CAN WE PREDICT INTERANNUAL AND REGIONAL VARIATION IN DELIVERY OF PELAGIC JUVENILES TO NEARSHORE POPULATIONS OF ROCKFISHES (GENUS *SEBASTES*) USING SIMPLE PROXIES OF OCEAN CONDITIONS?

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ABSTRACT

Rates of larval delivery and population replenishment of many marine species, including nearshore temperate reef fishes are notoriously variable between years and across geographic ranges. The inability to explain and predict this variation hampers our understanding and forecasting of population dynamics and our attempts to manage fisheries proactively. Environmental proxies of interannual and regional variation in rates of population replenishment may provide scientists and managers with tools to forecast regional stock dynamics and adjust rates of fishing mortality to maintain sustainable fisheries. Rockfish (genus *Sebastes*) constitute important fisheries throughout the California Current large marine ecosystem. Since 2000, we monitored rates of onshore delivery of pelagic juveniles (defined here as settlement) of two groups of nearshore rockfishes (kelp, gopher, black and yellow and copper [KGBC] and olive, yellowtail, and black [OYTB]) using artificial collectors placed just offshore of rocky reefs at five locations ranging from Southern California to Northern Monterey Bay. These species complexes are based on similarities in their life history and larval attributes. We attempt to relate interannual patterns of settlement to easily accessible, regional indices of ocean conditions including upwelling, alongshore transport, sea surface temperature (SST) and Chlorophyll-a (Chl-a). In the Santa Barbara channel locations (south of Pt. Conception), interannual variation in settlement of the two species groups is concordant and settlement is strongly and positively correlated to regional upwelling in summer months. North of Pt. Conception, timing of settlement of the two species groups is less concordant. In that region, settlement of KGBC was also positively correlated with summer upwelling, while that of the OYTB group was highly variable and poorly related to any ocean indices. In general, upwelling and alongshore transport were better predictors of delivery than SST or Chl-a. Our results indicate that (1) readily available oceanographic metrics like upwelling indices can be used as reasonable proxies for explaining and forecasting actual rates of replenishment (i.e. delivery of pelagic juveniles to nearshore adult populations) and (2) recognition of the regional variation in these relationships will better inform efforts to more accurately forecast stock dynamics, especially at regional spatial scales.

Keywords: Larval delivery, Settlement, Rockfish, *Sebastes*, Upwelling, Alongshore transport, Chl-a, Temperature, Ocean indices, Proxies

INTRODUCTION

The rate at which young are delivered to and replenish populations is highly variable in time and space and is a critically important determinant of population size and dynamics for many marine organisms (Doherty and Williams 1988; Roughgarden et al. 1988; Caley et al. 1996; Doherty 2002; Osenberg et al. 2002). However, understanding the dynamics of marine populations is often difficult, when input of new individuals is fluctuating in seemingly unpredictable ways. Physical and biological processes affecting growth, survival, and transport of pelagic stages have been shown to affect recruitment and hence, population sizes, for coral reef and temperate fishes (Doherty and Fowler 1994; Chambers 1997; Carr and Syms 2006) as well as marine invertebrates (Connell 1985; Ebert and Russell 1988).

For fisheries species, the inability to accurately predict or forecast the strength of recruitment to a fishery has hampered management efforts. It is clear for most nearshore, demersal fisheries, that reliance on stock-recruitment relationships is inadequate to forecast year class strength (Frank and Leggett 1994). This is due, in part, to the spatially heterogeneous and 'open' nature of these stocks and their associated fisheries. In addition, stock recruitment relationships are confounded by environmental factors affecting survival of pelagic larvae and delivery to settlement habitats.

Given declines in many nearshore fisheries, including rockfishes on the west coast of North America (Love et al. 1998; Mason 1998; Berkeley et al. 2004), improved knowledge of larval recruitment may allow more proactive management measures. The ability to predict patterns of intra- and interannual variation in delivery of larvae or pelagic young to adult populations offers the potential to dramatically improve fisheries management by allowing for better predictions of year class strength and future stock biomass. For example, Shanks and Roegner (2007) and Shanks et al. (this volume) correctly predicted catch rates of *Cancer magister* based on measurements of settlement and timing of the onset of spring upwelling four years prior. Similar lagged correlations between larval or juvenile abundance and commercial harvest have been made for western rock lobster in Australia (Morgan et al. 1982) and for a number of temperate fish species (Mearns et al. 1980; Parrish et al. 1981; Hollowed et al. 1987; Ralston and Ianelli 1998; Jenkins 2005; Laidig et al. 2007; Hare and Able 2007). Moreover, population dynamics of exploited species can be more sensitive to recruitment dynamics because of their typically truncated size distribution (Hsieh et al. 2006).

While recent increases in ocean observing networks are providing accessible environmental data at unprecedented spatial and temporal scales, monitoring interannual and geographic patterns of larval and/or pelagic juvenile replenishment for nearshore marine species at scales relevant to management, remains a challenging and potentially costly endeavor. Thus, understanding the strength and form of linkages between environmental variability and delivery of young may allow the use of 'proxies' for rates of population replenishment that are both easier and cheaper to measure. The utility of simple proxies will increase if the spatial scale and geographic areas for which they apply are identified.

In this study, we test the ability of simple oceanographic proxies to predict rates of delivery of pelagic juveniles of two groups of nearshore rockfishes (genus *Sebastes*) by investigating correlations between delivery to onshore adult populations and four, readily available, regional indices of ocean conditions that have previously been shown to influence delivery of young rockfish to reefs (Laidig et al. 2007; Caselle et al. 2010) on the West Coast of North America: upwelling, alongshore transport, sea surface temperature (SST) and Chl-a. Specifically, we document annual and geographic variability in rates of delivery of pelagic juvenile rockfish across roughly 400 km from central California to southern California, relate interannual patterns to readily available, regional indices of ocean conditions, and discuss the predictive ability of these indices among species and locations. This is the first study to explore potential relationships between oceanographic drivers and actual rates of larval delivery to populations of rockfishes on shallow rocky reefs at such large regional geographic scales.

METHODS

Pelagic juvenile rockfish species complexes

Rockfishes (genus *Sebastes*) are a speciose group of cold temperate fishes, most common in the Northeast Pacific (Love et al. 2002). Rockfishes undergo internal fertilization, bear live, feeding larvae, and have a gestation period that likely depends on water temperature (Sogard et al. 2008). Females of the rockfish species in this study are thought to release larvae once per season (Larson 1992; Gilbert et al. 2006). Two groupings of nearshore rockfishes are common settlers to rocky reefs in the study region, each with a distinct set of shared morphological and early life-history characteristics.

The OYTB group consists of three species, olive, yellowtail, and black rockfishes (*Sebastes serranoides*, *S. flavidus* and *S. melanops*, respectively). All share similar larval characteristics including larval release during the winter, pelagic duration ranging from 3.5–4 months and large size at settlement (2.8–5cm TL). This group settles from early to late spring in central California (Anderson 1983; Carr 1991; Ammann 2004) and from spring through the summer, with most settlement occurring in the late spring, in the Channel Islands (Love et al. 2002; Caselle et al. 2010).

The KGBC group includes kelp, gopher, black-and-yellow and copper rockfishes (*Sebastes atrovirens*, *S. carnatus*, *S. chrysomelas*, and *S. caurinus*). These species range from Alaska (*S. caurinus*) or northern California (the other three species) in the north to central Baja California in the south. KGBC rockfish release larvae from late winter through spring and following larval durations of approximately 1–3 months (Moser 1996; Gilbert 2000), fish settle to kelp canopy and rocky reef habitat at lengths of less than 2cm total length (TL). Settlement of these species occurs from late spring through late summer (Anderson 1983; Carr 1991; Love et al. 2002; Ammann 2004; Caselle et al. 2010) with the majority of settlement occurring in June through August (Ammann 2001; Caselle et al. 2010; Carr and Caselle, unpublished data). Although there is evidence that timing of delivery of *S. caurinus* may be as similar to that of the OYTB complex as it is to the other members of the KGBC complex in central CA (Anderson 1983; Carr 1991), previous work (Ammann 2004) suggests that this species responds to oceanographic drivers more similarly with the KGB group than with the OYTB, perhaps reflecting more similar life history attributes and larval processes. For this reason, and because their timing of settlement overlaps substantially with *S. carnatus* and *S. chrysomelas* in central California, and overlaps completely with members of this complex in the Channel Islands, we included them in the "KGBC" group for analyses.

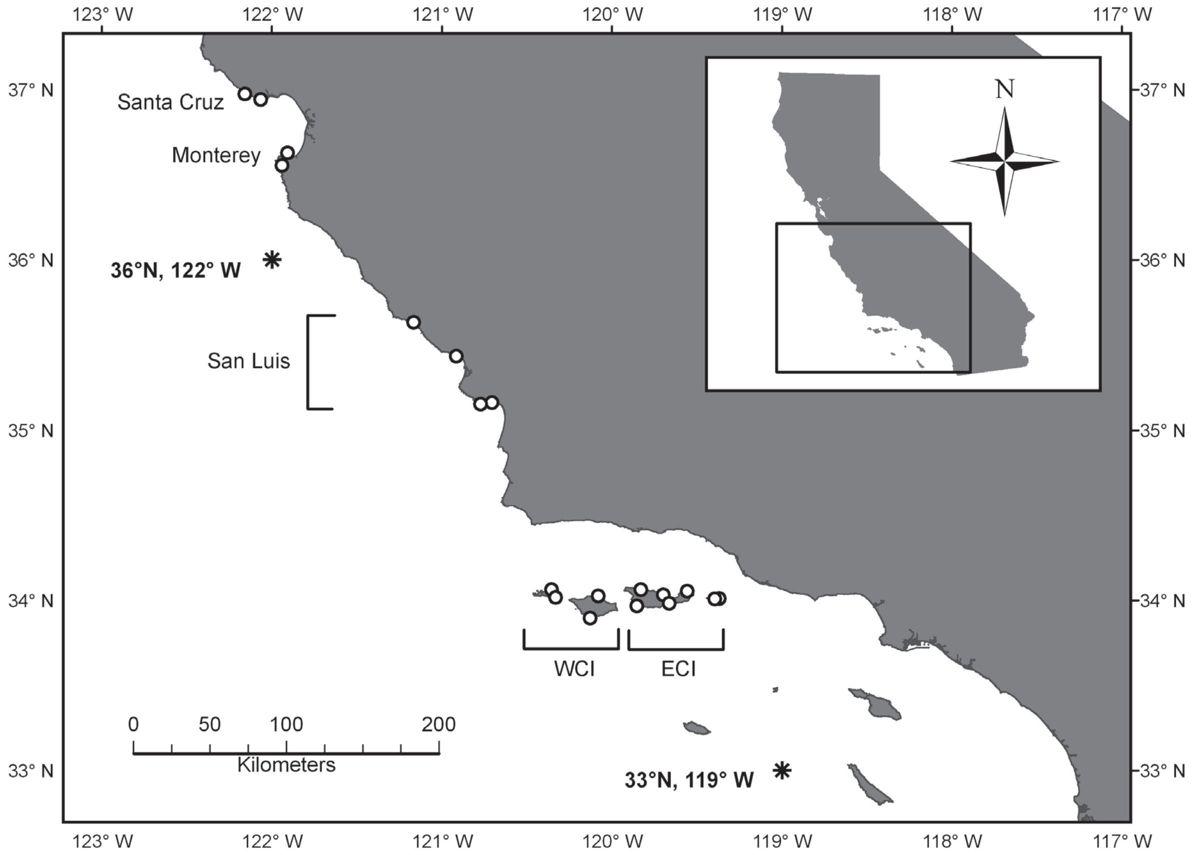

Figure 1. Map of study area. Gray circles show locations of settlement collection sites within each location. West Channel Islands (WCI) sites are on San Miguel and Santa Rosa and East Channel Islands (ECI) sites are on Santa Cruz and Anacapa. Stars mark the locations for the ocean indices: Southern California (So Cal:119W 33N) and Central California (Cen Cal: 122W 36N).

We present settlement data from these taxonomic groupings because (1) their combined abundances provide stronger statistical power to detect temporal and geographical patterns, (2) it is not possible to visually distinguish between all species within each group (e.g., gopher, [*Sebastes carnatus*], and black and yellow, [*Sebastes chrysomelas*], rockfish) and genetic analyses have not been completed for all samples, and (3) the species are treated as complexes in some fisheries (e.g., California recreational nearshore fishery).

Settlement to SMURFs

We monitored arrival of newly settled rockfishes on artificial collectors known as SMURFs (Standard Monitoring Units for Recruitment of Fishes; Steele et al. 2002; Ammann 2004) at 5 locations in California (fig. 1). Rates of settlement to SMURFs provide measures of delivery of competent larvae or pelagic juveniles in close proximity to adult populations, but independent of, and not confounded by, the availability and quality of nearby settlement habitat (Steele et al. 2002; Ammann 2004). Nonetheless, settlement to SMURFs can also correlate with recruitment to reefs as measured by visual surveys (Ammann 2001). Throughout this paper, we use the term 'settlement' to SMURFs to mean the rate at which young fish appear on the SMURFs and we interpret these measures as rates of onshore delivery of pelagic juveniles to the site where SMURFs are located.

All SMURFs were placed on individual mooring lines approximately 100–500 m from one another and 50–200 m offshore of kelp beds at sites where kelp was present, or 200–500 m from shore at sites where no kelp was present. Moorings were located in approximately 15 m of water depth and SMURFs were placed 3 m below the surface buoy. We sampled several sites within each location, ranging from 2 in Monterey and Santa Cruz to 7 in the East Channel Islands (fig. 1). Within each site, from three to eight replicate SMURFS were sampled. The sampling interval, the seasonal timing of collections, and the number of years sampled also varied slightly between locations. In the East Channel Islands (ECI), West Channel Islands (WCI) and San Luis locations, we removed fish settlers from each SMURF biweekly, while in Monterey and Santa Cruz sampling was approximately weekly. Earlier studies with daily sampling regimes indicated that biweekly sampling is suffi-

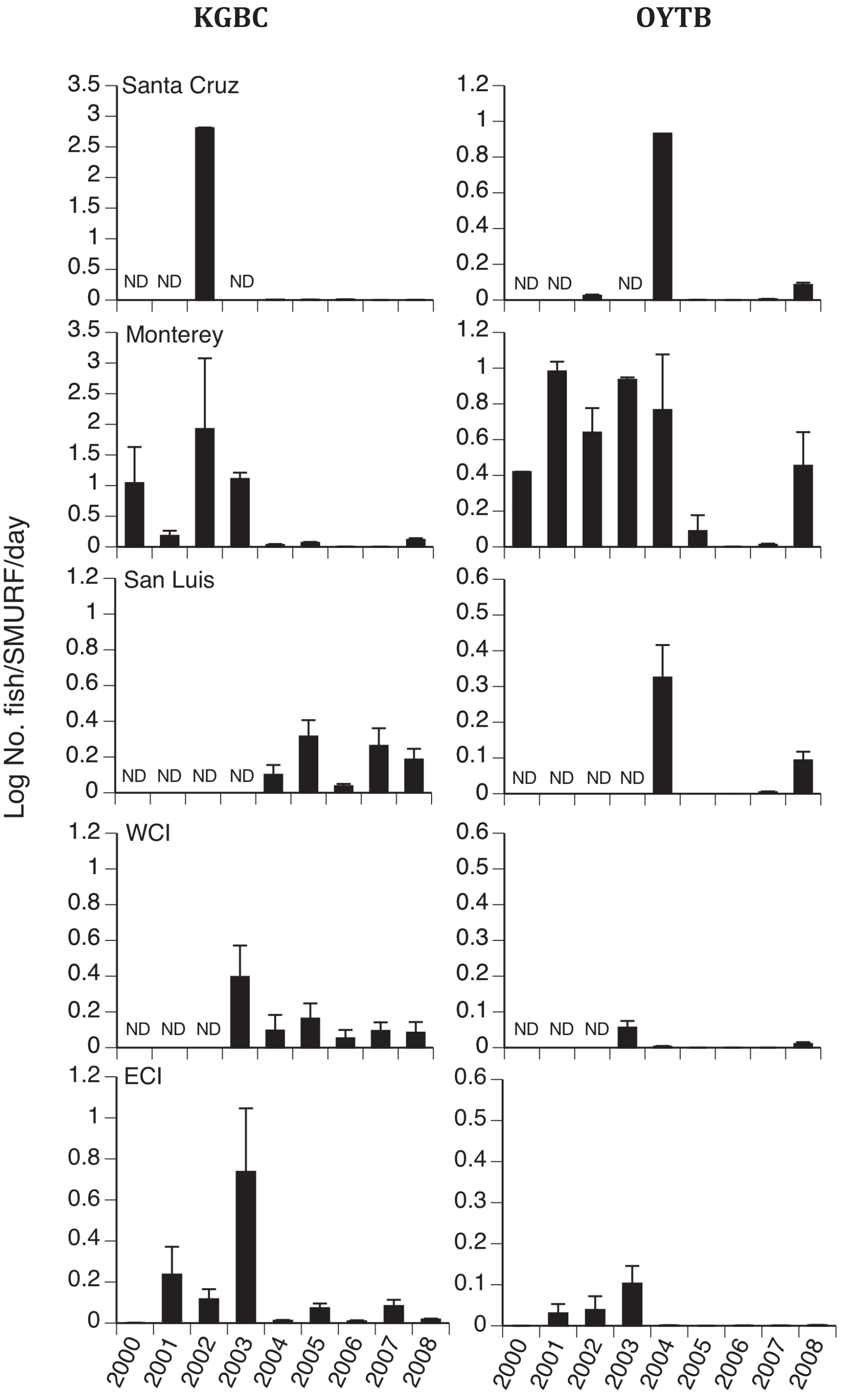

Figure 2. Mean number of settlers per SMURF per day + 1 SE (untransformed data) for KGBC (left panels) and OYTB (right panels). ND indicated = No data. Note different scales for y-axes.

ciently frequent to minimize post-settlement mortality on a SMURF (Steele et al. 2002; Ammann 2004). While variation in the sampling interval is unlikely to influence the relative abundance and interannual patterns of settlement, it may influence the number of fish settling and caution is suggested in comparing the absolute magnitude of settlement (i.e., rates of delivery) among sites. Sampling at all locations commenced in early- to mid-April and concluded in mid- to late-October. Sampling began in 2000 in Monterey and ECI followed by Santa Cruz in 2002, WCI in 2003 and San Luis in 2004. Years with missing data are noted on Figure 2.

Time series of oceanographic variables

We generated monthly means of four coastal oceanographic variables (hereafter referred to as "ocean indices") to test for relationships with regional interannual variation in settlement. These were offshore and alongshore components of upwelling, sea surface temperature (SST) and satellite derived estimates of Chlorophyll-a (Chl-a) concentration at the sea surface. Chl-a concentration was used as a near-term (monthly) proxy of productivity as it relates to availability of prey (i.e., zooplankton abundance). Upwelling indices were obtained from NOAA Fisheries Southwest Fisheries Science Center's Environmental Research Division (formerly the Pacific Fisheries Environmental Laboratory, publically available at http://www.pfel.noaa.gov/, Schwing et al. 1996) at 2 locations chosen to represent regional-scale variation around the settlement locations (fig. 1, southern California ('So Cal'): 119W 33N and central California ('Cen Cal'): 122W 36N). Chl-a and SST indices were calculated for the same locations (details below). These locations are 2 of 15 'historical' locations where ocean indices are routinely calculated and made accessible online (Perez-Brunius et al. 2007).

We used time series of both the offshore and alongshore components of upwelling. The magnitude of the offshore component of upwelling is considered to be an index of the amount of water upwelled from the base of the Ekman layer. Positive values are, in general, the result of equatorward wind stress. Negative values imply downwelling, the onshore advection of surface waters accompanied by a downward displacement of water. We refer to this index as the 'Bakun Index' throughout. We also used values for the alongshore component of upwelling with positive values indicating equatorward transport and negative values indicating poleward transport.

We used satellite-based measurements of SST and Chl-a concentration to develop indices of the thermal environment and phytoplankton abundance from the same two locations. To create the SST time series, we used weekly composite of daytime SST from NOAA Advanced Very-High-Resolution Radiometer (AVHRR) 18-km gridded satellite images (available at http://poet.jpl.nasa.gov/). We then calculated the mean monthly SST in a 1×1 degree box centered on each of the locations for direct comparison with the upwelling indices.

We described pelagic primary productivity in the 2 regions of interest using surface chlorophyll a (Chl-a) concentration from SeaWiFS (sea-viewing Wide Field-of-View Sensor, GeoEye, Dulles, Virginia, USA). We used the 8d, 4km standard mapped images available for research use (http://oceancolor.gsfc.nasa.gov/SeaWiFS/). Values of the Chl-a concentration derived parameter were again averaged over a 1×1 degree box centered on each the two locations and interpolated to a daily time interval. From that time series we calculated monthly averages.

Tests of relationships between oceanographic variables and settlement

Annual settlement density is expressed as the mean number of fish/SMURF/day to account for the differences among locations in sample interval and/or replication. In order to better visualize and test for coherence among locations and species groups over time, we standardized settlement density for each location as follows:

Log (Annual Mean) – Log (Grand Mean) /
Log (Standard Deviation of Grand Mean).

We used this standardized index of settlement in pairwise correlations among locations for each species group.

To investigate regional variation in interannual relationships between settlement and ocean indices, we first calculated pairwise Pearson correlation coefficients between mean annual settlement (log10 + 1 transformed, not standardized) for each species group at each location and the monthly averages of the four ocean indices. The log transform improved normality and reduced heterogeneity in variance. We used monthly averages for January through August, corresponding to times ranging from egg production through the period when the majority of settlement to SMURFs occurs for these species. Although SMURF sampling continued through October, very little settlement occurred after August in any year at any location (this study and see Ammann 2004; Wilson et al. 2008; Caselle et al. 2010). Here we present only the results of correlations between settlement to SMURFs at the three northern locations (i.e., San Luis, Monterey and Santa Cruz) with central California indices (Cen Cal: 122W 36N) and the two Southern locations (i.e., WCI and ECI) with southern California indices (So Cal: 119W 33N). We did not statistically correct for multiple comparisons (e.g., Bonferroni type corrections) because we are simply interested in the relative strength of the correlations and not statistical significance, *per se*. A number of monthly ocean indices were significantly correlated with settlement and we next used these significant variables in stepwise multiple regression models to assess the relative importance of particular indices across regions to assess their relative applicability to predicting interannual variation. Finally, we asked whether a composite of those ocean indices is a better predictor of settlement than any single, highly correlated variable. Using only data from the two locations with the longest time series,

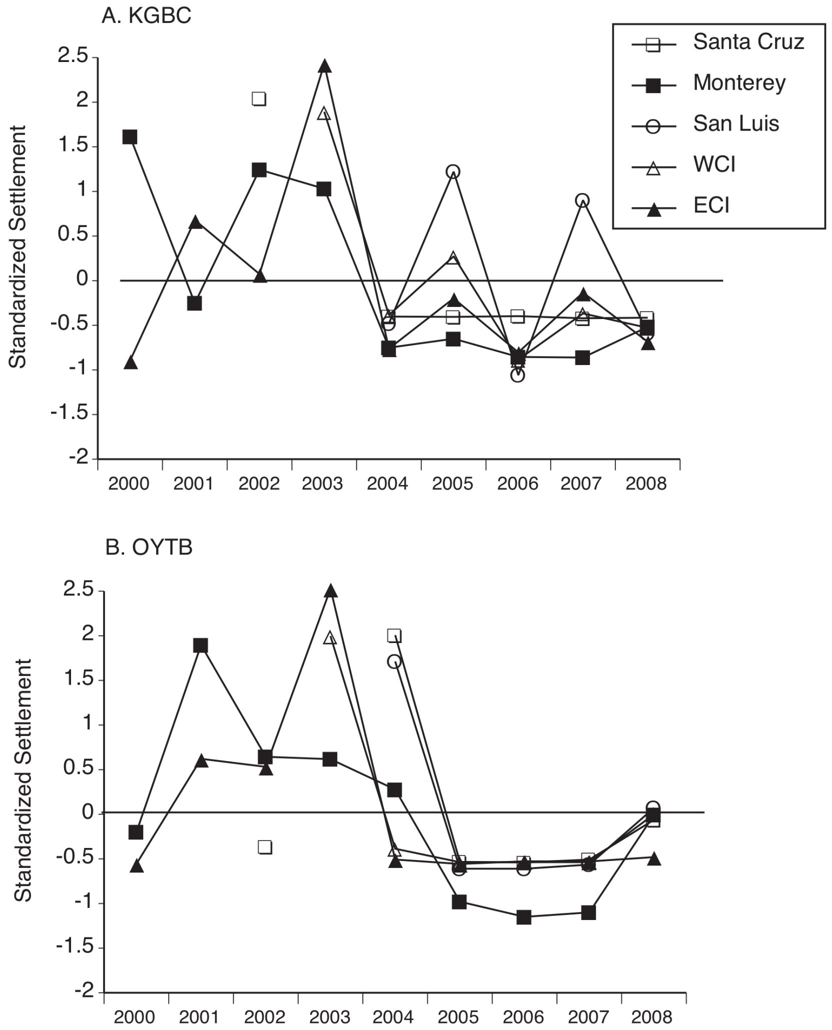

Figure 3. Standardized number of fish per SMURF per day for A. KGBC and B. OYTB. Standardization is described in the methods. Site legend is the same for both panels.

ECI and Monterey, we combined all individual variables that were significant in pairwise correlations into a single index using principal component analysis. The first principal component and the best single predictor (that with the highest correlation in the pairwise tests) were regressed against settlement and we compared the R^2 of the two relationships.

RESULTS

Spatial and temporal variation

Settlement of both groups of nearshore rockfishes was characterized by large interannual fluctuations (fig. 2). Most locations had one or a few strong years and little to no settlement in other years. The year of peak settlement differed among locations and species groups. Focusing on the two sites with a complete time series (Monterey and ECI sampled from 2000–2008) indicates that on average, settlement was higher prior to 2003, declining to low levels in 2004 (OYTB at ECI and KGBC at both locations) or 2005 (OYTB in Monterey) and remaining low. Although absolute abundance of settlers should be interpreted with some caution due to slight sampling differences, both species groups settle in greater numbers to the two northernmost locations (Monterey and Santa Cruz) compared with San Luis, ECI and WCI (fig. 2). OYTB rockfish, in particular settle in very low numbers in the two Channel Islands locations.

Standardized settlement densities allow easier visualization of temporal trends among locations (fig. 3). Again, most locations showed very low settlement of both species groups during the second half of the time series relative to the first part of the study. During the first half of the study, the peak years of settlement differed

TABLE 1
Pairwise Pearson correlation coefficients of standardized annual rockfish settlement among locations for A) KGBC and B) OYTB.

A. KGBC	Santa Cruz	Monterey	San Luis	WCI
Monterey	0.97**	.	.	.
San Luis	–0.49	0.02	.	.
WCI	–0.19	0.91*	0.84	.
ECI	0.62	0.41	0.96**	0.94**

B. OYTB	Santa Cruz	Monterey	San Luis	WCI
Monterey	0.68	.	.	.
San Luis	0.99***	0.90*	.	.
WCI	0.30	0.67	0.40	.
ECI	–0.15	0.58	0.55	0.98***

* $p<0.05$, ** $p<0.01$, *** $p<0.001$

between locations and species groups (fig. 3). Settlement of the KGBC group in Monterey was highest in 2000 and 2002 while in the ECI, settlement of this group was high in 2001, peaked in 2003 and was low in 2000 and 2002 (fig. 3A). For the OYTB group, settlement was more similar between the Monterey and ECI locations with high settlement density from 2000 through 2003 (for ECI) or 2004 (Monterey) and low to no settlement following those years (fig. 3B).

Settlement was significantly correlated between the two southern locations, WCI and ECI for both taxonomic groups (tab. 1A, B). Settlement to the two northernmost locations, Monterey and Santa Cruz, was significantly correlated for the KGBC group (tab. 1A) but not for the OYTB group (tab. 1B). The lack of a correlation for the OYTB group was driven by very low settlement in Santa Cruz in 2002. Sampling at Santa Cruz that year commenced relatively late in the summer, potentially resulting in an underestimate of OYTB settlement, which tends to occur in late spring/early summer. Settlement to the central location, San Luis, was more strongly correlated to the two southern locations for KGBC and to the northern locations for the OYTB group (tab. 1A, B). It must be noted the time series at San Luis was the shortest in the study (5 years) and occurred only during a period of apparently low settlement of both rockfish groups throughout the study region. In addition to spatial coherence between the WCI and the ECI for a given species complex, the two complexes settle contemporaneously at these locations but show more complex patterns and less coherent patterns at the three other locations (fig. 3).

Oceanographic proxies for settlement

Upwelling was greater, on average, from 2000 to 2003 and declined in both regions beginning in 2004 (fig. 4A, Mean Bakun index both regions: 2000–2003 = 138, 2004–2008 = 116). From 2000–2002, peak upwelling was greatest in the Cen Cal region (usually in June and July) while in subsequent years peak upwelling was equal or greater in the So Cal region (usually in April, May or June). Alongshore transport tended to be positive (equatorward) in the Cen Cal region and negative (poleward) in the So Cal region throughout the study period (fig. 4B). Chl-a concentration was greater on average as well as more variable in the Cen Cal region relative to So Cal but showed no obvious temporal trends over the study period (fig. 4C). SST was consistently lower in Cen Cal than in So Cal and increased slightly after 2002 in both regions (fig. 4D, Mean SST Cen Cal: 2000–2002 = 16°C, 2003–2008 = 16.5°C, So Cal: 2000–2002 = 13.3°C, 2003–2008 = 14.0°C).

Upwelling and alongshore transport were more strongly correlated with annual settlement of both taxonomic groups than SST or Chl-a (tab. 2, tab. 3). In addition, these indices for the summer months tended to correlate with settlement more strongly than either winter or spring months. Finally, we found stronger correlations between ocean indices and settlement for the KGBC group than for the OYTB group. The exception was at the two Channel Islands locations where settlement of both species groups was highly correlated and similarly related to the upwelling.

In the southern locations (ECI and WCI), the Bakun index in the summer months of June, July and August was strongly and positively related to settlement of both KGBC and OYTB groups (tab. 2, 3) respectively. In the ECI, KGBC settlement was also correlated with Chl-a in August, while OYTB settlement was significantly correlated with alongshore transport in May and June and Chl-a in August. In the WCI, KGBC settlement was positively correlated with alongshore transport in June and Chl-a in May, while OYTB settlement did not relate to any other indices beyond the Bakun index.

At the San Luis location, KGBC settlement was negatively related to Chl-a levels in July and August; no other indices were correlated (tab. 2). Interestingly, OYTB settlement at this location showed no significant correlations with any index (tab. 3).

Settlement of KGBC at Monterey and Santa Cruz was strongly and positively correlated with the Bakun

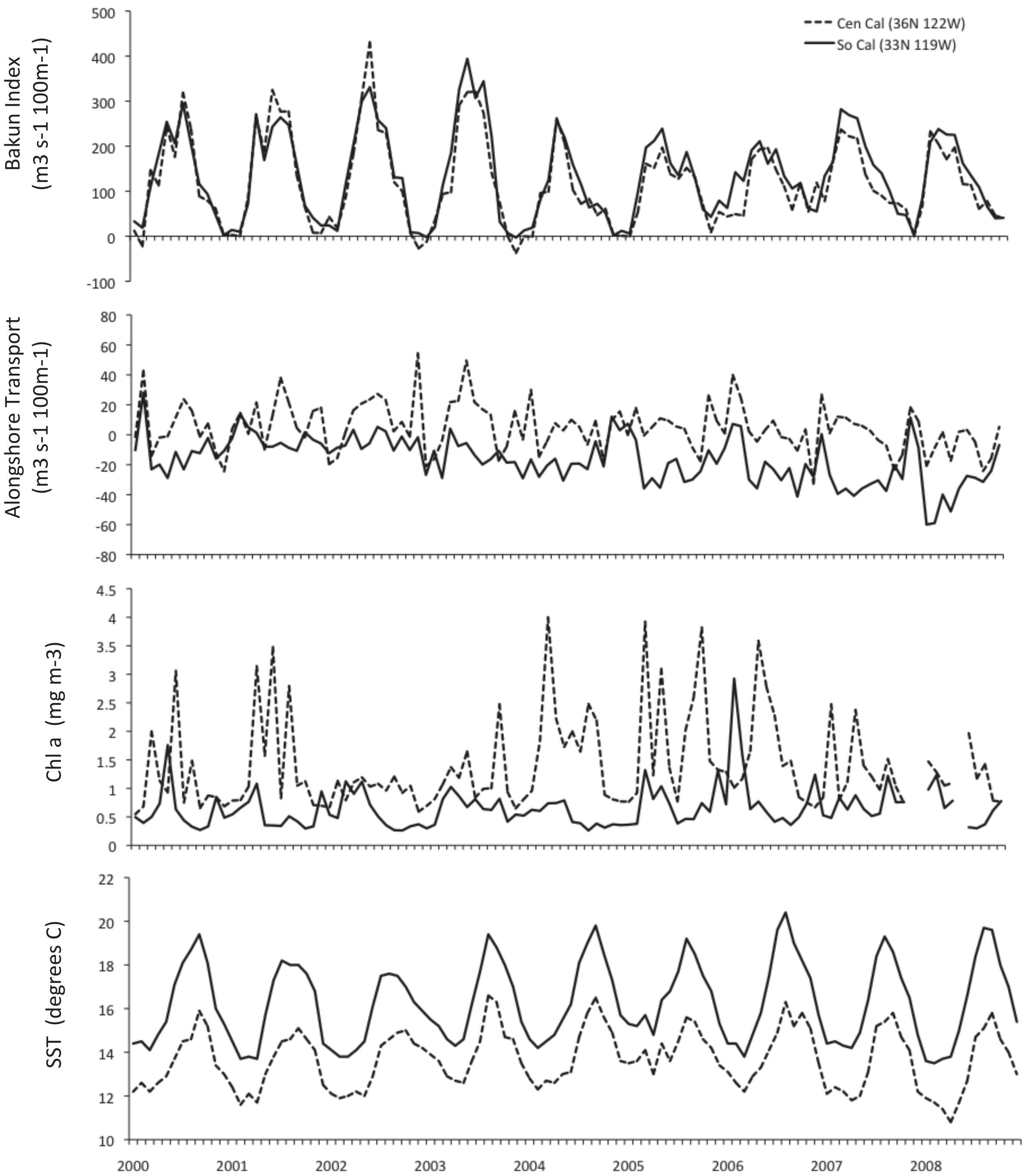

Figure 4. Time series of monthly averages of physical oceanographic indices. A) Offshore Ekman transport (Bakun index) (m^3 s^{-1} 100m coastline^{-1}), B) Alongshore Ekman transport (m^3 s^{-1} 100m coastline-1), C) Chl-a concentration (mg m^{-3}), D) Sea surface temperature (SST) (degrees C).

index in summer months, the same pattern found in the Channel Islands locations (tab. 2). This was not the case for the OYTB group (tab. 3). In marked contrast to the strong positive correlation of OYTB settlement with upwelling in the Channel Islands, OYTB settlement was not significantly correlated with the Bakun index at either Monterey or Santa Cruz. OYTB settlement did correlate with alongshore transport in July and August at Monterey. With the exception of the KGBC group in the Monterey, SST was not a good predictor of settlement for either group in any location.

Multiple regression allowed us to assess the relative importance of particular indices identified in the correlation analysis (tab. 4). For both species groups and most locations, upwelling during summer months explained the majority of variance in settlement, with partial R^2

TABLE 2

Pearson correlation coefficients of annual rockfish settlement (log10 + 1 transformed) and mean monthly oceanographic indices from January through August for KGBC at five locations. ECI and WCI locations show correlations with So Cal indices while San Luis, Monterey and Santa Cruz show correlations with Cen Cal indices.

Month	J	F	M	A	M	J	J	A
Bakun Index								
Santa Cruz	0.067	–0.239	–0.208	0.195	0.749	0.995	0.784	0.882
Monterey	–0.269	–0.426	0.011	–0.141	0.681	0.475	0.802	0.745
San Luis	0.245	–0.095	–0.062	0.625	–0.114	0.466	–0.223	–0.092
WCI	–0.601	–0.475	–0.357	0.056	0.780	0.943	0.897	0.812
ECI	–0.459	–0.242	–0.239	0.234	0.447	0.873	0.618	0.841
Alongshore transport								
Santa Cruz	–0.416	–0.683	–0.058	0.365	0.862	0.692	0.937	0.955
Monterey	–0.329	–0.136	–0.337	0.105	0.342	0.624	0.626	0.736
San Luis	–0.357	0.060	–0.003	–0.157	0.588	0.749	0.528	–0.489
WCI	–0.194	0.010	–0.081	0.362	0.726	0.856	0.511	0.401
ECI	–0.236	–0.153	0.051	0.444	0.646	0.568	0.375	0.115
Chl-a concentration								
Santa Cruz	–0.361	0.360	–0.478	–0.305	–0.230	–0.518	–0.526	–0.419
Monterey	–0.576	–0.242	–0.145	–0.391	–0.490	–0.244	–0.677	–0.339
San Luis	–0.802	–0.917	0.216	0.253	–0.474	0.164	–0.957	–0.969
WCI	–0.729	–0.820	–0.393	–0.220	0.865	–0.264	0.741	0.764
ECI	–0.420	–0.360	–0.184	–0.047	–0.201	–0.317	0.489	0.853
SST								
Santa Cruz	–0.360	–0.376	–0.228	–0.003	–0.343	–0.329	–0.656	–0.720
Monterey	–0.044	0.107	–0.115	0.165	–0.220	0.023	–0.671	–0.317
San Luis	0.161	0.620	0.639	0.137	0.290	–0.099	–0.005	–0.402
WCI	0.776	0.697	0.453	–0.094	–0.372	–0.517	–0.701	–0.364
ECI	0.613	0.372	0.168	–0.362	–0.401	–0.318	–0.440	–0.170

P<0.05 P<0.001

values as high as 0.99 (tab. 4). This result was particularly strong for the KGBC group compared to the OYTB group, in particular for the Channel Islands locations relative to the other more northern sites.

For the two sites with complete time series (ECI and Monterey), we asked whether a composite of multiple monthly indices was a better 'proxy' for settlement than any single monthly variable. To do this, we created an index using principal components analysis on all significant single monthly correlates (from tabs. 2 and 3) and compared that with the best single predictor by comparing R^2 values from regressions (figs. 5 and 6). Since the monthly ocean indices tend to correlate with one another, PC1 loadings were quite high (60%–90%). In the ECI, we compared the strength of the relationships between settlement vs. PC1 and settlement vs. June upwelling for the KGBC complex (fig. 5A–B) and settlement vs. PC1 and settlement vs. August upwelling for the OYTB complex (fig. 5C–D). Although all fits were good, settlement was more strongly related to the composite variable (PC1) than the single best predictor variable in all cases. This was particularly true for KGBC (fig. 5A–B: $R^2 = 0.92$ for PC1 vs. 0.76 for June Bakun Index). For Monterey, we contrasted PC1 vs. July Bakun Index for KGBC settlement (fig. 6A–B) and PC1 vs. July alongshore for OYTB settlement (fig. 6C–D). For the KGBC group both relationships were strong and significant and the difference between the R^2 values was negligible (fig. 6A–B: $R^2 = 0.77$ for PC1 vs. 0.74 for July Bakun Index). For OYTB in Monterey, both relationships were poor and R^2 values were equal (fig. 6C–D $R^2 = 0.36$ for both).

DISCUSSION

Spatial and temporal variation

Similar to previous studies (reviewed in Carr and Syms 2006), we found that settlement of two nearshore rockfish groups was highly variable among years. Yet notably, the 9 years of this study did not encompass any large climatic events such as ENSO (El Niño Southern Oscillation), which have previously been linked to extreme fluctuations in rockfish settlement and recruitment (Norton 1987; Lenarz et al. 1995; Ralston and Howard 1995; Carr and Syms 2006). We also documented good spatial coherence in interannual patterns of settlement for both species groups among the closely located study locations such as ECI–WCI and Monterey–Santa Cruz.

TABLE 3

Correlation coefficients of annual rockfish settlement (log10 + 1 transformed) and mean monthly oceanographic indices from January through August for OYTB at five locations. ECI and WCI locations show correlations with So Cal indices while San Luis, Monterey and Santa Cruz show correlations with Cen Cal indices.

Month	J	F	M	A	M	J	J	A
Bakun Index								
Santa Cruz	–0.449	–0.453	0.024	–0.317	0.382	–0.160	–0.532	–0.539
Monterey	–0.512	–0.370	–0.046	0.369	0.372	0.659	0.472	0.646
San Luis	–0.479	–0.465	0.080	–0.244	0.765	0.170	–0.680	–0.820
WCI	–0.538	–0.313	–0.083	–0.007	0.790	0.929	0.925	0.902
ECI	–0.465	–0.344	–0.248	0.079	0.517	0.893	0.693	0.912
Alongshore transport								
Santa Cruz	0.027	0.590	–0.543	–0.508	–0.055	–0.126	0.006	–0.197
Monterey	–0.063	–0.142	–0.443	0.222	–0.110	0.372	0.818	0.708
San Luis	–0.012	0.639	–0.631	–0.542	0.146	–0.096	0.429	–0.141
WCI	–0.208	–0.335	–0.293	0.417	0.683	0.797	0.404	0.211
ECI	–0.252	–0.215	0.024	0.565	0.734	0.674	0.491	0.253
Chl-a concentration								
Santa Cruz	–0.110	–0.088	0.309	0.592	0.817	–0.337	0.191	0.194
Monterey	–0.316	–0.192	–0.336	0.224	0.179	–0.204	–0.552	0.366
San Luis	–0.200	–0.024	0.260	0.534	0.760	–0.593	0.107	0.174
WCI	–0.531	–0.540	–0.135	–0.158	0.643	–0.648	0.602	0.729
ECI	–0.461	–0.312	–0.067	–0.082	–0.072	–0.425	0.370	0.743
SST								
Santa Cruz	0.040	–0.217	0.025	0.070	0.008	–0.277	–0.070	0.178
Monterey	–0.118	–0.438	–0.264	–0.307	–0.224	–0.067	–0.604	–0.376
San Luis	–0.104	–0.389	–0.090	–0.028	–0.131	–0.437	–0.266	–0.004
WCI	0.475	0.370	0.011	–0.323	–0.637	–0.459	–0.441	–0.089
ECI	0.500	0.253	–0.002	–0.345	–0.511	–0.336	–0.424	–0.218

P<0.05 P<0.001

TABLE 4

Results of multiple stepwise regressions of significant variables from pairwise correlations (Table 2 for KGBC, Table 3 for OYTB) on annual rockfish settlement of A. KGBC and B. OYTB.

A. KGBC

Site	Variable	Model Step	Sign	Partial R-Square	Model R-Square	F Value	Pr>F
Santa Cruz	Upwelling June	1	(+)	0.9904	0.9904	414.26	<.0001
	Alongshore transport May	2	(-)	0.0079	0.9983	13.97	0.0334
Monterey	Upwelling July	1	(+)	0.6428	0.6428	12.6	0.0094
San Luis	Chl-a conc. August	1	(-)	0.9333	0.9333	27.99	0.0339
WCI	Upwelling June	1	(+)	0.8893	0.8893	32.13	0.0048
	Chl-a conc. May	2	(+)	0.1067	0.996	79.6	0.003
	Alongshore transport June	3	(-)	0.0037	0.9997	23.84	0.0395
ECI	Upwelling June	1	(+)	0.7624	0.7624	22.46	0.0021
	Chl-a conc. August	2	(+)	0.1494	0.9119	10.17	0.0189

B. OYTB

Site	Variable	Model Step	Sign	Partial R-Square	Model R-Square	F Value	Pr>F
Santa Cruz	Chl-a conc. May	1	(+)	0.6681	0.6681	8.05	0.047
Monterey	Alongshore transport July	1	(-)	0.6699	0.6699	14.21	0.007
San Luis	N/A						
WCI	Upwelling June	1	(+)	0.863	0.863	25.21	0.0074
ECI	Upwelling August	1	(+)	0.8326	0.8326	34.81	0.0006
	Upwelling June	2	(+)	0.0837	0.9162	5.99	0.0499

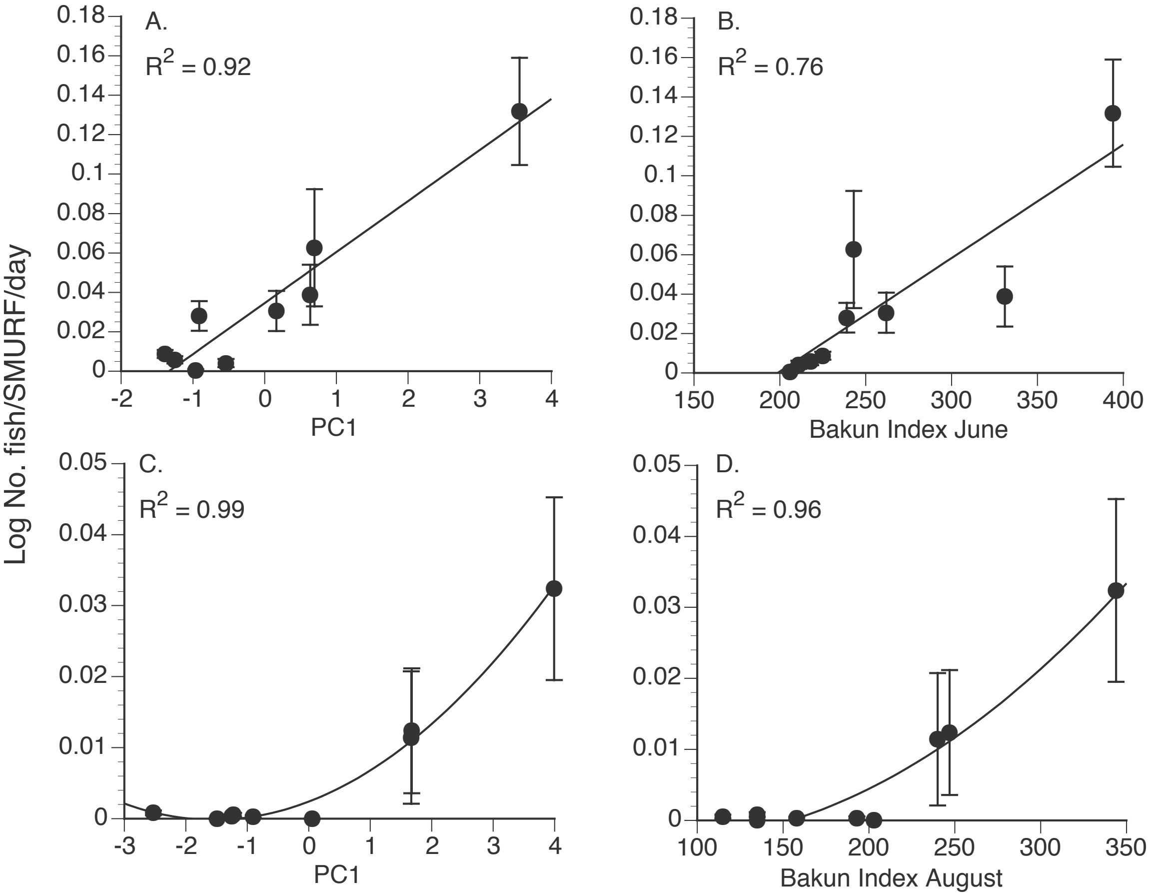

Figure 5. Comparisons of the performance of PC1 versus individual predictors for the East Channel Islands location (ECI). A) Settlement (log No. fish/ SMURF/ day) of KGBC vs. principal component 1 (PC1 of significant individual correlates for a given species group and location-see methods), B) Settlement of KGBC vs. Bakun index June, C) Settlement of OYTB vs. PC1, D) Settlement of OYTB vs. Bakun index August. R^2 values are shown.

Correspondence in the interannual patterns among larger regions (e.g. sites south of Pt. Conception versus sites north of Pt. Conception), which span a distance of approximately 400 km, were generally weaker. While we know of no other studies that compare settlement patterns of fishes in both Central and Southern California, the regional differences we see here corroborate regional differences in temporal patterns of recruitment among intertidal invertebrates recorded across the same geographic range (Broitman et al. 2008).

Although correlations between distant locations were weaker than closely spaced locations, the interannual patterns of settlement to SMURFs were broadly synchronous over time across the entire study region in that both species groups exhibited very little or no settlement in the later years of the study. The two locations with the longest times series (ECI and Monterey) show a precipitous decline in settlement beginning in 2004 or 2005. This was notable for the OYTB group in which settlement failed between 2004–2008 in the southern locations and between 2005–2007 in the northern locations. The lack of continuous SMURF settlement data from the other locations (WCI, San Luis and Santa Cruz) prior to 2003–2004 makes it difficult to assess the degree to which settlement may have declined at those locations relative to earlier years. However, interannual patterns of recruitment to kelp forests measured by SCUBA surveys (beginning in 2000 and corresponding to sites in Santa Cruz, Monterey and San Luis in this study) were similar to those observed from SMURFS and reflected the overall decline in the later years of this study even at sites with no SMURF sampling (Carr and Caselle, unpublished data, available at www.piscoweb.org). This is the first study to document coherent failures in rockfish settlement to nearshore areas at such large spatial scales.

The spatially extensive nature of the settlement failure likely indicates decline or failure in production and/or larval survival rather than changes in processes affecting larval transport or delivery, which are more likely to act at smaller spatial scales. Several studies have documented anomalous oceanographic conditions in the Northeast Pacific ocean in 2005 including delayed spring upwelling, increased water temperatures, low Chlorophyll-a, anomalous zooplankton concentrations and distributions as well as declines in recruitment of invertebrates and pelagic nekton (Brodeur et al. 2006; Schwing et al.

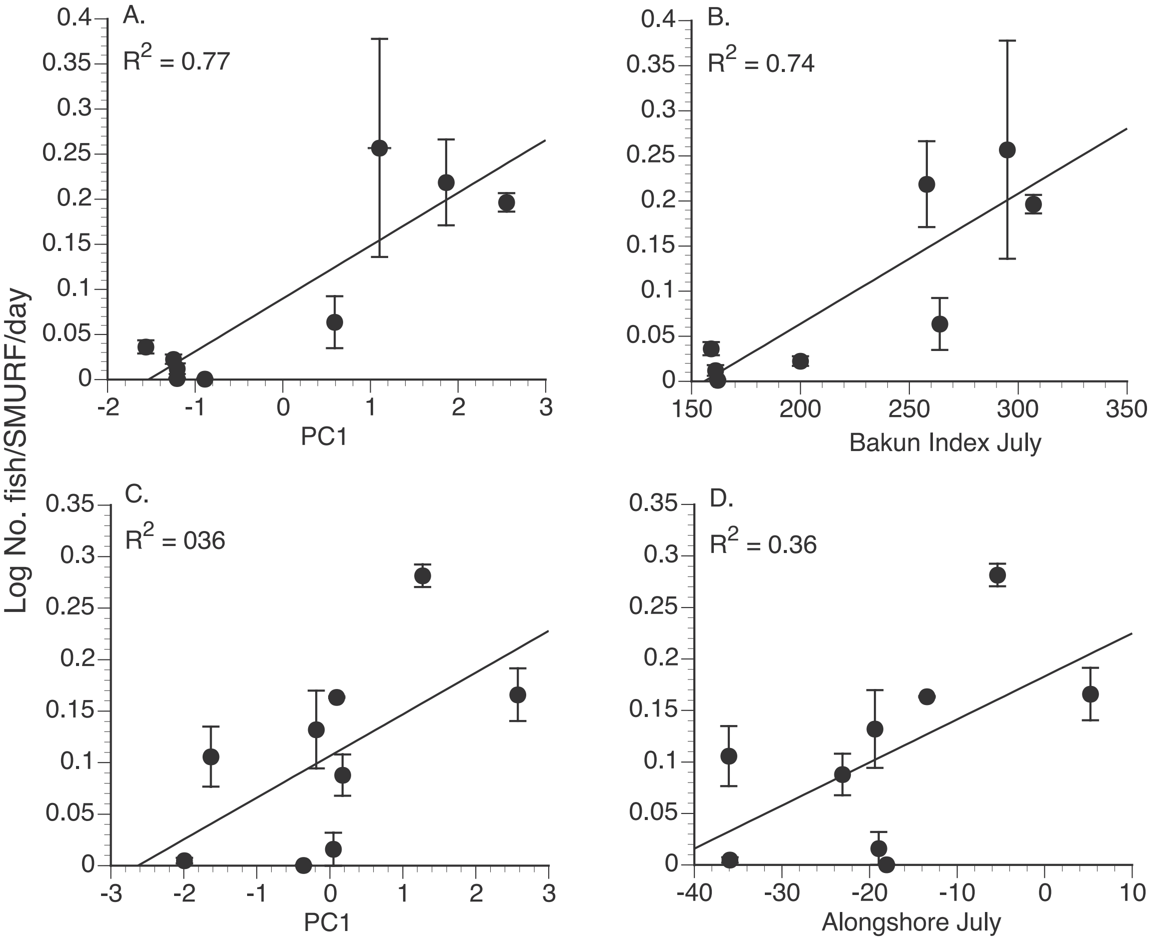

Figure 6. Comparisons of the performance of PC1 versus individual predictors for Monterey. A) Settlement (log No. fish/ SMURF/day) of KGBC vs. principal component 1 (PC1 of significant individual correlates for a given species group and location—see methods), B) Settlement of KGBC vs. Bakun index July, C) Settlement of OYTB vs. PC1, D) Settlement of OYTB vs. Alongshore transport July. R^2 values are shown.

2006; Barth et al. 2007). It appears from this study, that these anomalous conditions, especially those relating to late upwelling, also influenced survival and settlement of nearshore rockfishes. Further, our results indicate that the effects of conditions so well documented in 2005, continued in central and southern California at least until 2008, when settlement of the OYTB group recovered in the locations North of Pt. Conception.

Field and Ralston (2005) investigated the general assumption that, for populations with similar life histories and exposure to environmental variability, there is spatial synchrony in year class strength. They found broad spatial coherence in year class strength of winter spawning rockfishes (including yellowtail rockfish studied here) over scales of 500–1000 km. That study, which back-calculated year class strength from fishery landings data, and others (Hannah 1995; Hollowed and Wooster 1995; Botsford and Lawrence 2002) have suggested that large scale physical forcing mechanisms acting on scales of 1000s of kms are more important than regional or meso-scale processes in influencing recruitment to a fishery. However, the regional comparisons made by those studies are all to the north of Point Conception within an upwelling dominated section of the California Current. In contrast, the stronger regional differences in spatial synchrony of recruitment and oceanographic drivers that we observed in this and previous studies (Caselle et al. 2010), likely reflect our comparisons between regions to the north and south of Pt. Conception and the greater differences in conditions of the California Current, including upwelling dynamics.

While settlement failures were broadly coherent across all regions, during times of settlement, locations within regions tended to be more highly correlated to one another than across regions (e.g. WCI and ECI). While inferences from these comparisons are limited due to short time series at three of five locations, the strongest correlations within a region were between the two Channel Islands locations (i.e., south of Pt. Conception) for both species groups. Previous studies have documented a strong east-west gradient of environmental conditions over short geographic distances across the northern Channel Islands (Hickey et al. 2003; Broitman et al. 2005) resulting in differences in community structure (Blanchette et al. 2006; Blanchette et al. 2009; Hamilton et al. 2010) and recruitment (White and Caselle, 2008; Broitman et al. 2005) of both subtidal and intertidal organisms. Consequently, the eastern and western islands have a tendency to be treated as separate units when considering spatial management such as marine protected areas (Airamé et al. 2003). Despite differences in SST, productivity and exposure to storms between the eastern and western islands, we found very strong coherence in annual settlement in time and between species groups. This result has important implications for interpretation of changes to both populations and communities in a recently placed network of marine protected areas located in these islands (Hamilton et al. 2010).

Relationship to ocean environment

While a wide range of environmental parameters have been related to settlement of marine organisms, upwelling and downwelling circulation are among the more intensively studied processes for fishes and invertebrates in temperate coastal habitats (Norton, 1987; Ainley et al. 1993; Ralston and Howard 1995; Bjorkstedt et al. 2002; Mace and Morgan 2006). Previous work has also shown that year class strength for many rockfishes in the California Current system is likely set at some point during the larval phase (Ralston and Howard 1995; Yoklavich et al. 1996), prompting a number of studies focused on identifying environmental variables that may be related to the dispersal and survival of larvae, planktonic juveniles and settlers (Lenarz et al. 1995; Sakuma and Ralston 1995; Nishimoto and Washburn 2002; Laidig et al. 2007). For rockfishes, both the timing and the strength of coastal upwelling can influence successful recruitment and the relationships are complex (Yoklavich et al. 1996; Bjorkstedt et al. 2002). We found that a simple index of regional upwelling during summer months strongly correlated with rockfish settlement at locations both north and south of Pt. Conception, explaining more variance in combined models than indices of alongshore transport, SST or Chl-a. This study builds on earlier work that attempted to identify the spatial and temporal scales of influence of several oceanographic parameters on biweekly recruitment of nearshore rockfishes (similar to groups studied here) to the Santa Barbara Channel (Caselle et al. 2010). In that study, a number of wind-driven processes (e.g., Ekman upwelling and transport, Ekman pumping, and wind stress) were significantly related to settlement but with lags that varied between species groups (very short and very long for the KGB group, intermediate for the OYT group). In the simpler analyses done here, the Bakun index predicted settlement (more strongly for the KGBC group) but at relatively short lags for both groups. Unlike results of Laidig et al. (2007) in a study of rockfish recruitment to reefs in Northern California, we found that no ocean indices from winter or spring months (Jan through April) were correlated with settlement to any location. The strong positive relationship with the Bakun index occurring in the months directly preceding or even during settlement suggest that either the effects of upwelling on larval dispersal, delivery, or survival later in the pelagic stage are more important than effects on early larval phases and/or that the Bakun upwelling index, measured at regional scales is not a true measure of upwelling, *per se*, but describes or covaries with a number of processes that eventually determine larval settlement.

The coast of California is part of an Eastern boundary system characterized by persistent upwelling, especially from the Oregon border to Pt. Conception (Parrish et al. 1981). Coastal upwelling is typically described by low SST, high productivity and high offshore flow and can affect settlement of nearshore organisms negatively, by increasing offshore transport, or positively through increased availability of food resources. Whereas regions north of Pt. Conception are better characterized, fewer studies have documented oceanographic-recruitment correlations south of Pt. Conception (but see Stephens et al. 1984; Mearns et al. 1980; Broitman et al. 2005). South of Pt. Conception, the coastline runs in an east-west orientation, and although upwelling remains an important process, the typical pattern of upwelling-relaxation dynamics observed on the central and northern part of California (Davis 1985) is less prominent. Instead, wind-driven and other circulation processes interact with the unique geomorphology of the region to generate a variety of circulation patterns (Harms and Winant 1998). Thus, while the Bakun index measured at the central California location ("Cen Cal" in this study) may accurately reflect coastal upwelling (Bograd et al. 2009), the southern California index ("So Cal" in this study) may not represent upwelling per se (Perez-Brunius et al. 2007) but instead be a proxy for other processes that clearly relate to survival and/or transport of rockfish larvae in the region. The end result is that the Bakun upwelling index provides a very good proxy for settlement of these nearshore rockfish complexes in both the Monterey and the Channel Islands regions, although the actual mechanisms are likely to differ in the two regions.

In conclusion, our results suggest that simple oceanographic proxies can provide useful predictors of year-to-year variation in settlement of at least some nearshore rockfish species. However, the best oceanographic proxies for settlement varied both regionally and between species groups, indicating that a single metric applied across the entire range of a stock or for multiple species that differed markedly in key life history traits (e.g., larval duration, spawning season) would likely prove a poor predictor for regional patterns of settlement and recruitment of particular species. Nonetheless, our results suggest that such relationships, in contrast to the poor predictability of spawner-recruit relationships, could prove useful tools for forecasting year-class strength and population dynamics. The next step for these nearshore rockfish groups will be to determine the relationship between settlement variation and recruitment to the fishery. The growing time series used here and geographic extent of settlement monitoring will allow these relationships to be determined in the future. In conjunction with the increasing accessibility of ocean indices to fisheries ecologists and managers, their use for forecasting settlement, recruitment and year-class strength can greatly enhance our ability to adjust catch proactively to better correspond with stock dynamics. While we are not arguing here against pursuing a detailed mechanistic understanding of the causes of variation in larval delivery, settlement and recruitment, in the face of declining fisheries and ecosystems worldwide, the utility of simple, cheap and readily accessible proxies for these complex processes should not be ignored.

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