sea level data, and scores from the first two principal components were evaluated for their relationship to rockfish abundance. Results presented in Tables 5 and 6 demonstrate that there are strongly held, coherent common trends in upwelling and sea level anomalies off the coast of California, as demonstrated by the first component eigenvalues and eigenvectors. For example, 62% of upwelling variance between latitudes 33° and 42°N is explained by a shared common trend and all four sites load similarly onto the first component. Likewise, 87% of sea level variability at San Diego, San Francisco, and Crescent City is accounted for by the shared common trend, again with very similar loadings at all three sites. Note also that the first two components for these regional oceanographic variables explain 90–96% of the total variance. Finally, the second component eigenvectors

Figure 9. Annual seawater properties at 30 m depth in the survey region. Plotted values are mean estimates based on ANOVA; error bars are ±1.0 SEM. The number in each symbol corresponds to the year (1987–2009).

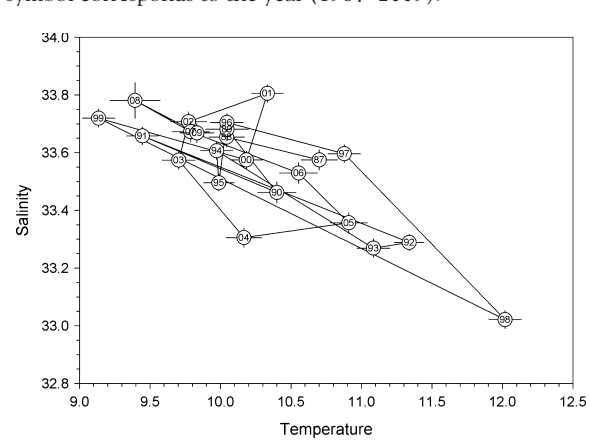
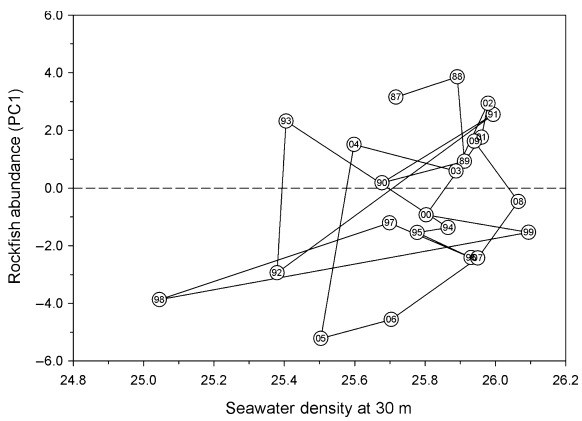


Figure 10. Interannual variation in the relationship between the hydrographic properties of seawater during the survey and the abundance of juvenile rockfish. The number in each symbol corresponds to the year (1987–2009).



for both variables (Table 6) shows a latitudinal aspect to its behavior, with positive loadings in the south and negative loadings in the north.

Results of the correlation analysis between oceanographic indices and pelagic juvenile rockfish abundance are presented in Fig. 11. All six panels are structured identically, with estimated correlation coefficients plotted on the *y*-axis against the lagged month plotted on the *x*-axis. Correlations between rockfish PC1 and the monthly values of the indices are plotted as symbols (closed circles and open squares), whereas correlations based on 3 month running means of the indices are presented as solid or dashed lines. The dotted horizontal lines at +0.374 and −0.374 represent the 95% confidence band for H_0: $r = 0.00$. For the regional indices (upwelling and sea level anomalies) there are two lines, one each for the 1st and 2nd principal components.

There is little to indicate that the basin-scale indices (MEI, PDO, NPGO, and NOI) have a meaningful influence on the abundance of pelagic juveniles in the central California region during May–June. Of the four indices, the NPGO appears to have a somewhat positive relationship with rockfish PC1 derived from Δ-GLM analysis, either immediately before (April of year *t*) or well before (October of year $t-1$) the survey. Likewise, there is some suggestion that the NOI in February–March is positively correlated with PC1. However, our general conclusion is that the basin-scale indices are largely uninformative in predicting pelagic juvenile rockfish abundance off the central California coast during May–June.

Likewise, upwelling anomalies have at best a limited relationship to pelagic juvenile rockfish abundance. At no point during the 8 months that precede the survey does upwelling PC1 have a substantial correlation with rockfish PC1. There is some suggestion that upwelling PC2 has a positive effect in May and a negative effect in February. Given the second component eigenvector loadings, this implies that (i) positive anomalies in the south and negative anomalies in the north during May are associated with increased pelagic juvenile rockfish abundance, and (ii) negative anomalies in the south and positive anomalies in the north during February are also beneficial.

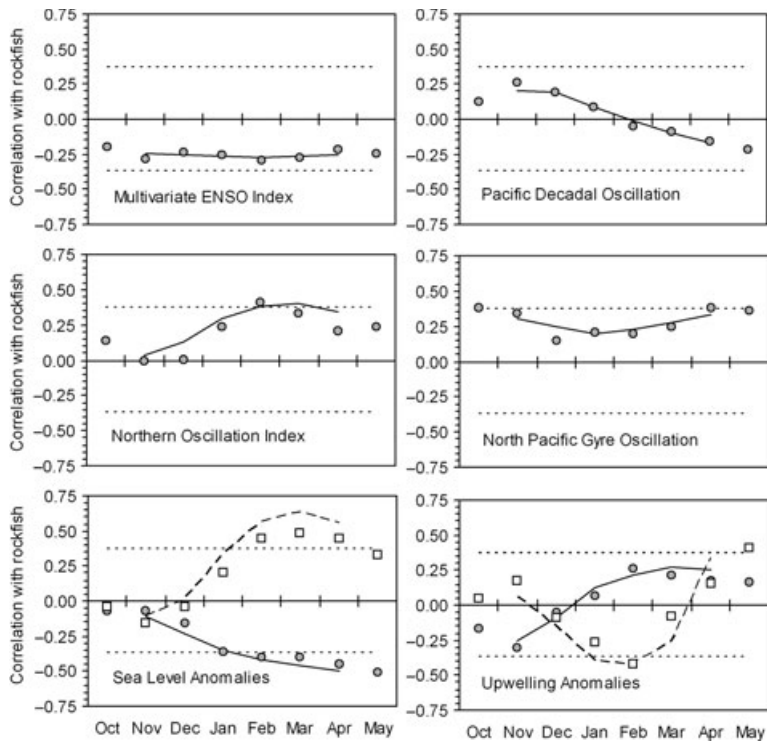
Of all the oceanographic variables examined, sea level anomalies seem to be the most influential. There is a negative relationship between pelagic juvenile rockfish abundance and sea level PC1 during April–May and a positive relationship between abundance and sea level PC2 during February–April. Based on the component loadings provided in Table 6, this implies that coastwide poleward transport anomalies in April–May have an adverse impact on pelagic juvenile rockfish catch rates and, conversely, equatorward transport anomalies have a favorable effect. Eigenvector loadings for sea level PC2 imply that positive scores, which are 'favorable' to rockfish, arise when negative (=equatorward) sea level anomalies occur at San Francisco and Crescent City, but a positive anomaly (=poleward) exists at San Diego.

DISCUSSION

Biological conditions

We describe long-term patterns in the distribution, abundance, and size structure of pelagic juvenile rockfishes off the central California coast. There is a very strongly developed common trend in the time series of pelagic juvenile rockfish abundances (Fig. 2), with 77% of the collective variation of ten species encompassed by PC1. We conclude from this result that rockfish larvae spawned during the winter months are biologically exchangeable, which implies that environmental conditions conducive to survival affect all these species similarly and that collectively their reproductive success should be positively correlated. Confirmation of this prediction exists to some extent in the PCA of recruitment estimates obtained from five rockfish stock assessments conducted for the PFMC (Tables 5 and 6), with 48% of the combined variance explained by a positively correlated, shared common trend. That the recruitments estimated based on catches and survey data have strong, but not as strong, covariation likely reflects the expectation that post-settlement processes (e.g., different habitats, growth rates and species interactions) continue to contribute to recruitment variability, although the major

Figure 11. Lagged correlation plots relating the abundance of pelagic juvenile rockfish (PC1) to oceanographic indices. Lines represent correlations with centered 3-month running means of the indices, whereas symbols plot the correlations with monthly values. In the two lower panels the solid line and closed circles are for PC-1 and the dashed line and open squares represent PC-2 (see text for more discussion).



mode of such variability has occurred by the pelagic juvenile stage. In view of their morphological, dietary, and ecological similarities during their early life history (Matarese *et al.*, 1989; Reilly *et al.*, 1992; Moser, 1996), these findings are not surprising.

Superimposed on the primary positive covariation in abundance patterns is an effect that is apparently due to variation in the geographic distribution of spawning adults (Fig. 3). Interannual variation in alongshore flow during the winter spawning season (December to March) would be expected to result in a shifting pattern of representation of northern versus southern species within the central California region. Specifically, years with positive poleward anomalies in flow would be expected to have enhanced representation of southern species (e.g., *S. hopkinsi*, *S. jordani*, and *S. paucispinis*), which are abundant south of Point Conception. Conversely, equatorward anomalies should result in a shift in species composition towards northerly distributed stocks, including *S. flavidus* and *S. pinniger*. Although these two factors (PC1 and PC2) explain 85% of the interannual variability in abundance of the species considered, there are clear differences in their spatial distributions within the survey area (Fig 5a,b). Note that the highest catches of the more northern species, *S. entomelas*, *S. flavidus*, *S. mystinus*, and *S. pinniger*, all tend to occur in the northern portion of the Gulf of the Farallones (>37.5°N), whereas the more southerly distributed *S. auriculatus*, *S. goodei*, *S. jordani*, and *S. saxicola* all have strong centers of abundance in the Monterey Bay region. Also evident is an offshore distribution of *S. paucispinis*, which has the shallowest depth distribution of these species during the pelagic juvenile stage (Ross and Larson, 2003). This shallow distribution may lead to greater offshore advection from Ekman transport (see Petersen *et al.*, 2010).

There is independent information that confirms that the observed patterns of abundance detected by the survey are real and are ecologically significant. In particular, the importance of pelagic juvenile rockfish in seabird diets, as well as the reproductive success of several species of seabirds at the Farallon Islands (37°42′N, 123°00′W) has long been observed to be related to the abundance of pelagic juvenile rockfish within the Gulf of the Farallones (Ainley *et al.*, 1995; Sydeman *et al.*, 2001; Mills *et al.*, 2007; Field *et al.*, 2010b). These

correlations were particularly noticeable during the 1990s when survey and seabird predation estimates of pelagic juvenile rockfish declined, indicating that pelagic juvenile rockfish act as a conduit of variable ocean productivity by modulating its impacts to higher trophic levels (Miller and Sydeman, 2004; Wells *et al.*, 2008). Analysis of salmon food habits data also suggests a strong relationship between the abundance of pelagic juvenile rockfish in the ecosystem and their occurrence in salmon diets (Mills *et al.*, 2007; J. Thayer *et al.*, Farallon Institute for Advanced Ecosystem Research, unpublished data). Thus, interannual variability in pelagic juvenile rockfish abundance is an important ecosystem indicator, with respect not only to forecasting the productivity of adult rockfish populations but to understanding the population dynamics of a considerable number of co-dependent predators at higher trophic levels.

It is interesting to speculate on the biological factors that might lead to interannual variation in rockfish reproductive success. An obvious candidate is variability in the prey field encountered by larval rockfish (Houde, 1987, 2008). Some limited information exists concerning the feeding habits of larval and pelagic juvenile rockfish (Sumida and Moser, 1984; Reilly *et al.*, 1992), which appear to rely primarily on copepod nauplii, copepodites, and larval stages of euphausiids (e.g., eggs, calyptopis, and furcilia). Importantly, Reilly *et al.* (1992) found that the diets of five species of pelagic juvenile rockfish varied considerably from year to year but that there was high dietary overlap among species within a year, an observation that is consistent with our findings of shared covariability in abundance. Similarly, Santora *et al.* (2011) found considerable year-to-year variation in the abundance of krill in the central California region. More broadly speaking, there is recognition that varying ocean conditions in the California Current, as revealed by the oceanographic variables we have summarized (e.g., the PDO, NPGO, and the MEI), is associated with significant alterations in the plankton community that forms the trophic basis for larval rockfish production (Peterson and Schwing, 2003; Hooff and Peterson, 2006; Brodeur *et al.*, 2008; Thompson *et al.*, 2012).

Our results represent a 28-year time series of survey catches taken within a study area that spans a relatively narrow latitudinal range (Fig. 1). The spatial extent of the survey was expanded in 2004 to cover the entire U.S. west coast (Sakuma *et al.*, 2006), and since then sampling effort in terms of days-at-sea has nearly doubled. Even though the long-term results we present are limited to a narrow range of coastline (185 km), and the distributional range of many of these species can be as much as 10× greater (Love *et al.*, 2002), the survey is still able to detect variation in rockfish year-class strengths, as determined by PFMC groundfish stock assessments (Fig. 4). The utility of the survey in providing informative pre-recruit indices for use in groundfish stock assessment depends directly on the precision of the relationship between survey indices and subsequent recruitment. If prediction errors exceed residual recruitment variation, then incorporation of a pre-recruit index simply adds unwanted noise to an assessment. Recruitment process error in rockfish stock assessments (σ_r) is large, with CVs typically in the range of 50–100%. In comparison, the arithmetic scale CV of the prediction error in Fig. 4 is approximately 200%, indicating that survey results derived from the core area (Fig. 1) are generally too imprecise for use in groundfish stock assessments. In theory, implementation of the coastwide survey should reduce and improve recruitment prediction errors, but it is too soon to know how substantial the improvement will be.

While the limited spatial scale of the midwater trawl survey likely affects the precision of recruitment predictions for stocks with a coastwide distribution, the fact that survey abundances generally track coastwide rockfish recruitments provides support for the conclusion that the spatial scale of these recruitment events is quite large. For example, Field and Ralston (2005) showed that 51–72% of the year-to-year variance in the recruitments of *S. entomelas*, *S. flavidus*, and *S. goodei* is based on coastwide patterns, with a lesser fraction associated with finer scale geographic features. In particular, they showed that the *e*-folding scale of recruitment events (Myers *et al.*, 1997) for these three species was 670–800 km. With respect to among-stock covariation in recruitment trends, Hollowed *et al.* (1987) and Mueter *et al.* (2007) demonstrated temporal concordance in groundfish stocks in the Gulf of Alaska ecosystem. Mueter *et al.* (2007) also found strong within-group correlations within two groups of groundfish stocks in the Eastern Bering Sea/Aleutian Islands (flatfish and gadids), although the correlations between these groups were negative. Megrey *et al.* (2009) expanded the scope of these prior studies to demonstrate comparable within- and between-ocean basin covariation in recruitment, which tended to be positively correlated within north Pacific and North Atlantic ecosystems but negatively correlated between the two. The collective interpretation from these studies is that large-scale physical forcing typically regulates

the reproductive success of ground fish stocks (see also Francis *et al.*, 1998; Hare and Mantua 2000).

With respect to within-year temporal variability, it is clear that the vulnerability of these species to capture by the midwater trawl varies seasonally (Fig. 6). Some (*S. auriculatus*, *S. goodei*, and *S. saxicola*) peak in availability during March–April, whereas all of the others peak during May–June. It is again worth noting that the three species whose availability peaks early in the year have more southerly distributions as adults (Fig. 3). Peak availabilities of the two species with the most northerly distribution as adults (*S. flavidus* and *S. pinniger*) are strongly centered in late May and early June. These findings are consistent with the generalization that spawning in rockfishes, both intra- and interspecifically, shifts later in the year as one progresses from south to north (Love *et al.*, 2002).

There is a relationship between abundance and the size structure of pelagic juvenile rockfish (Fig. 8), with large fish occurring when catch rates are high. A logical explanation for this phenomenon is the 'stage-based mortality' hypothesis (Houde, 1987), which posits that rapid growth quickly transitions individuals through smaller size classes, which are more vulnerable to predation, and that increased survival arises from fast growth. While interannual variation in growth rates does occur, it is insufficient to explain the large changes in size structure that are observed (Fig. 7). Based on ages determined from otolith microstructure (e.g., Laidig *et al.*, 1991; Woodbury and Ralston, 1991; Ralston, 1995), interannual variation in the growth rate of *S. jordani*, the most abundant species in the survey, results in a 9% coefficient of variation in estimated size at age 100 days (Ralston S., unpublished data). In contrast, interannual variation in the mean length of survey catches (Fig. 7) is 35%. The primary cause of among-year length variation is due to differences in the birthdate distributions of those fish that survive to May–June, when the survey occurs (see Woodbury and Ralston, 1991). When catch rates are high, fish tend to be much older than when catch rates are low.

Oceanographic conditions

We analyzed the relationship between variation in survey catches of pelagic juvenile rockfish and selected oceanographic variables in order to evaluate processes potentially responsible for their variability. However, for a full understanding it is important to identify limitations in our conclusions. In particular, because the midwater trawl survey is conducted in May–June and year-class strength is almost certainly established during the first 30 days of life (Houde, 1987, 2008), there is a 4-month lag between spawning and the timing of the survey. As a consequence, aside from CTD data collected during the survey, we rely on published monthly oceanographic indices to characterize environmental conditions and events preceding the survey (see Fig. 11).

However, it is reasonable to expect that critical mortality events that affect the establishment of year-class strength might occur on weekly or even daily time scales. For example, Lasker (1975, 1978, 1981) developed the 'stable ocean' hypothesis, asserting that good larval feeding conditions for northern anchovy (*Engraulis mordax*) are dependent on reduced turbulence in the upper water column. Peterman and Bradford (1987) subsequently found strong statistical support for the hypothesis by calculating the number of times that wind speeds fell below 10 m s^{-1} for four consecutive days (so-called 'Lasker events'), which they showed was inversely correlated with mortality rates. Hence, events occurring over relatively short time intervals can, in some instances, have a profound effect on larval survival. The monthly indices we report integrate out high-frequency signals that may be of importance to larval survival. A similar concern was identified by Zabel *et al.* (2011), who showed that monthly indices performed better than indices averaged over 3 months in accounting for *S. paucispinis* year-class strength.

Our findings regarding hydrographic conditions encountered at the time of the survey show that water properties vary considerably from year to year (Fig. 9). Of particular note was 1998, when warm, low-salinity water was found in the study area. This was a strong, persistent El Niño year, when the MEI exceeded a value of 2.0 over the 12 months that preceded the survey. Even so, there is little to suggest that the water type encountered at the time of the survey has a definitive effect on pelagic juvenile rockfish abundance (Fig. 10). Rather, the weak but positive correlation with PC1 indicates that seawater with an upwelling signature, while generally associated with increased catch, is neither necessary (see 1993) nor sufficient (see 1999) to account for years with high rockfish abundance (PC1 > 0).

Our analysis of a variety of published time series of oceanographic indicators (Fig. 11) suggests that basin-scale indices, including the MEI, PDO, NOI, and the NPGO, provide little predictive capability vis-à-vis rockfish reproductive success. In contrast, the two regional data sets (sea level and upwelling anomalies) have greater predictive power. It is revealing that for both of these, PC2 (dashed lines in Fig. 11) is best correlated with survey catch rates. This is especially true for sea level anomalies. In particular, there are

relatively strong positive correlations (r = 0.56–0.64) between the running mean of February–April sea level PC2 and rockfish abundance during May–June. Moreover, the running mean of sea level PC1 also correlates significantly with pelagic juvenile rockfish abundance. While variation in sea level is influenced by variation in wind-driven upwelling, we highlight the importance of sea level simply because it correlates best with pelagic juvenile rockfish abundance (Fig. 11).

How do we interpret the effect of sea level anomalies on the establishment of rockfish year-class strength? Following on Reid and Mantyla (1976), Chelton *et al.* (1982) showed that sea level anomalies along the California coast are well correlated with alongshore geostrophic flows calculated from CTD dynamic height data collected during CalCOFI surveys. Specifically, positive sea level anomalies are associated with poleward flow anomalies and vice versa. More recently, Saraceno *et al.* (2008) used sea level data from tide gauge stations in concert with satellite altimeter data to improve estimates of nearshore sea surface height and geostrophic flow. In general, poleward advective anomalies during February–April can be seen to have an adverse effect on survival, whereas equatorward anomalies in the flow field are associated with improved survival. Clinal variation in the flow field as captured in PC2 suggests further that conditions are best for rockfish when there is a poleward anomaly in San Diego and equatorward anomalies in San Francisco and Crescent City (see Prin2 eigenvector; Table 6). We interpret this condition as a relative 'convergence' of the flow field within the central California study region (not to be confused with that term as used in standard oceanographic parlance). Conversely, the greatest negative score on PC2, corresponding to the poorest conditions for survival, occurs during 'divergent' flow conditions after the spawning season, arising from an equatorward anomaly in the south and poleward anomalies in the north during February–April.

We emphasize that, because an anomaly is a deviation from expectation, an equatorward anomaly could occur when the flow is actually poleward. For example, Petersen *et al.* (2010) calculated dispersal statistics for rockfish larvae based on the release of Lagrangian floats within a ROMS model developed for the central California coast. They showed strong poleward advection at all depths for 'floats' released over the continental shelf in the winter, in general agreement with the observations and conclusions of Largier *et al.* (1993). Thus an equatorward anomaly might arise simply from a poleward flow that is weaker than expected.

Our findings agree with Laidig *et al.* (2007), who described annual variation in the abundance of settled YOY rockfish off the northern California coast, including *S. flavidus*, *Sebastes melanops*, and *S. mystinus*. They observed strong positive covariation in the summer settlement of these three species in kelp forest habitats. They also identified sea level and nearshore temperature during the preceding winter spawning season as key indicators of oceanographic processes responsible for the establishment of year-class strength. Prior work by Ralston and Howard (1995) had demonstrated that the abundance of pelagic juveniles of these species is correlated to and coupled with their abundance following settlement. The importance of winter conditions has also been highlighted by Black *et al.* (2011), who associated variation in rockfish growth (*Sebastes diploproa* and *Sebastes ruberrimus*), as well as seabird reproductive success (*Uria aalge)* with winter upwelling modes. Moreover, Hannah (2010) developed an informative pre-recruit index for Oregon pink shrimp (*Pandalus jordani*) that was based on catch rates of age-0 shrimp in commercial catches (which are primarily composed of age 1+ individuals), relative to sea level height off Oregon, and a wind-based upwelling index.

We conclude that regional interactions in the winter alongshore flow field, and to a lesser extent the cross-shelf flow field (i.e., upwelling), are related to the establishment of year-class strength for these winter-spawning rockfishes. For both variables, correlation analyses show that PC2, representing a clinal effect in latitudinal expression (Table 6), is most closely associated with our midwater trawl survey catches. Our analysis of ocean conditions accounts for high-frequency variation in rockfish reproductive success, which is the dominant mode expressed in the trawl survey data (Fig. 2). Low-frequency variation is nonetheless present, as evidenced by the gradual decline in catch from 1984–98, which may account for the persistent but weak correlations with basin scale indices.

The importance of variability in the physical flow field that is encountered by larvae in establishing year-class strength has long been appreciated (Sinclair, 1988). Advection of larvae away from suitable settlement habitats can lead to recruitment failure and vice versa (Harden-Jones, 1968). However, it would be presumptuous to attribute the reproductive success of these 10 rockfish species to a single causative agent. As argued by Houde (2008), much more likely is a complex interaction of multiple factors operating on the early life history, or in his own words, a 'realization that recruitment variability is the outcome of complex trophodynamic and physical processes acting over

many temporal and spatial scales'. Houde (2008) also noted the critical importance of extended time series of survey data in defining and understanding the conditions that control recruitment. The time series presented here is likely among the longest such time series for post-larval (but pre-settlement) recruits and thus should continue to provide useful insights into the mechanisms responsible for the variable recruitment observed in both exploited and unexploited species, as well as the long- term ecological interactions between rockfish and the higher trophic level predators that depend on them.

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