

## SPATIAL AND TEMPORAL PATTERNS OF INVERTEBRATE RECRUITMENT ALONG THE WEST COAST OF THE UNITED STATES

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**Abstract.** Patterns of recruitment in marine ecosystems can reflect the distribution of adults, dispersal by ocean currents, or patterns of mortality after settlement. In turn, patterns of recruitment can play an important role in determining patterns of adult abundance and community dynamics. Here we examine the biogeographic structure of recruitment variability along the U.S. West Coast and examine its association with temperature variability. From 1997 to 2004 we monitored monthly recruitment rates of dominant intertidal invertebrates, mussels and barnacles, at 26 rocky shore sites on the West Coast of the United States, from northern Oregon to southern California, a span of 1750 km of coastline. We examined spatial variation in the dynamics of recruitment rates and their relationship to coastal oceanography using satellite-derived time series of monthly sea surface temperature (SST). Recruitment rates showed a biogeographic structure with large regions under similar dynamics delimited by abrupt transitions. The seasonal peak in recruitment rates for both mussels and barnacles changed from a late summer–early fall peak in Oregon to winter or early spring in northern California, and then back toward summer in southern California. Recruitment rates varied greatly in magnitude across the latitudinal range. The barnacle *Balanus glandula* and mussels (*Mytilus* spp.) showed a decline of two orders of magnitude south of Oregon. In contrast, recruitment rates of barnacles of the genus *Chthamalus* showed a variable pattern across the region examined. The spatial distribution of associations between raw SST and recruitment rates for all species showed positive associations, indicating recruitment during warm months, for all species in Oregon, northern California, and several sites in south-central California. By considerably extending the spatial and temporal scales beyond that of previous studies on larval recruitment rates in this system, our study has identified major biogeographic breaks around Cape Blanco and Point Conception despite considerable spatial and temporal variation within each region and among species. These large differences in recruitment rates across biogeographic scales highlight the need for a better understanding of larval responses to ocean circulation patterns in the conservation and management of coastal ecosystems.

**Key words:** advanced very-high resolution radiometer (AVHRR) satellite; *Balanus glandula*; *Chthamalus* spp.; community structure; geographic variation; intertidal invertebrates; *Mytilus* spp.; recruitment; West Coast, USA.

### INTRODUCTION

Temporal and spatial variation in the availability of propagules is increasingly recognized as a strong ecological driver of population and community dynamics in a wide range of ecological systems (Roughgarden et al. 1988, Rees et al. 2001, Bolker et al. 2003, McCauley 2006). Although variability in recruitment

can be large and can drive correspondingly large variation in population size, the mechanisms underlying recruitment variation are often poorly understood (Gaines and Bertness 1992, Shima 1999, Morgan 2001, Hughes et al. 2002, Navarrete et al. 2005). In many cases, the source of the variation is presumed to be the interaction between the spatial distribution of adults and the scales of propagule dispersal (Hanski 1999). Sites that are distant from sources of propagules with limited dispersal potential may have chronically low recruitment (Tilman et al. 1997, Hanski 1999, Hughes et al. 2000). Scales of propagule dispersal vary enormously among species and locations (Clark et al. 1999, Nathan and

Manuscript received 30 October 2006; revised 9 November 2007; accepted 11 December 2007; final version received 23 January 2008. Corresponding Editor: J. J. Stachowicz.

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Muller-Landau 2000, Kinlan and Gaines 2003). Much of this variability is tied to characteristics of the propagules themselves (e.g., size, shape, behavior), but the physical setting into which propagules are released can be equally or more important. The prominent role of physical drivers of dispersal variability is especially true in the sea, where physical transport processes can play a critical role in the dispersal of planktonic larval stages from their natal populations (Roughgarden et al. 1988, Gaines and Bertness 1992, Leonard et al. 1998, Cowen et al. 2006). Since larval recruitment rates may ultimately determine the persistence of sessile adult populations and the predominant community regulation pathway, assessing the spatial patterns of ocean conditions that deliver larvae to shallow benthic habitats is particularly important for coastal ecosystem management and conservation (Underwood and Fairweather 1989, Menge 1991, Minchinton and Scheibling 1993, Airame et al. 2003).

Associations between large-scale gradients in ocean circulation processes and spatial variation in larval delivery rates have been found worldwide (Harris et al. 1998, Hughes et al. 1999, Connolly et al. 2001, Menge et al. 2003, 2004, Navarrete et al. 2005, Cowen et al. 2006). In several temperate regions, experimental evaluations have highlighted the linkage between recruitment rates and community regulation pathways (Menge et al. 2003, 2004, Navarrete et al. 2005). These studies suggest that shores experiencing persistent wind-driven offshore transport of surface waters tend to receive limited numbers of young from species with planktonic larvae. Consequently, space on the substratum is often unoccupied or dominated by algae, and top predators seem to play a limited role regulating community structure (Navarrete et al. 2005). In contrast, shores experiencing intermittent shoreward transport of surface waters may be dominated by filter-feeding invertebrates (Menge et al. 1997, 2003). In this oceanographic context predation can play a large role in determining community structure by freeing primary substrate that is otherwise monopolized by invertebrates (Menge et al. 2003, Navarrete et al. 2005).

Because of their large impact on coastal ecosystems, the circulation processes that may transport pelagic larvae to benthic habitats have received worldwide attention. Higher-frequency (hours to days) transport mechanisms such as tidal bores or internal waves (Shanks and Wright 1987, Pineda 1991) and river plumes (Vargas et al. 2006b) have been shown to influence larval delivery to shore at local and mesoscales. Due to its prominent role in large-scale ocean circulation along east boundary coastal ecosystems (Hill et al. 1998), coastal upwelling circulation has also received considerable attention as a larval transport mechanism at lower frequencies (days to weeks; Wing et al. 1995b, Poulin et al. 2002, Menge et al. 2003, dos Santos et al. 2007). During upwelling conditions, alongshore equatorward winds and the rotation of the earth displace

warmer surface waters offshore via Ekman transport, which are replaced by cold water emerging from deeper layers. When alongshore winds relax, coastal upwelling ceases and the warmer offshore waters usually move back toward the coast, generating downwelling and poleward coastal flow (Largier et al. 1993, Wing et al. 1995a). Larvae entrained in the surface layer are hypothesized to be swept offshore by Ekman transport during upwelling and collected in offshore frontal regions where they may remain in the surface or get moved to deeper waters (Roughgarden et al. 1988, Grantham 1997). This lower-frequency nearshore circulation pattern underlies two potential pathways for larval transport. First, if larvae remain in surface layers, they may be transported onshore through the sustained advection of the coastal front during relaxation from upwelling (Farrell et al. 1991, Shanks et al. 2000, Pfeiffer-Herbert et al. 2007). Second, if larvae are located in deeper layers, they may be transported through the shoreward movement of the bottom boundary layer during upwelling (Shanks et al. 2000, Garland et al. 2002, Shanks and Brink 2005). Although it has not been sufficiently explored, larvae could interact with these horizontal flow patterns by changing their vertical position (Garland et al. 2002, Poulin et al. 2002, Mace and Morgan 2006, Pfeiffer-Herbert et al. 2007).

Much of the research on larval transport mechanisms described in the preceding paragraphs was conducted in response to a hypothesis, the upwelling/relaxation hypothesis, about the manner in which spatial variation in the intensity of coastal upwelling might drive spatial variation in larval recruitment rates and consequently population dynamics of intertidal communities (Gaines et al. 1985, Roughgarden et al. 1988, Farrell et al. 1991, Alexander and Roughgarden 1996). The upwelling/relaxation hypothesis was later extended to an oceanographically based theory of community regulation (Connolly and Roughgarden 1999b) in which latitudinal variation in patterns of community structure were largely attributed to the latitudinal variation in the Coriolis effect and the intensification of equatorward winds on mid-latitudes associated with global atmospheric circulation patterns (Brink 1983, Huyer 1983). Along the West Coast of the United States, the Pacific Northwest (Washington–Oregon) region experiences a markedly seasonal upwelling regime in which frequent relaxation events take place during the upwelling season (May–September; Huyer 1983, Hickey 1992). Southward, between Cape Blanco (42° N) and Point Conception (34°30' N), the period of upwelling-favorable winds becomes longer (April–October), the average intensity of upwelling is substantially higher, and relaxation events become less frequent (Bakun and Nelson 1991). South of Point Conception, the complex coastal topography of the Santa Barbara Channel influences circulation patterns in the region. The east–west orientation of the channel topographically shelters it from the strong

upwelling-favorable winds of the open coast, generating a seasonal alternation of upwelling/relaxation and recirculation patterns (Hickey 1992, Cudaback et al. 2005).

Previous larval recruitment field studies, carried out in central California, identified a positive association between larval recruitment rates and adult abundances in the barnacle *Balanus glandula* (Gaines et al. 1985, Farrell et al. 1991). This positive association between larval recruitment and adult abundance follows the general equatorward increase in upwelling intensity along the U.S. West Coast. This species is a major component of the intertidal biota along the Washington–Oregon coast and becomes rarer and more spatially and temporally variable along the northern-central California coast (Connolly and Roughgarden 1998, Connolly et al. 2001). Interestingly, this association does not hold along most of the U.S. West Coast for many other species with planktonic larvae, including the mussel *Mytilus californianus*, the dominant intertidal invertebrate (Menge et al. 2004). Hence, the underlying causes of both local and biogeographic patterns of distribution of adults is more complex than a simple association with upwelling intensity, as earlier studies envisaged (Connolly and Roughgarden 1998, Connolly et al. 2001).

Both the low- and high-frequency circulation dynamics shown to transport pelagic larvae to the benthic habitat are associated with vertical and horizontal movement of ocean waters that is many times evident as thermal anomalies on the ocean surface. Conditions favorable to larval delivery are characterized by thermal anomalies, which may indicate the intrusion of warm offshore surface waters such as during relaxation from upwelling (Shanks 1995, Garland et al. 2002, Broitman et al. 2005) or of cold bottom waters from internal tidal waves and bores (Shanks and Wright 1987, Pineda 1994a) or river plumes (Vargas et al. 2006b). Temperature variability is straightforward to quantify, and its association with larval transport mechanisms therefore offers a potentially powerful tool for understanding variation in recruitment across various spatial and temporal scales.

Trade-offs inherent in studies of recruitment have influenced efforts to gain a mechanistic understanding of its causes and consequences. Sample processing is slow and expensive, larvae and recruits are microscopic and difficult to observe in the field, larval stages are of relatively short duration, and transport events tend to occur on short timescales. Further, settlement, defined as the process of attachment to the adult habitat (Connell 1985), and recruitment, defined as survival over some period of time after settlement (e.g., days to weeks), can be differentially affected by processes occurring during the transition from the plankton to the benthos (Connell 1985). For example, post-recruitment processes such as predation or desiccation can potentially decouple settlement and recruitment densi-

ties (Connell 1961). An additional complication is that oceanographic events promoting larval delivery to the shore may not yield recruitment if there are no larvae present in the water column (Narváez et al. 2006). Thus, although the ideal study would incorporate high-frequency sampling (e.g., hourly to daily) at all life stages (larvae, settlers, recruits, adults) across multiple spatial scales (centimeters to thousands of kilometers), under the current set of constraints, most studies emphasize some of these ideal traits at the expense of others. Some studies focus on high-frequency events and detailed examination of one or two life-history stages, but are necessarily limited to small spatial and temporal domains (Farrell et al. 1991, Wing et al. 1995b, Garland et al. 2002, Vargas et al. 2004, Ladah et al. 2005, Lagos et al. 2005, Porri et al. 2006). Other studies may sacrifice temporal, life-history, and physical resolution in an effort to understand longer-term and larger-scale patterns of recruitment and their relation to larger-scale oceanography and the dynamics of communities (Connolly et al. 2001, Menge et al. 2003, 2004, Broitman et al. 2005, Navarrete et al. 2005). In some cases, linking the high-frequency and low-frequency approaches is possible if distinct larval life-history stages occur during settlement (e.g., barnacle cyprids, indicative of higher-frequency events) and recruitment (barnacle juveniles, representing a summation of both higher- and lower-frequency events).

Oceanographic conditions in the nearshore can vary across many nested spatial scales, notably local (one to tens of kilometers), meso (tens to hundreds of kilometers), and regional or biogeographic scales (hundreds to thousands of kilometers; Abbott and Letelier 1998, Broitman and Kinlan 2006) and across a comparable range of temporal scales (see *Methods*). This large spatiotemporal variation stresses the need to monitor biological and physical processes at many sites spread over hundreds of kilometers over long periods of time in order to evaluate characteristic scales of variability. The ability of satellites to capture environmental conditions continuously over large spatial domains provides an opportunity to characterize oceanographic conditions simultaneously over extended spatial scales. Sea surface temperature (SST) derived from remote sensing may provide unique insights into mechanisms of larval delivery when paired with long-term monitoring of larval recruitment rates (Broitman et al. 2005, Lagos et al. 2005). The combination of field data and remote sensing may allow us to understand variability in larval recruitment rates over extended spatial and temporal domains at the expense of restricting our efforts primarily to the study of low-frequency processes. The advantage is that monitoring programs can be maintained in time, which becomes explicitly important in order to assess and evaluate the potential impacts of large environmental variability on coastal ecosystems (IPCC 2001, Kennedy et al. 2002, Harley et al. 2006).

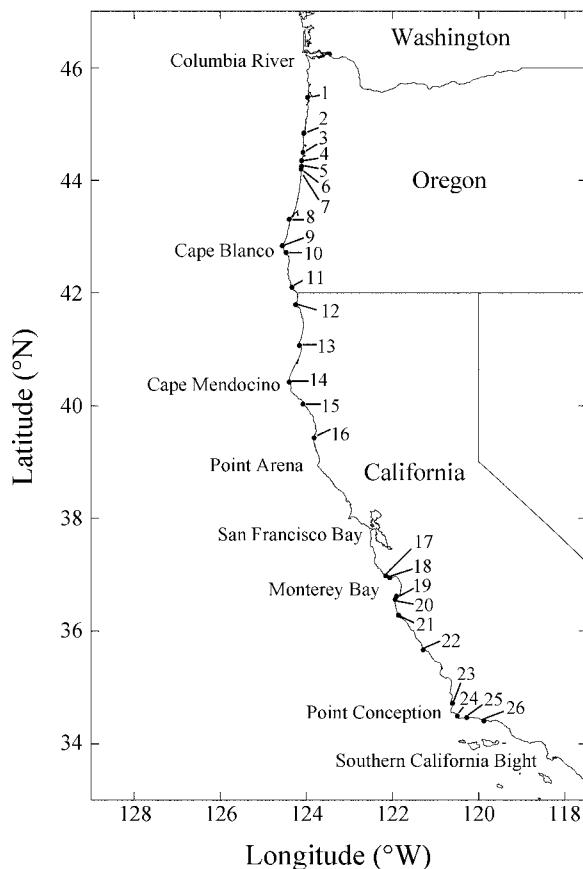


FIG. 1. Map of the West Coast of North America with numbers showing the locations of the study sites where recruitment of mussels and barnacles was monitored. The geographic coordinates, names of the study sites, and corresponding site numbers are listed in Table 1.

Here we focus on the spatial and temporal variability in the recruitment rates of two groups of dominant intertidal invertebrates, mussels and barnacles, and their association with oceanographic variability using satellite-based SST. We present results from a long-term, large-scale monitoring program carried out by the Partnership for Interdisciplinary Study of the Coastal Oceans (PISCO) along the U.S. West Coast. Using monthly time series of recruitment rates of two genera of barnacles and one genus of mussels and based on previous studies, we test three hypotheses: (1) recruitment rates of the three taxa show a similar geographic pattern; (2) the three taxa respond similarly to coastal SST; and (3) seasonal patterns of recruitment are similar across the region.

## METHODS

### *Study sites and organisms*

We surveyed larval recruitment of two groups of abundant intertidal invertebrates, mussels (*Mytilus* spp.) and barnacles (*Balanus glandula* and *Chthamalus* spp.), for eight years at 26 sites over 11 degrees of latitude

along the West Coast of the United States (Fig. 1). Eleven sites were located in Oregon (sites 1–11; Table 1) and 15 sites were located in California (sites 12–26; Table 1). The number and locations of sites were determined in part by accessibility and other logistical constraints, and sites were selected to be as similar as possible in terms of geomorphology, wave exposure, and habitat type (see Appendix A: Table A1 for detailed site descriptions).

The mussel *Mytilus californianus* is the dominant intertidal filter-feeding species along western North America (Paine 1974, Menge et al. 1994, Smith et al. 2006). It spawns during summer (June–July) in the northwest Pacific and year-round in southern California, and its larvae are estimated to stay in the plankton for 9–21 d (Hines 1979, Trevelian and Chang 1983, Strathmann 1987). Chthamaloid barnacles brood and spawn almost year-round, predominantly from spring to fall. Life in the plankton may last from 14 to 21 d (Hines 1978, Strathmann 1987). The barnacle *Balanus glandula* broods and spawns from winter through late summer and its larval development may last for four to eight weeks (Barnes and Barnes 1956, Hines 1978, Brown and Roughgarden 1985, Strathmann 1987, Leslie et al. 2005). Several barnacle species use food supply as a cue to spawning (Crisp 1956), and phytoplankton blooms may act as a cue for the release of larvae (Hines 1978).

### *Recruitment methods*

We measured larval recruitment of barnacles and mussels using techniques described in detail elsewhere (Farrell et al. 1991, Menge 1992, Menge et al. 1999, Navarrete et al. 2008). Mussel recruitment rates were quantified using standardized plastic mesh collectors (Tuffys; Clorox, Oakland, California, USA), while barnacle recruitment rates were quantified using 10 × 10 cm plexiglass or PVC plates covered with SafetyWalk (3M Company, Saint Paul, Minnesota, USA). The mesh of the mussel collectors attracts mussel recruits by mimicking the structure of finely branched macro algae (e.g., *Endocladia muricata*) and adult byssal threads, which are known to be a favored natural settlement substratum for mussel plantigrades (Paine 1974). Similarly, the textured surface of the SafetyWalk mimics the rugose rock surface, which is a favored natural substratum for the cyprid (settling) larval stages of barnacles.

Five to eight replicate collectors were fastened to the rock in gaps in mussel beds, the dominant feature of the middle intertidal zone at each site, using stainless-steel lag screws. Gaps were either natural or created manually, but were located midway between the upper and lower edge of the mussel bed (i.e., at approximately mean sea level [MSL]). Although the tidal range and thus MSL varies from north (larger) to south (smaller; Schoch et al. 2005), placement of collectors in the middle of the mussel bed was done to ensure that submergence times were as similar as possible across the latitudinal

range of the study (see Schoch et al. 2005). Retrieved collectors were held in  $-20^{\circ}\text{C}$  freezers until processing. In the laboratory, mussel recruits were detached from the mesh using diluted bleach solutions or by spraying with a strong jet of water, collected in sieves, and counted using a dissecting microscope. Recently metamorphosed barnacles and cyprids were counted directly on the plates under a dissecting microscope. Uniformity in protocols for sorting and counting was maintained among the PISCO groups by conducting regular coordination workshops. Mussel recruitment rates were standardized to the number of individuals per collector ( $\sim 100\text{ cm}^3$ ), barnacle recruitment rates were standardized to the number of individuals per plate ( $100\text{ cm}^2$ ), and both are expressed as monthly rates indicating the number of individuals per collector per day (Navarrete et al. 2008).

We present monthly data from 26 sites for barnacles and mussels, starting January 1997 (late 1999 for sites 11–21; Table 1), with most sites starting October 1999, until December 2004. While most sites were visited monthly, some were visited every two months due to their remote location (see Fig. 1), and in some cases rough ocean conditions precluded sampling during stormy periods. In these cases collectors were changed out at the earliest subsequent low-tide period. Densities in collectors left out longer than one month were adjusted to a per-month basis. Although it is possible that collector devices may saturate with larvae when left in the field for prolonged periods of time, prolonged deployment was necessary only during winter periods in Oregon and northern California when recruitment rates were minimal (see *Results*). In the case of barnacle settlement plates, the highest number of individuals observed was  $\sim 15\,000$  individuals/plate, while the mean density was 178 individuals/plate overall ( $\sim 1.1\%$  of the absolute maximum). The next highest numbers were 14,000 and 13,000 individuals/plate (these accumulated over three months in winter at Tokatee Klootchman, Oregon), and after those, 7,000 were reached on plates a few times, once over three winter months at Strawberry Hill, Oregon, and once over one month at Fogarty Creek, Oregon. Hence, it is unlikely that barnacle recruitment plates became saturated between sampling periods. In the case of mussel larval collectors (Tuffys) in Oregon, where recruitment was the highest (see *Results*), the maximal density we recorded was  $\sim 36\,000$  mussel larvae/collector, while the average overall was 412 mussel larvae/collector or 1.14% of the maximum observed. So again, mean densities almost never approached maximum densities. Observations with Tuffys on the New Zealand coast (Menge et al. 2003) recorded  $\sim 60\,000$  mussel settlers in a collector, so the highest U.S. observation was still only 60% of the highest observation on record, and the U.S. average was only 0.7% of this maximum. As with settlement plates, it seems unlikely that mussel larval collectors became saturated between sampling periods.

TABLE 1. Name and geographical coordinates of the 26 study sites along the West Coast of the United States.

Site number	Site	Latitude (N)	Longitude (W)
1	Cape Meares	45°28'	124°14'
2	Fogarty Creek	44°50'	125°56'
3	Boiler Bay	44°49'	125°56'
4	Seal Rock	44°30'	125°55'
5	Yachats Beach	44°21'	125°53'
6	Strawberry Hill	44°15'	125°53'
7	Tokatee Klootchman	44°12'	125°52'
8	Cape Arago	43°18'	125°35'
9	Cape Blanco	42°50'	125°26'
10	Rocky Point	42°43'	125°31'
11	Lone Ranch	42°6'	125°39'
12	Point St. George	41°47'	125°45'
13	Trinidad Head	41°4'	125°50'
14	Cape Mendocino	40°25'	125°35'
15	Kibesillah Hill	40°1'	125°55'
16	Fort Bragg	39°25'	124°10'
17	Sand Hill	36°58'	123°50'
18	Terrace	36°57'	123°55'
19	Hopkins Marine Laboratory	36°37'	122°52'
20	Stillwater Cove	36°33'	122°33'
21	Andrew Molera	36°16'	122°8'
22	Piedras Blancas	35°40'	122°42'
23	Lompoc	34°43'	121°23'
24	Jalama	34°30'	121°30'
25	Alegria	34°28'	121°43'
26	Coal Oil Point	34°24'	120°7'

We used linear interpolation between sampling dates to standardize monthly recruitment rates to fall between the first day and the last day of each month across the sampling period (Connolly et al. 2001). Not all sites were started at the same time, and some were terminated before 2004. The maximum number of months a site was monitored was 96 and the minimum was 40. Hence, all sites presented and subject to statistical analysis have a minimum of three years of continuous data.

#### *Recruitment vs. settlement*

As noted earlier, recruitment estimates do not equate to settlement estimates. Quantification of the latter requires high-frequency sampling, which is logistically unfeasible across the large spatial and temporal scales considered here. Recruitment estimates are the net result of a number of transport, settlement, and post-settlement events that occur at sub-monthly scales, raising the issue of a mismatch between what we measured as recruitment and the mechanisms that we infer to be responsible for the recruitment patterns. For example, if post-settlement mortality varies latitudinally, then observed patterns of recruitment might reflect processes occurring after settlement that are not related to the processes that drive settlement.

In our sample processing for barnacles, we identified and counted both cyprids and metamorphs of each taxon. Cyprids, which metamorphose within  $\sim 24$  h or less after settlement, thus provide a measure of settlement during the previous day (Strathmann 1987). In our monthly sampling regime, metamorphs are thus

individuals that range between 24 h and 30 d in age. We thus define cyprids as “settlers” and metamorphs as “recruits.” As a simple test of the strength of post-settlement factors as determinant of patterns of recruitment in our study, we examined the hypothesis of no correlation between recruitment and settlement rates. A lack of significant associations indicated that post-settlement processes decouple the number of cyprids attaching to the standardized collectors (settlement plates) and the number of metamorphosed individuals later counted as recruits. In contrast, a positive correlation provided support for the alternative hypothesis of an association between the numbers of cyprids settling to the plates and the number of metamorphosed individuals recorded as recruits.

#### *Remote sensing of sea surface temperature*

We characterized oceanographic conditions at each site using ocean surface temperature from the advanced very-high resolution radiometer (AVHRR) satellite (Casey and Cornillon 1999). These data are available as weekly (7-d) composites at a nominal resolution of 4 km processed with the Pathfinder Version 5 algorithm for 1997–2003 and the NASA interim algorithm for 2004. The data set examined here spans the duration of the larval recruitment data set, 8 yr, from January 1997 to December 2004. From the AVHRR data set we selected the pixels surrounding the location of the study sites in order to increase the temporal coverage in the data set. By averaging over five pixels along-shelf and six pixels cross-shelf (e.g., 10 km alongshore in each direction and 24 km offshore or an area of  $20 \times 24$  km in front of the site) we characterized thermal conditions in the vicinity of the sites. Spatial averaging was required because missing pixels were common in the nearshore, and selecting the pixel corresponding only to the site would have severely curtailed the available degrees of freedom for statistical analysis (Broitman et al. 2005). Thus, the 480-km<sup>2</sup> square represented in our spatial averages are a compromise between adequate temporal cover (53–87% of valid observations) and a representation of local (site-scale) SST patterns. Raw SST corresponds to the 7-d temperature record at each site interpolated to monthly resolution. Monthly SST anomalies (SSTA) were calculated by subtracting the long-term monthly mean (1996–2005) from each month. We used a longer time series of ocean temperature to calculate long-term means, averaging the effects from the strong oceanographic variability observed between 1997 and 2002 in the Pacific Coast region, which included a major El Niño event and a prolonged La Niña event (Schwing et al. 2002).

#### *Statistical analyses*

To examine the seasonality of recruitment rates we calculated the long-term standardized anomaly for every recruitment rate time series by subtracting the series mean and dividing by the series standard deviation and

then computed a long-term recruitment anomaly for each calendar month using all available data in each time series. A pattern of variability in ocean temperature commonly reflected in biological responses is the seasonal cycle in SST. On the coast of Oregon and southern California, we observed SST maxima around August and minima during February (early spring). This seasonal pattern was shifted in northern-central California, where SST maxima occurred during September–October and minima during April (Strub et al. 1987, Legaard and Thomas 2006). Although geographic variation in the timing of spawning has never been examined across the U.S. West Coast, the literature review does not indicate that reproductive patterns have a true seasonal structure. Instead, spawning takes place episodically (during a few months) or is nearly year round (Hines 1978, Parrish et al. 1981, Strathmann 1987, Reitzel et al. 2004, Leslie et al. 2005, Shanks and Eckert 2005). Because of the brief larval periods in our study species, it can be expected that recruitment rates will follow, with a lag, the temporal patterns of spawning, which in many species do not necessarily fluctuate with temperature (Hines 1975). To test for the presence of a seasonal signal in recruitment rates, we compared monthly recruitment rates with SST. This comparison allowed us to assess the phase-match between recruitment rates and ocean temperature, where positive (negative) associations indicate recruitment during warm (cold) months. Beyond the seasonal cycle, recruitment rates may be associated with anomalous temperature conditions in the nearshore indicative of transport processes that favor larval delivery to the coast (Farrell et al. 1991, Shanks et al. 2000). To evaluate the association between larval recruitment and nearshore circulation processes, we compared monthly anomalies in larval recruitment rates and the monthly anomalies from the long-term monthly mean sea surface temperature. In this case positive (negative) correlations are indicative of increased recruitment associated with anomalously warm (cold) months.

The relationship between variability in ocean temperature and larval recruitment rates is extremely scale dependent. Upwelling/relaxation cycles last from days to weeks and have a seasonal distribution that varies geographically (Send et al. 1987, Bakun and Nelson 1991, Largier et al. 1993), and higher-frequency oceanographic events delivering larvae may last hours (Pineda 1994b, Garland et al. 2002), days (Vargas et al. 2004, Narváez et al. 2006), or weeks (Connolly and Roughgarden 1999a, Broitman et al. 2005) or repeat fortnightly (Shanks 1995, 2006, Pineda and Lopez 2002). By examining correlations between larval recruitment rates and temperature on the same month and over several months before collectors were retrieved, we may aggregate several of these events in order to detect ocean conditions promoting the delivery of larvae to shore. Preliminary results (not shown) indicated that across the region examined, maximal lagged correlations

were observed with ocean temperature during the month before collectors were deployed. Hence, for the compact presentation of results, all analyses were conducted between larval recruitment and one-month lagged ocean temperature.

Due to uneven temporal sampling of SST by the AVHRR sensor (due mostly to clouds), particularly in the southern Oregon–northern California region, and the episodic nature of larval recruitment, we used a nonparametric estimator of concordance, Kendall's tau ( $r_\tau$ ), to calculate temporal correlations between monthly recruitment rates and ocean temperature patterns on the month preceding the deployment of larval collectors. Calculating a correlation between two time series sharing a signal (e.g., a seasonal cycle) may generate a spurious pattern of correlation, thus increasing the probability of a type II error (Legendre and Legendre 1998). In the case of SSTA and monthly anomalies in recruitment rates, temporal autocorrelation was removed by subtracting the long-term monthly mean, but raw monthly recruitment rates, particularly at some of the Oregon mussel time series (Navarrete et al. 2008) and the SST time series showed a seasonal signal. The use of  $r_\tau$  avoids (to some degree) the effects of autocorrelation as it is a nonparametric estimator of concordance (Kruskal 1958). To reduce the probability of type II error, we used Monte Carlo resampling and bootstrapped the calculation of  $r_\tau$  10 000 times. Then, as a highly conservative estimation of the significance of the association between time series, we used the resulting 95% confidence interval of the correlations as a two-tailed test of the hypothesis that the correlations between temperature and recruitment rates were significantly different from zero (Manly 1997, Martinez and Martinez 2002). In correlations between barnacle settlement and recruitment, we computed  $r_\tau$  using recruitment rate anomalies to remove temporal autocorrelation and used a large-sample approximation to estimate significant probabilities (Kruskal 1958). All analyses were carried out using MATLAB 7 R14.0.2 (MathWorks, Natick, Massachusetts, USA).

## RESULTS

### *Spatial patterns*

We observed extreme spatial variation in recruitment rates of all intertidal invertebrates, which ranged five orders of magnitude across the study region. The central Oregon region, from Cape Meares to Tokatee Klootchman (45°28' to 44°12' N, sites 1–7), experienced the highest recruitment rates for *Mytilus* spp. (Fig. 2) and *Balanus glandula* (Fig. 3) with a drop of one order of magnitude in recruitment rates immediately southward, around Cape Arago (43°18' N). Recruitment of *Mytilus* and *Balanus* remained low from Cape Arago to Hopkins Marine Laboratory (36°37' N, sites 8–19), on the southern end of Monterey Bay. Between Hopkins Marine Laboratory and Point Conception (sites 20–23) recruitment rates were extremely low but diverged south

of Point Conception (~34°30' N, sites 24–26), with *B. glandula* increasing and *Mytilus* spp. remaining at low levels compared to sites immediately north.

A different spatial pattern was observed in *Chthamalus* spp. (Fig. 4), which exhibited high geographic variability in recruitment rates across the region. The highest *Chthamalus* spp. recruitment rates were observed at the southernmost site, Coal Oil Point (34°68' N, site 26), located in the Santa Barbara Channel. North of Point Conception, recruitment of *Chthamalus* spp. was one order of magnitude lower than in the Santa Barbara Channel, but at the north side of Monterey Bay (Sandhill and Terrace, site 17–18) recruitment levels were similar to those southeast of Point Conception. Spatial patterns were extremely patchy in the northern California–central Oregon region, where we observed a small area that experienced high recruitment rates around the Oregon–California border (Trinidad Head to Lone Ranch, 41°11' to 42°16' N, sites 11–13). Northward of this, recruitment rates declined one order of magnitude toward southern Oregon and increased again north of Tokatee Klootchman.

### *Temporal patterns*

We examined the spatial structure of temporal variability in larval recruitment using recruitment rate climatologies for each site. Recruitment rate climatologies of *Mytilus* spp. (Fig. 5A) showed that high larval recruitment in the central Oregon–northern California region took place during late summer–fall and peaked during August–October. South of Cape Mendocino (40°–42° N) and across the central California region, maximal recruitment rates were displaced toward winter (November to January), except sites on the north of Monterey Bay, which showed a seasonal pattern similar to central Oregon. The sites in the Santa Barbara Channel showed a marked shift in seasonality, with maximal recruitment rates spread over summer and fall, with maxima in September–October.

Recruitment rates of *B. glandula* (Fig. 5B) showed a similar annual cycle in central Oregon but toward northern California exhibited a narrower seasonal peak during late summer (August to October). South of Cape Mendocino recruitment rates of *B. glandula* showed a marked temporal displacement with a broad peak between late winter and early spring. This displacement of seasonality was abruptly reversed southward, where recruitment took place around the year and peaked during late summer south of Monterey Bay and during late spring in the Santa Barbara Channel. *Chthamalus* spp. (Fig. 5C) showed recruitment rates peaking during summer–early fall from central Oregon to Trinidad Head, with an earlier settlement season at Cape Mendocino. This seasonal pattern diverged southwards in a similar fashion, with *Mytilus* spp., with peak recruitment observed during winter–early spring. Sites located on the north side of Monterey Bay showed peaks of recruitment in both spring and late summer–early fall.

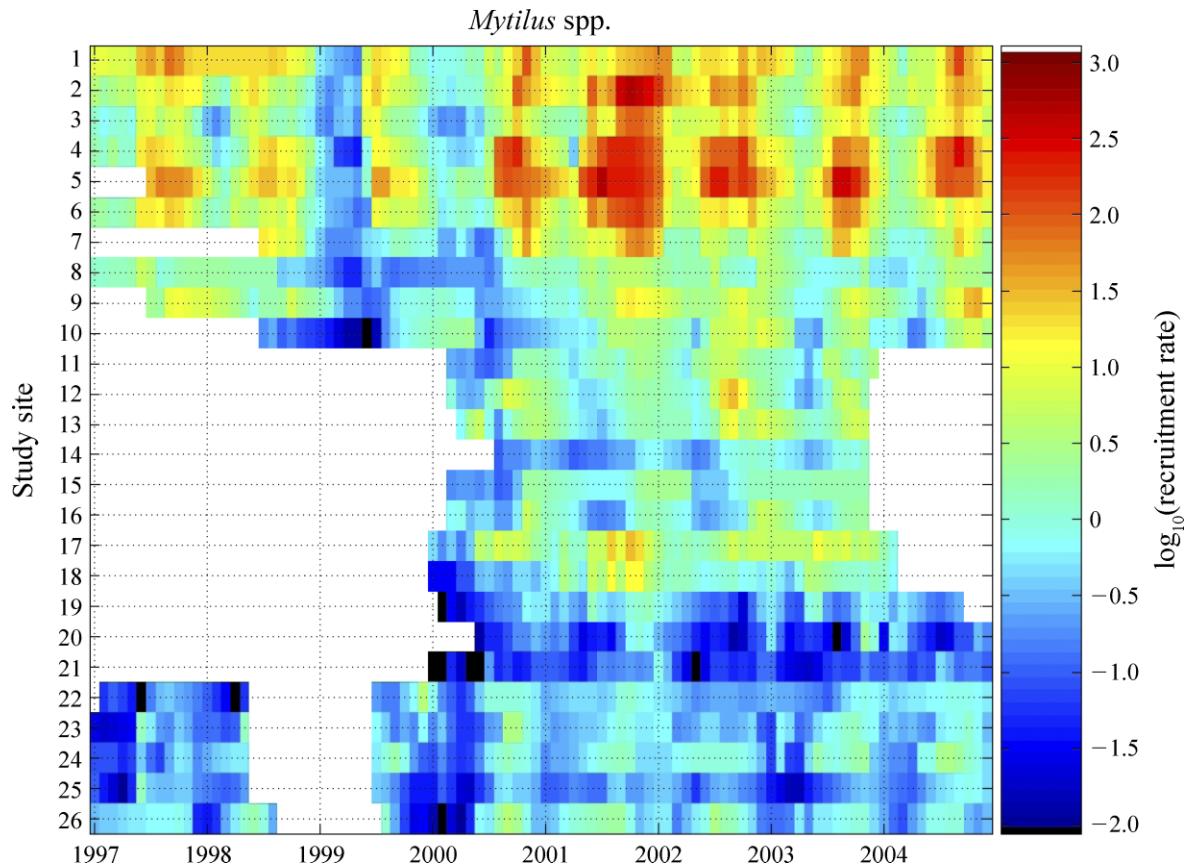


FIG. 2. Monthly larval recruitment rate time series from January 1997 to December 2004 for *Mytilus* spp. at the 26 study sites. Recruitment rate was measured as the number of recruits  $\cdot$  d<sup>-1</sup>  $\cdot$  (larval collector)<sup>-1</sup> and was transformed prior to analyses. Note the marked annual cycles across the region and the abrupt decline in larval recruitment rates south of Cape Arago (site 8). Black indicates zero recruitment, and white indicates no data.

In the Santa Barbara Channel, recruitment took place over most of the year and varied less than to the north.

#### *Relations with sea surface temperature*

*Mytilus* spp. recruitment rates were always in phase with seasonality, hence positively associated with SST. The associations were geographically coherent on the central–northern Oregon coast and sparser to the south, with one site on the north side of Monterey Bay (Sandhill) at Piedras Blancas in central California and at two sites around Point Conception (Lompoc and Alegría; Fig. 6A) showing positive correlations. Recruitment rates of *B. glandula* were also in phase with seasonal temperature variability and showed a similar spatial structure in their association with SST. Positive associations were observed at all sites across the north-central Oregon coast (Fig. 6B), at two sites in northern California, between Cape Blanco and Cape Mendocino (Point St. George and Trinidad Head), and at one site north of Point Conception (Lompoc). We observed anti-phased associations between recruitment rates of *B. glandula* and SST at two sites, one on the north side of Monterey Bay (Terrace) and at one site around Point

Conception, inside the Santa Barbara Channel (Coal Oil Point, Fig. 6B). Recruitment rates of *Chthamalus* spp. showed striking large-scale structure in the associations with SST. In-phase associations with the seasonal cycle in ocean temperature were of similar magnitude along the entire latitudinal extent of the study region, including all sites in north-central Oregon and across north and central California. The exceptions were several sites in northern California, between Cape Mendocino and the sites located on the northern side of Monterey Bay and inside the Santa Barbara Channel (Fig. 6C).

In contrast to the spatial pattern of associations between SST and raw recruitment rates, correlations between monthly ocean temperature anomalies (SSTA) and monthly recruitment rate anomalies were few and geographically widespread (Fig. 7). We observed positive correlations between SSTA and recruitment anomalies of *Mytilus* spp. at two sites in southern Oregon (Cape Blanco and Rocky Point; Fig. 7A), while one site in central California (Piedras Blancas) showed a negative correlation. Barnacles only showed positive correlations. For *B. glandula* (Fig. 7B) positive correla-

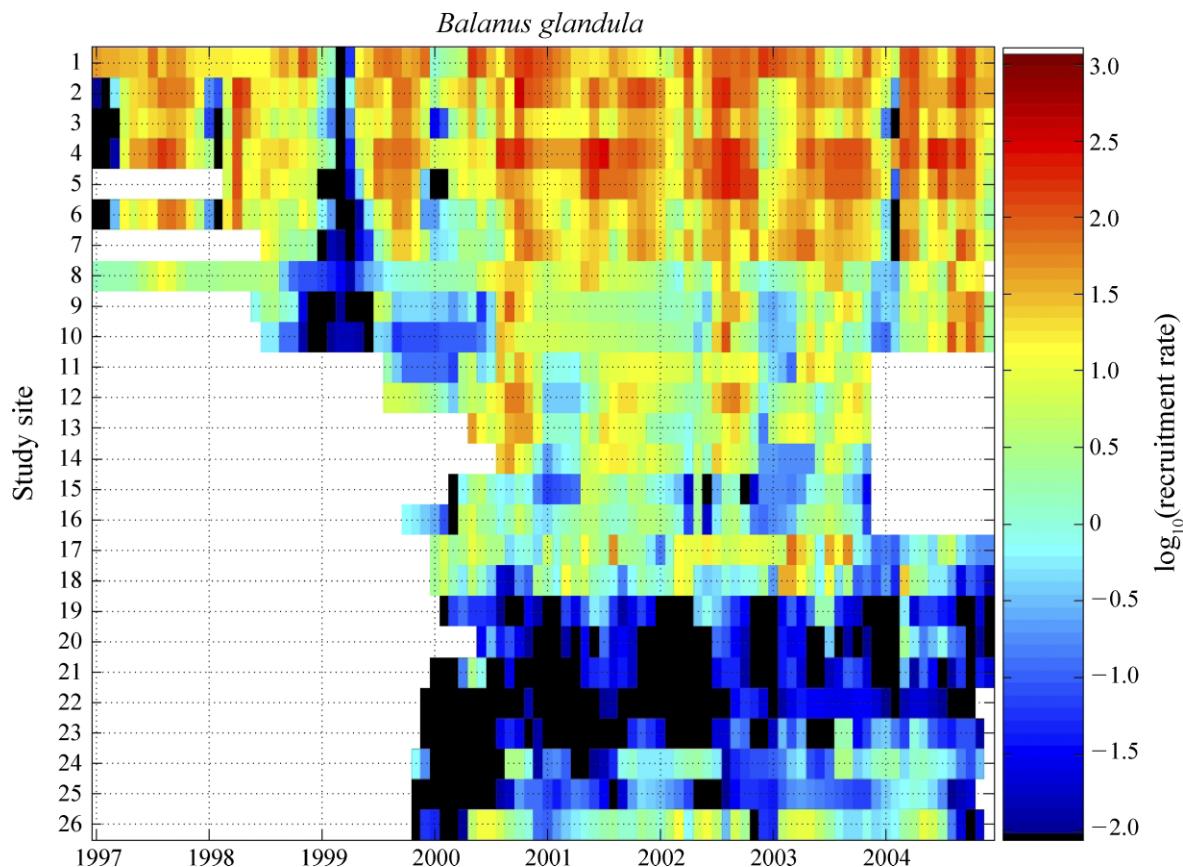


FIG. 3. Monthly larval recruitment rate time series from January 1997 to December 2004 for *Balanus glandula* at the 26 study sites. Recruitment rate was measured as the number of recruits  $\cdot$  d $^{-1}$   $\cdot$  (larval collector) $^{-1}$  and was transformed prior to analyses. Larval recruitment rates in central Oregon (sites 2–7) are more than five orders of magnitude greater than in central California (sites 19–22) but increase again toward Point Conception (Jalama, site 24). Note the marked decline south of Cape Arago (site 8) and the near-absence of recruits south of Monterey Bay ( $\sim$ 37° N). The color scale is the same as in Fig. 2.

tions were detected at two sites with in central Oregon (Yachats and Strawberry Hill), one site in northern California (Fort Bragg), and one site in central California (Andrew Molera). The correlations between SSTA and recruitment rate anomalies of *Chthamalus* spp. (Fig. 7C) showed positive associations at three sites along the coast of Oregon (Cape Meares, Yachats, and Cape Arago), at one site in central California (Hopkins) and one site just north of Point Conception (Lompoc).

#### Settlement vs. recruitment

An important fraction of the sampling period (52–85%) recorded the simultaneous presence of cyprids and metamorphs of *B. glandula* and *Chthamalus* spp. Recruitment rates of cyprids and metamorphs of each species showed a positive correlation at most of the 22 sites for which information was available (86% and 90% of the correlations for *B. glandula* and *Chthamalus* spp., respectively; see Appendix B: Table B1 for correlations and fraction of samples at individual sites). In the case of *B. glandula* three sites did not show significant correlations, one in Oregon and two in southern California.

For *Chthamalus* spp. two sites showed no significant correlation between the recruitment rate anomalies of cyprids and metamorphs, one in central California and one in southern California. Overall, we observed no geographic structure in the strength of the settlement–recruitment association.

## DISCUSSION

### *Spatial and temporal variation in recruitment*

Recruitment rates of the three taxa of sessile intertidal invertebrates studied varied enormously across the 11 degrees of latitude and eight years encompassed by our study. Contrary to our first hypothesis, we observed geographic differences in the recruitment rates among taxa. For mussels and the barnacle *B. glandula*, recruitment rates sometimes five orders of magnitude higher in Oregon than in the California region were a dominant feature of their geographic pattern (Figs. 2 and 3). In contrast, recruitment of the barnacle *Chthamalus* spp. was highly variable and increased markedly toward southern California (Fig. 4).

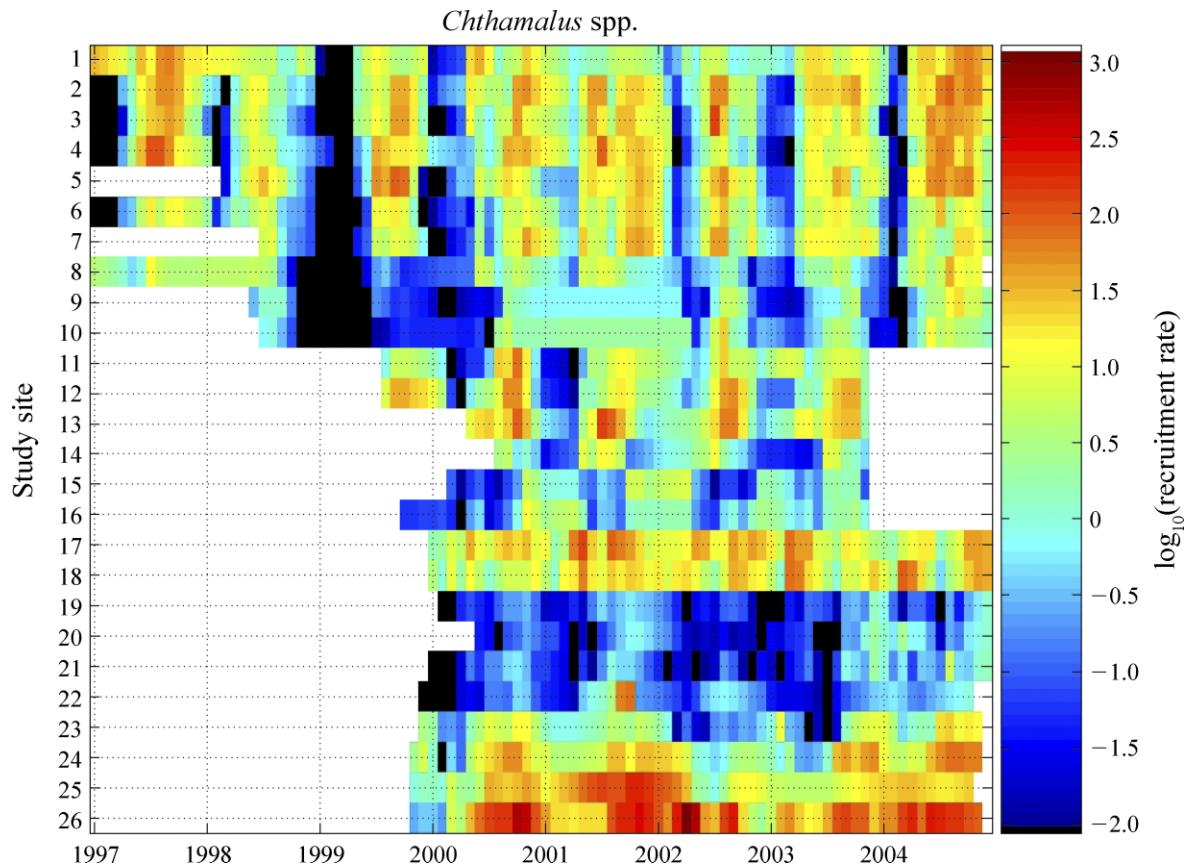


FIG. 4. Monthly larval recruitment rate time series from January 1997 to December 2004 for *Chthamalus* spp. at the 26 study sites. Recruitment rate was measured as the number of recruits  $\cdot$  d<sup>-1</sup>  $\cdot$  (larval collector)<sup>-1</sup> and was transformed prior to analyses. Larval recruitment rates are extremely high in central Oregon, decline south of Cape Arago (site 8), are negligible south of Monterey Bay, and increase again toward Point Conception. The color scale is the same as in Fig. 2.

As predicted by our second hypothesis, spatial variation in recruitment rates showed a similar spatial pattern in their association with SST. This spatial pattern was characterized by large areas positively associated to SST abutted by abrupt transitions around coastline features associated with major oceanographic transitions such as the Cape Arago–Cape Blanco area, Cape Mendocino, Monterey Bay, and Point Conception (Huyer et al. 1991, Barth et al. 2000, Pickett and Paduan 2003).

For all species, the annual cycle in recruitment rates was an important temporal pattern, particularly in the Oregon region. Seasonality was present as annually synchronous spikes in recruitment rates across many sites spanning large sections of coastline (Figs. 2–4). Contrary to our third hypothesis, however, the seasonality of recruitment rates did not vary consistently across the region, as the season of peak recruitment switched between the large regions outlined above (Fig. 5). For example, peak mussel recruitment rates were observed during late summer–early fall in Oregon, shifted toward winter south of Cape Blanco, and completely displaced to wintertime in northern and central California. South

of Monterey Bay peak recruitment rates of mussels abruptly reversed toward late summer–early fall in a pattern similar to that in Oregon (Fig. 5A). A similar spatiotemporal pattern was observed for *Chthamalus* spp., while peak recruitment rates of *B. glandula* were progressively displaced from summer in Oregon toward late winter–early spring in northern California and shifted to late summer in central California and early spring in southern California.

#### *Spatial structure of recruitment variability*

The spatial pattern of larval recruitment rates documented here is consistent with previous studies documenting a sharp decline in recruitment rates of mussels and barnacles from Oregon to California (Connolly et al. 2001). The large spatial extent and the long time period encompassed by the present study provide further insight into the potential mechanisms driving variation in larval recruitment rates and highlight some notable differences between this study and previous findings. Geographic variation in recruitment rates of mussels and barnacles are bounded by the distribution of sites across sections of the coastline

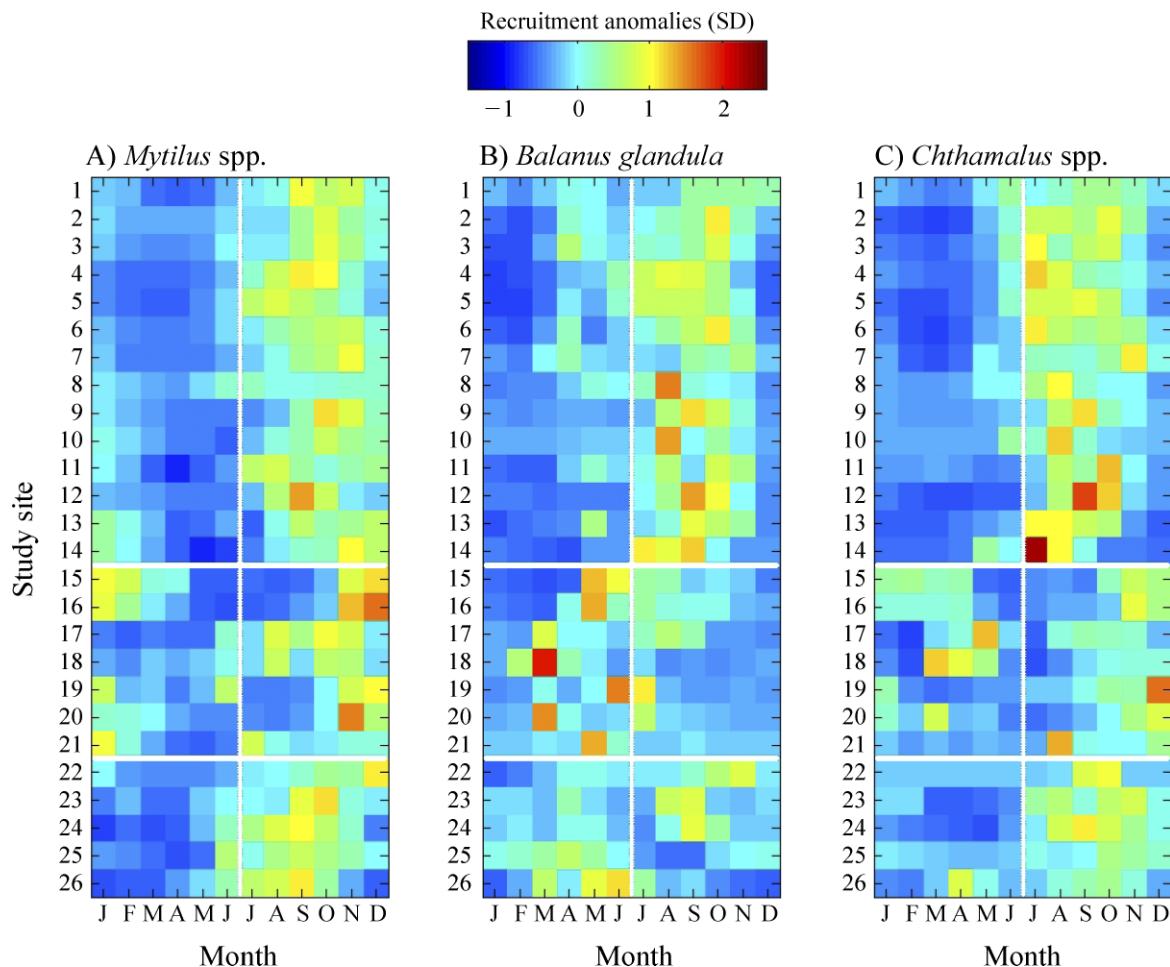


FIG. 5. Long-term monthly anomalies in larval recruitment rates for (A) *Mytilus* spp. mussels, (B) the barnacle *Balanus glandula*, and (C) *Chthamalus* spp. barnacles. Recruitment rate was measured as the number of recruits  $\cdot$  d<sup>-1</sup>  $\cdot$  (larval collector)<sup>-1</sup> and was transformed prior to analyses. Values in the color scales are standardized anomalies (SD). Note the shift in seasonality from late summer toward fall/winter or early spring in northern California south of Cape Mendocino and their displacement back to late summer in central-southern California. A vertical reference line is plotted on July to indicate the middle of the summer, and two horizontal reference lines are given to indicate Cape Mendocino (between sites 14 and 15) and the boundary between northern and central California (sites 21 and 22) to highlight transitions in seasons of maximal recruitment as mentioned in *Results*.

separated by areas where major changes in oceanographic conditions take place such as Cape Arago–Cape Blanco, Cape Mendocino, Monterey Bay, and Point Conception (Huyer 1983, Barth et al. 2000, Pfeiffer-Herbert et al. 2007). Although there are some notable spatial gaps in our study along the northern California coast, results presented by Connolly et al. (2001: Fig. 2) support the presence of abrupt changes in recruitment rates immediately around these transition areas, although their study did not extend to Point Conception. It is worth noting here that the abrupt increase in recruitment rates observed south of Point Conception seems to continue southward for *Mytilus* spp. and *Chthamalus* spp. at least until Point Mugu at the eastern end of the Santa Barbara Channel (results not shown), with relatively high recruitment rates of *Chthamalus* spp. being observed as far south as San Diego, California,

USA, and Ensenada, Baja California Norte, Mexico (Pineda and Lopez 2002, Ladah et al. 2005).

Whether overlapping biogeographic ranges may be driving geographic variation in recruitment rates is not clear. Currently, it is not possible to distinguish between the early recruits of *Chthamalus* spp. (*C. dalli* and *C. fissus*) or *Mytilus* spp. (*M. californianus*, *M. galloprovincialis*, and *M. trossulus*). In the case of barnacles, if the life histories and phenologies of the two species are different, the lack of large-scale geographic trends in recruitment rates for *Chthamalus* spp. may derive from the overlap of geographic ranges toward the southern end of the spatial domain examined. Alternatively, if their life cycles and phenologies are similar, then the pattern of recruitment suggests that *Chthamalus* spp. respond differently than mussels and the barnacle *B. glandula* to geographic variation in coastal oceanogra-

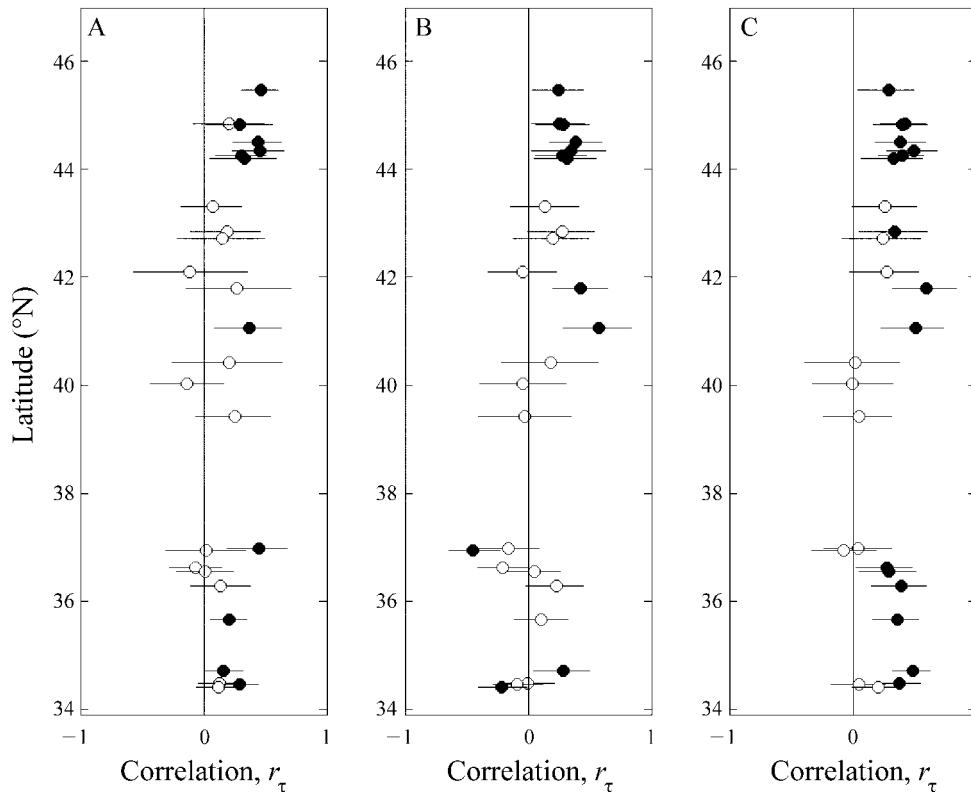


FIG. 6. Spatial structure of the temporal association between larval recruitment rates of (A) *Mytilus* spp. mussels, (B) the barnacle *Balanus glandula*, and (C) *Chthamalus* spp. barnacles and satellite sea surface temperature (SST) during the month before recruitment data were collected. Open circles represent the average Kendall's tau ( $r_\tau$ ) correlation between time series at each site after 10 000 Monte Carlo simulations, and the horizontal lines shows the 99% CI used to determine significant associations (solid circles). Note the large number of sites with in-phase association with seasonal temperature patterns along the coast of Oregon for all taxa, particularly for barnacles (B and C), and on the southern end of the study region for *Mytilus* spp. (A) and for *Chthamalus* spp. (C). Note the lack of significant correlations at most study sites in northern California ( $\sim 39^\circ\text{--}41^\circ\text{ N}$ ).

phy and environmental conditions. This latter interpretation is supported by the observation that *B. glandula* and *Chthamalus* spp. recruitment at sites in Monterey Bay varied in opposite ways with upwelling. *Balanus glandula* recruitment was low with strong upwelling, while *Chthamalus* spp. recruitment was high with strong upwelling (Roughgarden et al. 1988; S. D. Gaines, unpublished data; see also dos Santos et al. 2007). Understanding the factors underlying *Chthamalus* spp. recruitment patterns awaits more detailed study.

#### Relations with oceanographic patterns

Associations between raw recruitment rates and the seasonal cycle in ocean temperature (indexed through SST) provided a measure of the phase match between both cycles, as suggested by the recruitment climatologies (Fig. 5). In-phase associations with SST were observed along the coast of northern Oregon, between Cape Blanco and Cape Mendocino, and across south-central California. Thus, across all the taxa examined, recruitment rates at many adjacent sites, distributed over hundreds of kilometers, shared a comparable, positive response to monthly SST. These regions correspond to

coastline sections where flow during spring/summer is either intermittently onshore and offshore (Oregon; Menge et al. 1997, Castelao and Barth 2005) or characterized by complex coastal circulation features (southern California; Winant et al. 1999, Bassin et al. 2005, Cudaback et al. 2005). The area in northern California where we observed fewer correlations between SST and recruitment rates of any of the species examined,  $39^\circ\text{--}41^\circ\text{ N}$  (Figs. 6 and 7), is also the section of the coast where all recruitment rate climatologies show an abrupt departure from the coherent geographic pattern observed across the Pacific Northwest (Fig. 5). This region shows the smallest annual amplitude in the SST signal off the U.S. West Coast as it corresponds to the area of maximal summer upwelling across the west coast of North America (Bakun and Nelson 1991, Legaard and Thomas 2006). The intense offshore transport of surface waters characteristic of this region during the spring and summer months (Brink 1983) may prevent the development of a summer seasonal pattern of recruitment similar to the regions north and south, resulting in increased recruitment rates during winter or

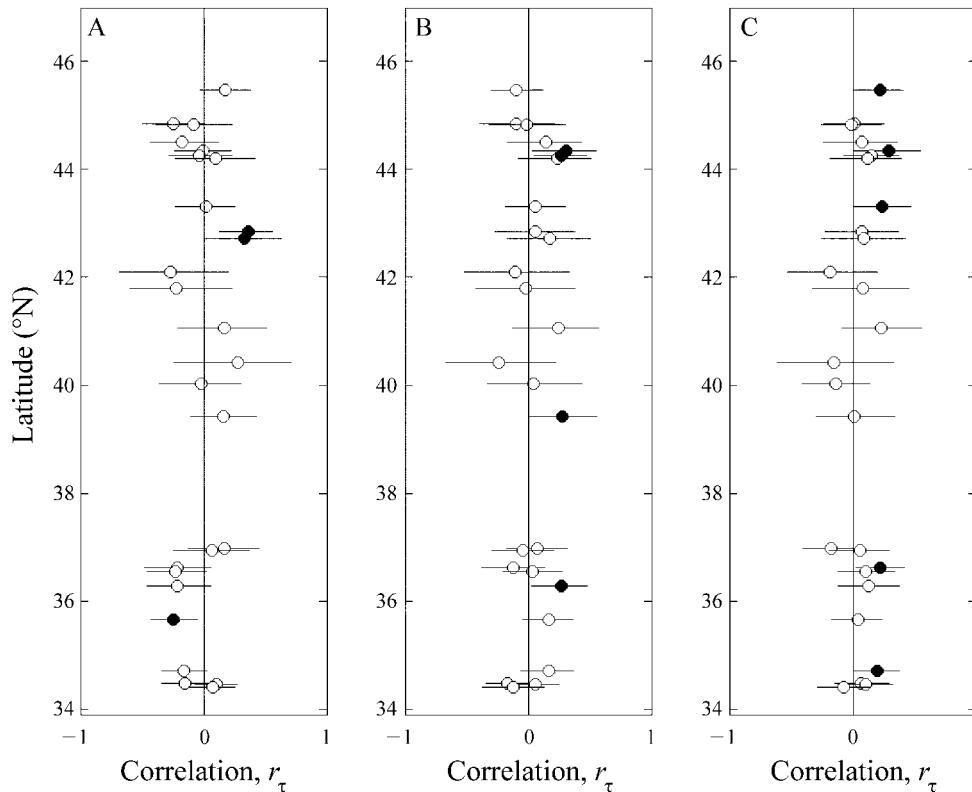


FIG. 7. Spatial structure of the temporal association between larval recruitment rates of (A) *Mytilus* spp. mussels, (B) the barnacle *Balanus glandula*, and (C) *Chthamalus* spp. barnacles and satellite sea surface temperature anomalies (SSTA) during the month before recruitment data were collected. Open circles represent the mean Kendall's tau ( $r_\tau$ ) correlation between time series at each site after 10 000 Monte Carlo simulations, and the horizontal lines show the 99% CI used to determine significant associations (solid circles). Note the paucity of correlations for all taxa and the lack of spatial structure in the few significant correlations.

early spring when offshore flow of surface waters is weaker.

The presence of a biogeographic mosaic in recruitment rates (the Pacific Northwest, north-central California, and southern California) was originally envisioned by Parrish et al. (1981). This biogeographic mosaic pattern is consistent with the presence of a genetic cline in populations of *B. glandula* between Oregon and southern California (Sotka et al. 2004). Sotka et al. (2004) suggested that although populations in Oregon and southern California showed evidence of connectivity among distant populations, the cline seemed to be maintained by recruitment limitation in north-central California. Nearshore circulation patterns along this large section of the U.S. West Coast seem to rarely favor the onshore transport of planktonic larvae (Parrish et al. 1981, Sotka et al. 2004, Shanks and Eckert 2005, Pfeiffer-Herbert et al. 2007). Hence, prevailing oceanographic conditions along the north-central California region may have an influence on recruitment patterns that is pervasive enough to disrupt gene flow over a biogeographic scale (Sotka et al. 2004, Byers and Pringle 2006, Pringle and Wares 2007).

The paucity of geographically coherent associations between SSTA and recruitment rates (Fig. 7) contrasts

with previous empirical studies in the central-southern California region (Connolly and Roughgarden 1999a, Broitman et al. 2005). These studies found an association between increased recruitment rates of barnacles and thermal anomalies in time series that included the strong 1997–1998 El Niño–Southern Oscillation (ENSO) event (Connolly and Roughgarden 1999a, Broitman et al. 2005). Our longer term study not only included the 1997–1998 ENSO event, but also the cold La Niña event afterward (Schwing et al. 2002). Although we detected several sites with positive associations between SSTA and recruitment of barnacles in the central-southern California region (Fig. 7B, C), we suggest that the lack of widespread associations in our study is likely to arise from having examined longer time series with a more conservative hypothesis-testing framework (see *Methods: Statistical analyses*).

Alternatively, the lack of associations may indicate a mismatch of scales between the thermal signature of single (or several) events associated with larval delivery to the shore and our monthly satellite temperature estimates and monthly monitoring of larval recruitment. For example, extensive work on larval delivery associated with internal tidal bores and waves has shown that these fortnightly features can be a predictable transport

mechanism for the larvae of coastal crustaceans, including barnacle cyprids (Shanks and Wright 1987, Pineda 1994a, Pineda and Lopez 2002, McCulloch and Shanks 2003, Queiroga and Blanton 2005). Vertical distributions of the larvae of the mussel and barnacle species included in our study have not been examined in detail. Preliminary results from sampling at nearshore moorings off the coast of Oregon suggest that mussel larvae tend to be far away from the surface, ranging from 1 to 8 m from the bottom (Rilov et al., *in press*). In the case of barnacle species, the cyprid stage (the non-feeding developmental stage immediately preceding settlement) tends to be near the surface (1–3 m from the surface; S. E. Dudas, B. A. Grantham, A. R. Kirincich, B. A. Menge, J. Lubchenco, and J. A. Barth, *unpublished manuscript*) and can accumulate at offshore surface fronts (Grantham 1997). The only study available, to our knowledge, that examined directly the vertical distribution of barnacle cyprids was carried out off Portugal (dos Santos et al. 2007). Their results showed qualitatively similar results with *Chthamalus* (*Chthamalus stellatus*) and Balanid cyprids (*Balanus perforatus*) located in shallow waters and accumulated at the coastal front. In this way, larval behavior may provide another source of geographic variability in recruitment rates as different species exploit different sections of the water column for shoreward transport and retention (Garland et al. 2002, Poulin et al. 2002, Queiroga and Blanton 2005, Queiroga et al. 2007). Although their importance is likely to vary along the coast, the interaction between larval behavior and transport mechanisms may be extremely important as a larval delivery process and should be a focus of future research (Shanks 1995, Queiroga and Blanton 2005).

*Alternative explanations of spatial patterns  
in recruitment rates*

Variation in rates of recruitment to open populations may arise from the many factors operating on the adults, the larvae, and the juveniles (Caley et al. 1996). Not much is known of the planktonic larval stage of our study species and postsettlement mortality can play a large role in shaping patterns of adult distribution, at least at local scales (Raimondi 1991, Menge 2000, Jenkins 2005). Our study was focused on identifying connections between geographic variation in recruitment rates and patterns of coastal circulation approximated by thermal satellite imagery. Although flow patterns can determine the sections of coast where planktonic larvae will be likely to arrive on shore (Gaylord and Gaines 2000), at least five alternative hypotheses can be considered as potential drivers of the biogeographic pattern of variation in recruitment rates identified by our study.

First, postsettlement mortality due to environmental stress may play a role in shaping the large-scale structure of recruitment rates detected through our recruit collectors. Both mean air and mean water temperatures

increase southward (Schoch et al. 2005), suggesting that higher thermal stress southward may cause higher mortality of recruits to the south than to the north. Under this scenario the lower recruitment of *Mytilus* spp. and *B. glandula* toward the south could result from similar or even higher settlement but higher post-settlement mortality in the south than in the north. Although post-settlement mortality clearly occurs, and our recruitment estimates are not true estimates of settlement, the widespread positive correlations between cyprid and metamorph densities in our collectors indicate that monthly recruitment estimates serve as a reasonable proxy for settlement. However, our non-parametric approach does not rule out completely the possibility of spatial heterogeneity in the strength of the settler–recruit relationship and the importance of postsettlement mortality as a determinant of adult distribution patterns (see *Results: Settlement vs. recruitment*). Recent studies suggest that intertidal thermal stress along the U.S. West Coast is greater at northern sites than at southern sites (Helmuth et al. 2006). This is due to the coincidence of summertime low tides during midday in northern regions and summertime low tides during the night in southern regions. Examination of the geographic variation in daily maximal body temperature of *M. californianus* in the sites studied by Helmuth et al. (2006) suggests that the months of maximal recruitment are not coincident with the months of maximal temperature, except in southern California. If anything, we expect the interaction between the geographic variation in the timing of low tides and between-sites patterns of heat stress to create a geographic mosaic in patterns of post-settlement mortality (Helmuth et al. 2006).

Second, spatial variability in recruitment rates may be related to ocean thermal conditions during the planktonic larval period. Ocean temperature influences pelagic larval duration by affecting metabolic demand (Thorson 1950, Pfeiffer-Hoyt and McManus 2005, O'Connor et al. 2007). The prolonged planktonic larval periods predicted to result from cooler temperatures to the north may reduce the probability of recruitment (Vance 1973). Alternatively, a prolonged larval period may increase the chance of dispersal and shoreward transport if pelagic predation is not severe, such as during the spring phytoplankton bloom (Reitzel et al. 2004). The effects of temperature on geographic patterns of recruitment await further study (O'Connor et al. 2007).

Third, ocean conditions influencing food availability may influence postsettlement survival of the planktonic larvae of our study species (Jarrett 2003, Phillips 2004, Emler and Sadro 2006). The existence of a strong latitudinal gradient of phytoplankton concentration, with high values to the north and low values to the south (Menge et al. 2004), is parallel to the pattern of recruitment and thus consistent with this alternative. However, within-region mesoscale patchiness of phyto-

plankton in the nearshore can be high (Menge et al. 2004, Leslie et al. 2005, Barth et al. 2007) and the lack of knowledge of where pelagic larvae are located vertically make this hypothesis difficult to evaluate across large spatial scales. The contrasting pattern for *Chthamalus* spp. compared to the other two taxa suggests that either food (measured as chlorophyll *a* concentration) is unimportant for the geographic recruitment patterns or that *Chthamalus* spp. do not respond to food concentration while the other taxa do (Vargas et al. 2006a).

Fourth, recruitment may reflect patterns of larval production by adults (Hughes et al. 2000). That is, is recruitment of some species higher to the north because adults are more abundant there? Prior studies yield contradictory results. One study suggests recruitment rates of mussels are unrelated to adult abundance (Menge et al. 2004). Overall, however, percent cover may underestimate the biomass of adults, as mussel beds in Oregon can be formed by several layers of individuals while in California they tend to be monolayers (Menge et al. 2004). Biomass seems likely to be a better metric of the abundance of larva-producing adults than does percent cover (MacCall 1990), so this relationship needs further study. In partial contrast to the mussel results, data from a separate set of intertidal surveys show that, in the case of *Balanus glandula*, recruitment rates do seem to be related to patterns of adult percent cover at 19 of our 26 study sites where information was available (Blanchette et al., *in press*). Assigning causation, however, is hard to determine. On more local scales, recruitment rates sometimes may be a poor indicator of overall abundance of adults as small recruitment events may be disproportionately important in determining population size due to temporally correlated mortality of settlers (Jarrett 2003, Pineda et al. 2006). Previous work suggests that a large spatial gradient in mussel abundance around Point Conception is not driven by variation in recruitment (Blanchette and Gaines 2007) but is associated with a strong gradient in mussel growth and predation (Blanchette et al. 2007). In contrast, results from nearby Santa Cruz island, California, suggested that abundances of mussel and barnacles were strongly correlated with recruitment rates (Blanchette et al. 2006), which appeared to be driven by oceanographic forcing (Broitman et al. 2005). Clearly, the adult–recruit relationship will vary across species and larval histories and will require further study (Hughes et al. 2000).

Fifth, differential post-settlement predation or biotic disturbances could influence recruitment patterns. Predators might include whelks, sea stars, and nemerteans, while disturbance might come from limpet “bulldozing” or dislodgement of cyprids or metamorphs while limpets are grazing (Dayton 1971). Tests of the latter possibility have been carried out in Oregon, showing a significant but weak effect of limpets on recruitment densities (B. A. Menge and M. Foley, *unpublished manuscript*), so

bulldozing by limpets can contribute to post-settlement mortality but probably with minimal consequences. This could vary geographically, however, and needs to be evaluated on a larger scale. Similarly, we rarely saw predators consuming barnacle recruits on settlement plates. After one month, recruits are still usually <1.5 mm in diameter and likely are not profitable prey for adult whelks or sea stars at such small sizes. Although we haven’t tested this possibility experimentally, nearly two decades of observations of recruitment to settlement plates suggests that post-settlement predation is not an important source of early mortality. Predation in mussel collectors also seems likely to be minimal for similar reasons, although we have not tested this possibility. No adult predators were observed in the mesh ovoids during sample sorting, and very few micro-predators (small whelks, nemerteans) were observed either.

#### CONCLUSION

Propagule delivery rates are a key component of community dynamics (Gaines et al. 1985, Hughes et al. 1999, Menge et al. 2003, Navarrete et al. 2005). In this study we have shown that larval recruitment rates of the dominant sessile intertidal invertebrates along the U.S. West Coast exhibit large spatial and temporal variation. Although our satellite-based monthly estimator of upwelling dynamics, SSTA, was not associated with recruitment variability, the biogeographic pattern of recruitment rates, their seasonal patterns, and their correlations to SST almost mirror the regional variability in SST, which is driven by upwelling intensity (Pickett and Paduan 2003, Legaard and Thomas 2006, Chhak and Di Lorenzo 2007). Coastal upwelling is one among several mechanisms shown to be involved in larval delivery to shore (Shanks 1995). However, the association between large-scale atmospheric circulation and larval recruitment rates of several species highlights the tight linkage of this key ecological process to global climate (Bakun 1990, Harley et al. 2006). Coastal upwelling is predicted to intensify along eastern boundaries of oceans in association with enhanced temperature gradients between the continents and the oceans (Bakun 1990, Snyder et al. 2003). Possible climate-driven changes in either the strength, timing, or spatial distribution in the upwelling regime along the U.S. West Coast have the potential to alter the magnitude of the larval recruitment rates of intertidal invertebrates. Although climate change prospects are highly uncertain in magnitude and timing (IPCC 2001), a climate-driven change in larval recruitment rates may have major consequences for the ecology of the coastal ecosystems (Harley et al. 2006). The possibility of forecasting ecological scenarios, even simplistic ones, should be a topic of active future research.

#### ACKNOWLEDGMENTS

We thank the legions of interns who have helped with field sampling and processing of the samples in the laboratory; without their help, such a massive sampling effort would have

been impossible. We also thank the many property owners who provided access to some of our study sites. C. Jones and J. Bennett provided crucial help in data and metadata management. B. R. Broitman acknowledges funding from the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-0553768), the University of California, Santa Barbara, and the State of California. This research was funded with support from the David and Lucile Packard Foundation, the Gordon and Betty Moore Foundation, the Andrew W. Mellon Foundation, the Wayne and Gladys Valley Foundation, and the National Science Foundation. We are grateful for the hard work of four anonymous reviewers, which significantly improved the focus and clarity of the original manuscript. This is publication number 288 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, a large-scale long-term consortium funded primarily by the David and Lucile Packard and Gordon and Betty Moore Foundations.

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#### APPENDIX A

The names, geographical coordinates, orientation, wave exposure, and geomorphological characteristics (rock type) of the 26 study sites along the West Coast of the United States (*Ecological Archives* M078-016-A1).

#### APPENDIX B

Kendall's  $\tau$  concordance between the density of settlers (cyprids) and metamorphs (recruits) at every site during the study period for *Balanus glandula* and *Chthamalus* spp. (*Ecological Archives* M078-016-A2).