Linking long-term, large-scale climatic and environmental variability to patterns of marine invertebrate recruitment: Toward explaining “unexplained” variation

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1. Introduction

The potential ecological consequences of changing climate on marine and coastal ecosystems are likely to be extensive and profound (Southward et al., 1995; McGowan et al., 1998; Peterson and Schwing, 2003; Feely et al., 2004; Harley et al., 2006; Helmsley et al., 2006; Helmut et al., 2011–this issue; Johnson et al., 2011–this issue; Philippart et al., 2011–this issue; Schiel, 2011–this issue), yet uncertainties remain about the mechanistic linkages between physical and biological change. For example, El Niño–Southern Oscillation (ENSO) cycles can offer valuable insights into the potential influences of large scale changes in climate (Glynn, 1988; Chavez et al., 1999), but effects vary with the intensity of the ENSO, perhaps in a non-linear manner (Holmgren et al., 2001). One issue is the extent...
Evidence suggests that temperate pelagic ecosystems may be highly sensitive to the PDO cycle (McGowan et al., 1998; Peterson and Schwing, 2003). Abundance of zooplankton off southern California, of northern-origin copepods off the Oregon coast, and survival of Coho salmon (Peterson and Schwing, 2003) were all low during a “warm” phase of the PDO (~1977–1998). In 1997–1998 several climate shifts occurred more or less simultaneously: one of the century’s two most intense El Niños occurred, followed in 1999 by an intense La Niña. Coincidentally, in 1998, oceanographic conditions seemed to shift to a “cold” phase of the PDO, although in 2002–2007 the PDO temperature anomalies had shifted back to warmer temperatures, and then shifted back to cooler temperatures in 2008–2009 (http://jisao.washington.edu/pdo/PDO.latest). Such fluctuations lend uncertainty as to whether or not the switch to cool conditions has yet occurred. Overlaid on all this was a steadily rising global temperature due to anthropogenic influences (Houghton et al., 2001). The ecological changes associated with these shifts led Peterson and Schwing (2003) to suggest that northeast Pacific ecosystems had entered a “new climate regime.” Other recent changes in the northeast Pacific (the sudden onset of persistent summer hypoxia in 2002 (Grantham et al., 2004), the “strange summer” of 2005 (Brodeur et al., 2006; Kudela et al., 2006; Schwing et al., 2006; Sydeman et al., 2006; Barth et al., 2007); the unusually intense upwelling summer of 2006 (Chan et al., 2008)) are consistent with the possibility of a regime shift in this region.

The supply of new individuals is obviously crucial for population persistence, and both models and evidence from a variety of systems suggest that under certain conditions, recruitment can be an important determinant of community structure (Underwood and Denley, 1984; Gaines and Roughgarden, 1985; Menge and Sutherland, 1987; Steele, 1997; Tilman, 1997; Connolly and Roughgarden, 1999; Menge, 2000; Gouhier et al., 2010). One assumption made in some models is that propagule supply varies in a consistent way along some environmental gradient, such as upwelling intensity (e.g., Connolly and Roughgarden, 1999). That is, among-species differences (e.g., in magnitude or seasonality) are unimportant or “average out,” and thus patterns of recruitment of different species tend to co-vary, at least on the scales that are relevant to determination of community structure.

Here we examine this assumption in the context of climate-related environmental variation in a rocky intertidal system. Along the US west coast, dominant space-occupying sessile invertebrates in the rocky intertidal region include barnacles and mussels (e.g., Schoch et al., 2006). On the Oregon coast, four of the most common of these species are the barnacles Balanus glandula and Chthamalus dalli, and the mussels Mytilus californianus and M. trossulus. These species co-occur, sharing rocky surfaces in the high, mid and low intertidal zones, and when abundant, can interact strongly (Dayton, 1971; Navarrete, 1996; Berlow, 1997; Berlow, 1999; Menge, 2000, 2003). In these “post-recruitment” processes, the mussel is the dominant competitor in mid and low zones (e.g., Paine, 1966, 1974; Dayton, 1971; Menge, 2003), and in all zones B. glandula usually outcompetes C. dalli, although when the latter is abundant relative to the former, it can reverse the outcome of competition (Menge, 2000). A further complexity is that B. glandula facilitates successful colonization of mussels, thereby sealing its doom as the mussels settle among, grow and eventually smother the barnacles (Berlow, 1997).

When recruitment is included in models of community structure, it is assumed to be a primary determinant of the strength of species interactions (Menge and Sutherland, 1987; Connolly and Roughgarden, 1999). High recruitment is assumed to lead to strong competition, and in conditions that are favorable for high levels of predator activity, strong predation. Low recruitment is assumed to underlie weak interaction strength. Whether or not among-species differences in recruitment magnitude or variation in temporal patterns of recruitment produce important alterations in interaction strength and thereby in community structure has not been well explored. Recently, we reported that (1) orders-of-magnitude increases in mussel recruitment occurred in association with the millennial transition (=1999–2000; Menge et al., 2009), but that, depending on site and zone, (2) this change led to no change or just small changes in community structure (Menge et al., 2010b). We suggested that the minimal response was due in part to the absence of comparable changes in barnacle recruitment, and thus to a lack of change in the strength of mussel–barnacle interactions. The factors underlying the changes or lack thereof in recruitment were, however, not investigated. In the context of inevitable climate change and uncertainty in the ecosystem consequences of these changes, it is increasingly important to gain insight into the factors underlying change in the input of recruits to ecological communities (see also recent work in Europe by Poloczanska et al., 2008; Hawkins et al., 2009).
Here our focus is on determining the relative contributions to variation in recruitment of large- to regional-scale environmental variation, as reflected in climate cycles and upwelling. We examine barnacle and mussel recruitment time series in detail, and analyze the variation we observed in relation to variation in large- to meso-scale variation in climatic and environmental cycles: PDO, ENSO, NPGO (all large scale), and coastal upwelling (a mesoscale factor that can be involved in transport of larvae to shore, and thereby recruitment). Our goals are: (1) to begin to understand the linkages between climate-related variability and the key ecosystem process of recruitment, (2) to determine if different species responded to these factors in similar or different ways, and (3) to examine correlations in recruitment between these species and how they were affected by the millennial transition. We evaluate three hypotheses:

$H_1$. Recruitment of barnacles and mussels is sensitive to climatic variability as expressed in the ENSO, PDO, NPGO climate indices and the Bakun upwelling index.

$H_2$. Recruitment of these species responded similarly between 1989 and 2008 to these sources of variability.

$H_3$. Relationships between recruitment of these species were altered by the millennial transition.

2. Methods

2.1. Study sites

Our study was conducted at rocky sites along the Oregon coast: Cape Meares (CM; 45° 34′ 12″ N, 123° 58′ 12″ W), Fogarty Creek (FC; 44° 50′ 24″ N, 124° 5′ 36″ W), Boiler Bay (BB; 44° 49′ 48″ N, 124° 3′ 36″ W), Seal Rock (SR; 44° 30′ N, 124° 5′ 24″ W), Yachats Beach (YB; 44° 19′ 12″ N, 124° 7′ 12″ W), Strawberry Hill (SH; 44° 15′ N, 124° 7′ 12″ W), Tokatee Klootchman (TK; 44° 12′ N, 124° 7′ 12″ W), Cape Arago (CA; 43° 18′ 36″ N, 124° 24′ W), Cape Blanco (CB; 42° 50′ 24″ N, 124° 34′ 12″ W), and Rocky Point (RP; 42° 43′ 12″ N, 124° 28′ 12″ W). Fig. 1 shows the locations of these sites along the Oregon coast. Data collection began in 1989 at BB and SH and through the 1990s began at additional sites in different years (Menge et al., 2009). Our present analysis includes data up through 2008. For brevity we refer to 1989–1999 data as the “1990s” and 2000–2008 data as the “2000s.”

Fig. 2. Time series of monthly $B.\text{glandula}$ recruitment (monthly mean number of recruits per day; error bars are not shown for clarity) at ten sites along the Oregon coast, arranged north to south from top to bottom. Note that ordinate scales differ among sites. The dashed vertical line separates the 1990s from the 2000s. Note that $B.\text{glandula}$ recruitment differed between decades at only two sites, SR and SH, where it was greater in the 2000s (two-way ANOVA on ln average recruitment by site and decade; decade p < 0.05).
2.2. Recruitment

Following Connell (1985), we define recruitment as the number of settlers surviving a period of time after metamorphosis, up to one month (e.g., Broitman et al., 2008; Menge et al., 2009, 2010a). Rates of recruitment of barnacles and mussels were estimated using replicated deployments of larval collectors in the mid and low intertidal zones (plastic mesh balls for mussels and settlement plates for barnacles; e.g., Farrell et al., 1991; Menge, 1992; Barth et al., 2007; Witman et al., 2010). Mussel planitgrade larvae attach to the filaments of the mesh balls (SOS Tuffy Pads, The Clorox Company, Oakland, CA, USA) that mimic the filamentous algal and mussel byssal thread surfaces that constitute common settlement sites in nature (e.g., Paine, 1974). We note that recruitment to tuffy collectors does not necessarily reflect realized recruitment to the intertidal as a whole, since realized recruitment is a function of the availability of the appropriate substratum. Thus, numbers of mussels in tuffies are probably most accurately considered “recruitment potential” and this is our meaning in this paper when we refer to mussel “recruitment.”

Following our earlier practice (Rilov et al., 2008), for mussels we analyzed only individuals between 230 and 280 μm. This excludes smaller pre-competent settlers and larger post-recruitment secondary settlers (e.g., Bayne, 1964), so most individuals are likely to have been recruits. Although some have reported success at visually identifying mussel species at the recruit stage (Martel et al., 1999), we have been unable to repeat this success. Recent genetic analyses indicate, however, that most (usually >90%) mussel recruits in our collectors are *Mytilus trossulus* with the remainder consisting of *M. californianus* (P. Raimondi and B. Menge, unpublished data).

Barnacle recruitment was estimated using 10×10 cm PVC plastic plates that are coated on the top side with Saf-T-Walk™ (3M, Minneapolis, MN, USA), a uniformly textured rubbery surface that facilitates barnacle settlement (e.g., Farrell et al., 1991; Menge et al., 1999; Witman et al., 2010). Collectors (*n* = 5) were established at wave exposed locations in the mid intertidal zone at all sites and also the high and low zones at BB and SH. Levels on the shore were similar across all sites. At BB and SH, collectors were also established in wave protected sites. Collector locations were the same each month, with occasional moves to a spot a few cm away when attachment holes needed redrilling due to erosion. The collectors were arrayed evenly-spaced across ~20–30 m of shore. They were replaced monthly, and recruits were identified and counted under a dissecting microscope in

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**Fig. 3.** Time series of monthly *C. dalli* recruitment at ten sites, arranged from north to south from top to bottom. Note that ordinate scales differ among sites. The dashed vertical line separates the 1990s from the 2000s. Note that *C. dalli* recruitment differed between decades at only one site, CM, where it was greater in the 1990s (two-way ANOVA on ln average recruitment by site and decade; decade *p* < 0.05).
the laboratory. Monthly samples were initiated in July 1989 at BB and SH; the number of sites sampled increased steadily starting in 1993 to a maximum of 10 sites from 2001 on. The month-long deployment of these collectors means that the collected juveniles include both settlers (individuals that have settled within the last 24–48 h) and recruits (individuals that settled between ~2 and 30 days prior to collection; Connell, 1985; Menge et al., 2010a). For barnacles, the pre-metamorphic cyprid phases are termed “settlers” and metamorphosed small barnacles are termed “recruits.” Analyses presented elsewhere (Broitman et al., 2008; Menge et al., 2010a) show that numbers of settlers and recruits are positively correlated, suggesting that post-settlement mortality was density independent. Barnacle recruits can be identified to species and we present data for the two most common species, *C. dalli* and *B. glandula*. As with mussel recruitment, densities of recruits on the uniformly-textured collector plates reflect recruitment potential; actual recruitment density on variably-textured rock surfaces is usually lower and more variable than on plates (Menge et al., 2010a). For simplicity, we refer to the numbers of juveniles counted on plate collectors as “recruits,” and to patterns of “recruitment” of barnacles.

### 2.3. Climate data

We obtained climate data from several online sources. ENSO data were obtained from [http://cdc.noaa.gov/ENSO/enso.mei_index](http://cdc.noaa.gov/ENSO/enso.mei_index), PDO data were obtained from [http://jisao.washington.edu/pdo/](http://jisao.washington.edu/pdo/), and NPGO data were obtained from [http://www.ocean3d.org/npgo](http://www.ocean3d.org/npgo). The Bakun upwelling index data were obtained from [http://pfeg.noaa.gov](http://pfeg.noaa.gov). In all cases, monthly averages were matched to monthly recruitment data lagged by one month, under the assumption that ocean conditions that affected larvae in the water column in one month were those that influenced recruitment in the following month (barnacle and mussel planktonic-larval durations are about two to four weeks; Strathmann, 1987).

### 2.4. Data analysis

Analyses were carried out using JMP 8.0 (SAS Institute Inc, 2008), R ([http://lib.stat.cmu.edu/R/CRAN/](http://lib.stat.cmu.edu/R/CRAN/)), and MATLAB ([http://www.mathworks.com/products/matlab/](http://www.mathworks.com/products/matlab/)). To reduce the number of climatic and environmental variables in our analysis and achieve orthogonality or independence of the independent variables, we used principle component analysis (PCA; Legendre and Legendre, 1998). To investigate the relationships between the environmental variables (climate cycles and upwelling), expressed as principle components, and recruitment of each species, we used three approaches: multiple linear regression (e.g., Legendre and Legendre, 1998), multiple quantile regression analysis (e.g., Cade and Noon, 2003), and wavelet analysis (e.g., Torrence and Compo, 1998). Multiple linear regression provides a coarse-scale look at which factors are most closely associated with recruitment of each species. By relating the mean of the response variable to explanatory variables, classical linear multiple regression assumes that this relationship is constant across different levels of the response variable. However, variation in this relationship can reveal important insights about the relative importance of each explanatory variable across different levels of the response variable. For example, recruitment may be unrelated to upwelling at low levels of recruitment, but strongly related to upwelling at high levels of recruitment. This type of variation would indicate that recruitment is (1) limited by processes unrelated to upwelling at low levels of recruitment and (2) limited by upwelling at high levels of recruitment. We explored this type of variability by relating the environmental and climate PCA axes to different levels...
(i.e. quantiles) of recruitment using multiple quantile regression analysis (Cade and Noon, 2003).

Investigation of how the magnitude and pattern of variability of recruitment varies through time is best achieved with time series analysis (e.g., Chatfield, 1996). Two key assumptions of classical time series analysis (i.e. spectral analysis) are that the time series is continuous, with no missing data, and “stationarity,” or that all moments of the time series (i.e. mean, variance, kurtosis, etc.) do not change in time (Chatfield, 1996; Torrence and Compo, 1998; Cazelles et al., 2008; Rouyer et al., 2008a, 2008b). Here, the assumption of stationarity is clearly violated: major changes in recruitment have occurred at several scales (decadal, in relation to ENSO, etc.). Wavelet analysis is ideal for non-stationary time series because it can quantify the dominant modes of variability and how these modes vary in time (Torrence and Compo, 1998; Cazelles et al., 2008). Recent work has shown that wavelet analysis can be highly robust to missing values (Cazelles et al., 2008). When they occurred (data were missing in 19 of 233 months or 8.25% for mussels, and 15 of 233 months or 6.44% for barnacles), gaps in our time series were filled in using linear interpolation prior to conducting wavelet analysis. Cubic spline interpolation gave nearly identical results. We provide a complete overview of wavelet analysis in Appendix 1. Briefly, we used cross-wavelet and wavelet coherence to quantify, respectively, the covariance and the correlation between recruitment and each environmental variable in the time-frequency domain. These two methods provide complementary information about patterns of covariation between pairs of time series. Cross-wavelet analysis identifies regions where time series have high common power, whereas wavelet coherence identifies regions where time series show correlated (or coherent) fluctuations (Cazelles et al., 2008; Grinsted et al., 2004). We present the wavelet coherence results in the main text and provide the cross-wavelet analysis in Appendix 2.

3. Results

3.1. Recruitment

Previously, we reported that recruitment rates of mussels increased dramatically in the early 2000s (time series shown in Menge et al., 2009), and showed that on average, barnacles did not exhibit a similar increase. These time series ran up to 2006 in Menge et al. (2009), and have now been extended through 2008 (e.g., see Menge et al., 2010b). The detailed time series for the barnacles B. glandula and C. dalli show that recruitment has changed little since the 1990s (Figs. 2 and 3). In contrast to mussel recruitment, the time series of monthly B. glandula recruitment showed only slight inter-decadal changes in abundance (see Appendix Fig. 2 in Menge et al., 2010b). Of the six (out of ten) sites with time series that began in the mid-1990s or earlier, two (SR and SH) had higher recruitment in the 2000s and four did not (Appendix Fig. 2 in Menge et al., 2010b). For SR, this difference seems driven largely by the 2008 recruitment season, in which extraordinarily high recruit densities occurred (Fig. 2). At SH, the difference appears driven by the 2006, 2007 and 2008 recruitment seasons, all of which had denser recruitment than all previous years except 1995 (Fig. 2). We note that the 1990s data for CM, FC, and YB were limited in extent, so it is likely the inter-decadal trends are better reflected by the other four sites (Fig. 2). These differences were sufficient to make the effect of decade significant, but overall the total variance explained was modest (two-way ANOVA; decade $R^2 = 0.11$). In general, however, in comparison to mussels, changes in B. glandula recruitment after 1999 were minimal.

The barnacle C. dalli is a flatter, smaller barnacle than B. glandula and in Oregon is not a strong facilitator of mussels (B. Menge, personal observations). In predation-impact experiments (e.g., Dayton, 1971;
Menge, 2003), C. dalli is often the most abundant species in treatments with predators present, consistent with the view that C. dalli is an unattractive prey (Paine, 1981). Exclusion of predators commonly results in dense covers of B. glandula which are then overgrown by mussels M. trossulus. Nonetheless, because C. dalli can occupy significant amounts of space in the low intertidal at some sites and because chthamaloids elsewhere can facilitate mussel recruitment (Navarrete and Castilla, 1990), we also examined changes of this barnacle across the decadal shift from the 1990s to the 2000s.

As with B. glandula, recruitment of C. dalli also did not change between decades (Fig. 3). Comparing average rates of recruitment by site and decade reveals inter-decadal differences at only one of six sites with sufficiently long time series (Fig. 3; Cape Meares = CM), and this difference was opposite to that shown by both mussel and B. glandula recruitment (see Appendix Fig. 2 in Menge et al., 2010b). Finally, recruitment densities of this smaller barnacle were generally much lower than those of B. glandula (Fig. 3), suggesting a more limited capacity to reach the high densities that are needed for effective facilitation of mussels.

3.2. Seasonal shifts

Although inter-decadal differences in barnacle recruitment were limited, it is possible that the seasons of recruitment differed between decades, thus potentially altering their interaction with mussels. As we have shown previously, mussel recruitment peaks have generally shifted one to two months later in the season, from July/August to September/October (Menge et al., 2005).

Overall, seasonal shifts in barnacle recruitment were slight, and although statistically significant shifts occurred in a few cases, these shifts seem ecologically trivial. For example, at five of six sites (CM, FC, BB, SR, and SH), small seasonal shifts in recruitment occurred in B. glandula, and changes at CA, though not significant, show a trend similar to the other sites (Fig. 4, Appendix Table 1). In general, the season of recruitment at these sites has expanded, with higher recruitment occurring earlier (March), later (October–December), or both, in the year.

The small barnacle C. dalli showed no inter-decadal seasonal shifts although non-significant trends towards earlier recruitment were evident at all six sites (Fig. 5, Appendix Table 2). Thus, although B. glandula recruitment season appears to have expanded in the 2000s, these trends are not consistent with a shift in phenology that might have reduced the amount of barnacle substratum available for mussel recruits. In fact, the tendency for higher barnacle recruitment later in the year is in the same direction as that seen for mussels, suggesting that at some sites, if anything, barnacle substratum may be more, not less available.

3.3. Linear and quantile multiple regressions

We first performed a PCA of all 1-month lagged environmental variables in order to (1) reduce the number of independent environmental variables used in the multiple regressions of recruitment and (2) prevent any correlation between the independent environmental variables from affecting the estimates of the multiple regression coefficients (i.e., avoid the “bouncing beta” issue due to multi-collinearity). PCA of all 1-month lagged environmental factors (MEI, NPGO, PDO, and upwelling) resulted in four axes, the first three of which explained over 88% of the total variance in the environment (Fig. 6, Tables 1 and 2). PCA axis 1 mainly represents MEI (loading = 0.6) and PDO (0.59); PCA axis 2 mainly represents upwelling (0.96); PCA axis 3 mainly represents NPGO (0.82) (Fig. 6, Table 1).

We further limited the number of PCA axes used for each multiple regression of recruitment by conducting forward selection on all PCA axes using a double-stopping criterion based on α = 0.05 and the adjusted R² of the full multiple regression model containing all four PCA axes (Blanchet et al., 2008). This resulted in the selection of PCA axes 2–3 for Mytilus spp. recruitment (Table 3) and B. glandula recruitment (Table 4), and PCA axes 1–3 for C. dalli recruitment (Table 5).

Multiple linear regression of log-transformed recruitment against all forward-selected environmental PCA axes showed similar effects of upwelling (PCA axis 2) and NPGO (PCA axis 3) on recruitment across species: recruitment tended to increase primarily with upwelling and NPGO (Fig. 7). The strength of these relationships were similar among species (Mytilus spp.: p < 0.0001, Adj. R² = 0.298; B. glandula: p < 0.0001, Adj. R² = 0.386; C. dalli: p < 0.0001, R² = 0.369; see Fig. 7, Tables 3–5).

Multiple quantile regression of recruitment as a function of all forward-selected environmental PCA axes showed interspecific
differences in the relationships between recruitment quantiles and the environment. Overall, *B. glandula* recruitment was consistently and strongly related to both climatic (NPGO) and environment (upwelling) indices (PCA axes 2 and 3), respectively; (Fig. 8), whereas the effects of climatic and environmental indices were contingent upon recruitment rates for both *C. dalli* and *Mytilus* spp. The effect of climate (NPGO) on *C. dalli* recruitment was strongly unimodal, with low rates of recruitment being unrelated to climate, intermediate to high rates showing a strong positive relationship with recruitment, and the highest rate being unrelated to climate (PCA axis 3; Fig. 9). The response of *C. dalli* recruitment to the environment was saturating, with low rates being unrelated to the environment and high rates being strongly related to the environment. Mussel recruitment relationships to upwelling and NPGO were similar to those for *C. dalli*, and thus also show a saturating response to both climate and environmental indices (Fig. 10). Hence, the effect of climate and the environment on recruitment is strong and consistent across recruitment rates for *B. glandula*, but contingent upon recruitment rates for both *C. dalli* and mussels, with weak effects at low rates and strong effects at intermediate and high rates. These results suggest that factors other than upwelling, MEI, NPGO and PDO play an important role in controlling recruitment variability at low and high rates (Cade and Noon, 2003).

### 3.4. Relationship between recruitment and environmental variables

We used cross-wavelet and wavelet coherence analyses to determine the pair-wise relationships between recruitment and each environmental variable (see Appendix 1). Wavelet coherence and cross-wavelet describe, respectively, the correlation and the covariance between pairs of time series in the time-frequency domain (Cazelles et al., 2008). Since both analyses yielded similar results, we present the wavelet coherence results in the main text (Figs. 11–13) and include the cross-wavelet analyses in Appendix 2 (Figs. 3–5). We note that strong patterns of covariation in these analyses do not necessarily imply causation (Cazelles et al., 2008). A strong association at annual frequencies between recruitment and upwelling, for example, could simply reflect the fact that both have strong annual cycles.

The relationships between recruitment and environmental variables clearly varied among species, with periodicity, and through time (Figs. 11–13; Appendix 2, Figs. 3–5). For all species, most times of coherence between environment and recruitment occurred at low periods (~8–16 months), that is approximately on an annual scale, particularly with PDO and upwelling. Relationships were complex however, with both in-phase and anti-phase and longer period (16–32 months or ~2 year and 32–64 months or ~4–5 year) associations.

*B. glandula* recruitment was associated with MEI (in-phase) and NPGO (anti-phase). These relationships occurred only briefly, from the late 1990s to about 2000 (MEI) or 1999–2002 (NPGO), but varied dramatically in strength, with intermittent and weak-to-moderate levels of in-phase fluctuations with MEI, especially during the strong 1998 ENSO event and subsequent La Niña (Fig. 11B). The anti-phase fluctuations between recruitment and NPGO overlapped the La Niña period, extending into the early 2000s (Fig. 11C). PDO and upwelling were much more strongly associated with recruitment of *B. glandula*. PDO showed strong but fluctuating associations (in-phase and anti-phase fluctuations) at 8–16 month periods, strong and persistent in-phase fluctuations at ~2 year periodicities from 1993 to 2005, and even apparent strong and persistent relationships at 4–5 year periodicities (at least during the middle of the time series, Fig. 11D). Upwelling showed strong associations at 8–16 month periods in the mid 1990s and from about 2000 on, with a notable gap during the time of the 1997–2000 ENSO/La Niña and at 16–32 month period in the mid 1990s (Fig. 11E). Thus, overall, *B. glandula* recruitment varied with all environmental measures, most persistently at annual periodicities with PDO and upwelling, but with interesting gaps that seem to coincide with the strong 1997–2000 ENSO/La Niña and short-lived shift in PDO.

*C. dalli* recruitment showed very similar patterns of variation, with intermittent and brief in-phase fluctuations with MEI (~8–16 months) during the 1997–2000 ENSO/La Niña, weaker and sporadic in- and out-of-phase fluctuations with NPGO at low periods (~8–16 months), periodically strong in- and out-of-phase fluctuations with PDO, and more persistent in-phase fluctuations at low periods (~8–16 months) with upwelling (Fig. 12B–E). We again note the interesting coincidence of the strong association with El Niño/La Niña and gaps in PDO and upwelling coherence during this time. *Mytilus* spp. recruitment showed very similar patterns to those of the barnacles (Fig. 13).

### 3.5. Relationship between recruitment of different species

We also used cross-wavelet and wavelet coherence analysis to determine patterns of interspecific co-variation in recruitment (Fig. 14 and Appendix 2, Fig. 6). In general, all species showed strong and coherent fluctuations in recruitment at periodicities ranging up to ~two years. Recruitment of all species showed highly coherent

### Table 2

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Note: Forward selection based on double-stopping criterion (α = 0.05, Adj. R² of full model containing all four PCA axes) and 1000 permutations of the residuals under the reduced model.

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<td>0.684</td>
</tr>
<tr>
<td>Proportion of variance</td>
<td>0.469</td>
<td>0.255</td>
<td>0.158</td>
<td>0.117</td>
</tr>
<tr>
<td>Cumulative proportion</td>
<td>0.469</td>
<td>0.725</td>
<td>0.883</td>
<td>1</td>
</tr>
</tbody>
</table>

Note: Forward selection based on double-stopping criterion (α = 0.05, Adj. R² of full model containing all four PCA axes) and 1000 permutations of the residuals under the reduced model.

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fluctuations at very high frequencies (or lower periods). All associations were in-phase, or positively correlated. Recruitment of the barnacle species showed the most similarities in space/time (Fig. 14B), but mussel recruitment was generally similar in coherence with both barnacle species as well (Fig. 14C, D).

4. Discussion

The factors underlying the often massive variations in recruitment are notoriously difficult to discern. Recruitment can vary because of variation in climate, in oceanographic variability (e.g., upwelling, alongshore currents, offshore breezes, internal tidal bores, wave regime, and coastal geomorphology), in reproductive output, in larval availability and behavior, and in immediate post-settlement factors such as species interactions and disturbance (Pineda, 2000). In this analysis, we attempted to detect the relationships between large-scale climatic factors as expressed in the MEI, NPGO and PDO climatic indices and intermediate-scale variation in upwelling, and recruitment of three major component taxa of rocky intertidal communities along the US west coast. Our results suggest that recruitment shows surprisingly strong links to these regional to ocean-basic scale variables, but also that the relationships are highly complicated in space and time.

4.1. Patterns of recruitment

As with mussel recruitment (Menge et al., 2009), barnacle recruitment varied as a function of season, site and latitude, as well as in time (Appendix 2 Fig. 2, Figs. 2 and 3). Temporal and spatial variation in barnacle recruitment was, however, less than that observed for mussels. Despite these differences, all three analyses aimed at determining the relationship between climate, regional environment (upwelling) and recruitment led to similar results. Environmental variation, even at large, ocean-basin scales, can explain substantial amounts of variation in recruitment, ranging from 30 to 40%. Given the many local sources of variation, this amount of explanatory power is
surprisingly high. Thus, as expected from hypothesis H1, each taxon was sensitive to climate-related variation, and responded similarly to these sources of variability (hypothesis H2). However, contrary to hypothesis H3, barnacle recruitment showed only slight shifts between the 1990s and 2000s.

4.2 Large-scale forcing, sequential filters and the role of larval transport in determining recruitment

Pineda (2000) modeled the process by which larvae travel to the adult habitat as a series of filters that sequentially reduce the numbers of larvae as they progress towards recruitment into the adult habitat, with multiple filtering mechanisms. Our analysis suggests that, at large scales of space and time, these three taxa respond somewhat similarly to climate and environmental effects. At the same time, the 30–40% of variance explained by these factors means that >60% of the variance in recruitment is due to other factors, presumably including those highlighted above. The local-scale, among-site and temporal variations evident in the actual time series for each of these species (Figs. 2 and 3, Fig. 2 in Menge et al., 2009) is presumably a reflection of the influence of such factors.

The similarities in the responses of recruitment to climate and environmental variability at large spatio-temporal scales documented here and the differences observable in the time series data highlight how some processes can vary in their role as a function of the scale considered. For example, our analysis suggests that upwelling affects all species strongly, at least at longer time scales (annually or multi-annually). But upwelling also varies on scales of days to months within years, with alternations between upwelling and downwelling events at scales of days to weeks being a particularly strong short-term scale. The role of upwelling in influencing recruitment has been controversial, and current evidence is actually contradictory on the role of upwelling in recruitment of these species. For *B. glandula* for instance, some studies find an impact of upwelling regime, with apparent strong (e.g., Farrell et al., 1991), moderate (Dudas et al., 2009) or weak effects of upwelling relaxation on recruitment (Shanks, 2009), while others find no relationship with upwelling (Morgan et al., 2009; Shanks and Shearman, 2009).

At finer, within-region, among-site scales, a host of processes must be considered. Thus, different patterns between mussel and barnacle recruitment seen at these scales likely reflect both spatio-temporal and qualitative differences in larval transport mechanisms, although differences in susceptibility to post settlement mortality sources could also play a role. The most likely larval transport mechanisms involved at the more local and shorter scales include transport by short-term upwelling–downwelling fluctuations, wind-driven transport including diurnal fluctuations in sea breezes, current-related variation in larval behavior, wave forcing, and tidally-driven change, such as internal waves (Farrell et al., 1991; Hawkins and Hartnoll, 1982; Pineda, 1991, 1999; Shanks and Brink, 2005; Woodson et al., 2007; Rilov et al., 2008; Dudas et al., 2009; Morgan et al., 2009; Shanks, 2009; Shanks et al., 2010; Witman et al., 2010).

Recent studies have sharpened the focus on processes delivering larvae across the last few hundreds of meters to shore. For example, consistent with a growing number of examples for fish larvae (Warner and Cowen, 2002; Swearer et al., 2002; Cowen et al., 2006), extensive cross-shelf sampling off Bodega Bay, California, indicates that the larvae of the majority of invertebrates develop close to shore (<3 km; Morgan et al., 2009) rather than being swept far offshore during upwelling as previously postulated. In another example, spatial variation among sites in mussel recruitment was unrelated to abundance of larvae just outside the surf zone (Rilov et al., 2008), suggesting a key role for processes within the surf zone in determining spatial and likely temporal variation in recruitment. Shanks et al. (2010) found that recruitment of *B. glandula* to boulders tended to be higher on dissipative than on reflective sandy beaches, and was greater on days with higher significant wave heights, suggesting the importance of micro-hydrodynamical processes as larvae approach their final destination. Shanks et al. (2010) also note that these patterns may not translate to continuous rocky shores, and indeed, recruitment of both barnacles at our sites tends to be higher,
4.3. Interactive effects of climate patterns

The wavelet analyses suggest that recruitment rates respond in complex ways to the different climate and environment measures. In addition to the issues discussed above, the fact that coherences between climate and environment, and recruitment, vary in whether they are in-phase (positively correlated) or in anti-phase (negatively correlated) suggests that the indices are aliasing the actual factor(s) that larvae are responding to as oceanographic conditions fluctuate. Pairwise comparisons suggest that during the 1989–2008 time period, this is the case. MEI, PDO and NPGO show highly non-stationary (i.e. variable in time) patterns of co-variation (Appendix 2 Fig. 7). For example, MEI and NPGO showed strong and anti-phase patterns of fluctuations at high periods (~64 months), but also in-phase moderate-to-weak fluctuations at low periods (~8–16 months). Strong fluctuations occurring at high periods remained consistently anti-phase in time, whereas weak-to-moderate fluctuations tended to shift from in-phase (e.g. from 03–93 to 09–98) to anti-phase (e.g. 02–04 to 11–06) in

not lower, at steeper and presumably more reflective sites (e.g., SR, FC vs. SH, TK; Appendix Fig. 2).

Fig. 10. Quantile and linear regressions used to describe log-transformed Mytilus spp. recruitment ($y$) as a function of forward-selected environmental PCA axes 2 ($x_1$) and 3 ($x_2$).

\[
\log_{10} y = \beta_1 x_1 + \beta_2 x_2 + \beta_0 + \epsilon
\]

Linear multiple regression: p-value $2.2 \times 10^{-16}$, Adjusted $R^2 = 0.298$. See Fig. 8 caption for further explanation.

Fig. 11. Standardized time series and pairwise wavelet coherence of B. glandula recruitment and monthly (B) MEI, (C) NPGO, (D) PDO and (E) upwelling from 1989 to 2008. Wavelet coherence describes the amount of correlation (or coherence) in the fluctuations of two time series (color bar) in the time-frequency domain. Black arrows indicate the phase angle between the fluctuations of the two time series. Arrows pointing to the left indicate anti-phase fluctuations, whereas arrows pointing to the right indicate in-phase fluctuations. Black contour lines indicate regions in which the observed wavelet coherence values are statistically significantly ($\alpha = 0.05$) based on Monte Carlo randomizations applied to 1000 pairs of surrogate time series whose first-order autoregressive coefficients match those of the original time series. Blacked-out areas represent the “cone-of-influence” where edge effects can influence the analysis. Period is in units of months. The x-axis indicates the time (month-year).
MEI and PDO showed strong and persistent in-phase fluctuations at high periods (~64 months) and transient, weak-to-moderate in-phase fluctuations at low periods (~8–12 months; e.g. from 12–95 to 05–01). Finally, PDO and NPGO showed strong and persistent anti-phase fluctuations at high periods (~64 months), but transient and in-phase moderate-to-weak in-phase fluctuations at low periods (~6–16 months). Since all the climatic patterns are large, basin-scale phenomena, the specific mechanisms underlying the apparent teleconnections between these large-scale patterns to regional coastal conditions to region- and site-scale patterns of recruitment will clearly be challenging to identify.

5. Conclusions

In the quest to determine the causes of the often puzzling variation in patterns of recruitment of marine organisms, most attention has been focused on processes and mechanisms that operate on shorter
time scales at smaller spatial scales. In our analysis, we have taken advantage of unique recruitment time series for key components of rocky intertidal communities along the Oregon coast in an attempt to assess the possible role of climatic and environmental variation. We found that such large-scale, long-term variation can explain over a third of the variability in our time series, suggesting that much variation in recruitment may be due to factors operating on climatic scales. Thus, taking advantage of unique recruitment time series for key components of the Oregon coast. The research was supported by grants from the NSF, the Andrew W. Mellon Foundation, and the David and Lucile Packard Foundation, the Gordon and Betty Moore Foundation, and by endowment funds from the Wayne and Gladys Valley Foundation. This is contribution number 382 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans funded primarily by the Gordon and Betty Moore Foundation and David and Lucile Packard Foundation. [SS]

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References


