

INTERHEMISPHERIC COMPARISON OF RECRUITMENT TO INTERTIDAL COMMUNITIES: PATTERN PERSISTENCE AND SCALES OF VARIATION

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Abstract. Recruitment variation can be a major source of fluctuation in populations and communities, making it difficult to generalize results. Determining the scales of variation and whether spatial patterns in the supply of individuals are persistent over time can provide insight into spatial generality and the application of conservation and metacommunity models. We examined these issues using eight-year-long data sets of monthly recruitment of intertidal mussels (*Mytilus* spp., *Perumytilus purpuratus*, *Semimytilus algosus*, *Brachidontes granulata*) and barnacles (*Balanus glandula*, *Chthamalus dalli*, *Jehlius cirratus*, *Notochthamalus scabrosus*) at sites spanning >900 km along the coasts of Oregon–northern California (OR–NCA, 45.47–39.43° N) and central Chile (CC, 29.5–34.65° S). We evaluated four general “null” hypotheses: that despite different phylogenies and great spatial separation of these taxa, their similar life history strategies and environmental settings lead to similar patterns of recruitment (1) between hemispheres, (2) in time, (3) in space, and (4) at larger and smaller spatial scales. Hypothesis 1 was rejected: along the OR–NCA coast, rates of recruitment were between two and three orders of magnitude higher, and patterns of seasonality were generally stronger and more coherent across space and time than along CC. Surprisingly, however, further analysis revealed regularities in both time and space for all species, supporting hypotheses 2 and 3. Temporal decorrelation scales were 1–3 months, and characteristic spatial scales of recruitment were ~250 km. Contrary to hypothesis 4, for the ecologically dominant species in both hemispheres, recruitment was remarkably persistent at larger mesoscales (kilometers) but was highly stochastic at smaller microscales (meters). Across species, increased recruitment variation at large scales was positively associated with increased persistence. Our results have several implications. Although the two regions span distinct latitudinal ranges, potential forcing processes behind these patterns include similar large-scale climates and topographically locked hydrographic features, such as upwelling. Further, spatial persistence of the recruitment patterns of most species at the mesoscale supports the view that marine protected areas can be powerful conservation and management tools. Finally, persistent and yet contrasting spatial patterns of recruitment among competing species suggest that recent metacommunity models might provide useful representations of the mechanisms involved in species coexistence.

Key words: barnacles; Chile–Oregon–California; coastal oceanography; long-term time series; mussels; predictability; settlement; spatial scale; spatial statistics; supply-side ecology; upwelling.

INTRODUCTION

Understanding the processes that determine patterns of community structure on scales ranging from local to biogeographic remains a central goal of ecology. The desire to generalize the insights gained from local observations is usually hampered by large environmental variation and by the sensitivity of species interactions to these conditions (Lawton 1999, Peacor and Werner 2004, Navarrete and Berlow 2006). Over the past few

decades efforts to compile precise environmental and biological information over large areas have dramatically intensified (Connolly et al. 2001, Stenseth et al. 2002, Menge et al. 2004, Coleman et al. 2006). A major motivation for such studies has been the realization that our ability to anticipate the effects of climate change and other human impacts requires the integration of responses to local conditions over larger areas (Stenseth et al. 2003, Pandolfi et al. 2005, Berryman and Lima 2006, Helmuth et al. 2006, Barth et al. 2007). Results of these studies have revealed the existence of unsuspected patterns of variation and highlight their dependence on regional to global environmental drivers. For example, experiments at five sites on the European coast revealed

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the existence of a sharp gradient in the control by limpets of algal biomass, with generally stronger effects to the north (Coleman et al. 2006). Hughes et al. (1999) examined spatial patterns in corals on the Great Barrier Reef, across a spectrum of scales ranging from meters to >1700 km and showed that coral reef assemblages that are similar in terms of abundance may nonetheless show profound differences in dynamics and turnover, with major implications for their ecology and management. On the eastern Pacific coast, Menge et al. (2004) and Navarrete et al. (2005) found that the effects of predation as a structuring process in intertidal communities were highly dependent on large-scale (hundreds of kilometers) gradients in recruitment of competitively dominant sessile species in the northern and southern hemispheres, respectively. Evidence from localized studies on both shores (Menge et al. 1994, 1997*a, b*, Nielsen and Navarrete 2004, Lagos et al. 2005, Narváez et al. 2006) strongly suggests that oceanographic regimes drive rates of recruitment over regional spatial scales.

Because the majority of marine organisms have life stages that spend part of their development in the water column, where they are subject to multiple sources of mortality and advective–diffusive processes that transport them varying distances away from the parental populations, stochasticity and uncertainty in the arrival of new individuals to shore is expected to be high (Sale et al. 1984, 2005, Caley et al. 1996, Hughes et al. 1999, Pineda 2000). The influence of this stochasticity can vary, however. In many cases, fluctuations in recruitment do not produce substantial variation in local population abundances (e.g., Hughes et al. 1999, Menge 2000, Paine 2002). Further, the arrival of individuals from distant populations may dampen population fluctuations in comparison to species that reproduce locally (Eckert 2003). In other cases, recruitment is one of the major sources of fluctuations in population numbers. For example, many studies have shown the profound consequences of recruitment variation on population dynamics (Gaines and Roughgarden 1985, Roughgarden and Iwasa 1986, Hyder et al. 2001) and on the strength of species interactions (Navarrete and Menge 1996, Robles 1997, Connolly and Roughgarden 1999, Navarrete and Berlow 2006). Spatial scale seems key to understanding such differences. Despite the potential for unpredictability, several studies have shown that in some cases physical and biological factors can produce predictable, spatially persistent patterns of recruitment at some spatial scales (Flores et al. 2002, Lagos et al. 2005, Hamilton et al. 2006). Over sufficiently large scales in relation to dispersal (hundreds of kilometers), populations should be closed and recruitment variation should be correlated with overall larval production (Hughes et al. 2000, Hamilton et al. 2006). Over mesoscales (tens of kilometers), nearing the scales of dispersal of many marine organisms (Kinlan and Gaines 2003, Shanks et al. 2003), patterns of recruitment can be greatly influenced by topographically

modulated oceanographic processes (e.g., upwelling) and larval production, potentially generating temporally coherent recruitment patterns (Hughes et al. 1999, Broitman et al. 2005, Lagos et al. 2005, Hamilton et al. 2006). At small scales (centimeters to meters) many studies have shown large and unpredictable variation, probably because of stochastic variation in small-scale hydrographic processes interacting with larval behavior and settlement cues (Keough and Downes 1982, Bourget 1988, Pineda 2000, Levin 2006).

While several studies have quantified spatial scales of variation in recruitment using hierarchical sampling (e.g., Hughes et al. 1999, Flores et al. 2002), it is unclear whether increased variability at a particular spatial scale is associated with increased temporal persistence of the spatial pattern, or increased stochasticity at that scale (e.g., fluctuation of “good” and “bad” locations). Long-term studies at a range of scales are required to examine whether or not processes producing large recruitment variation are also topographically anchored. One can hypothesize that in regions where dominant oceanographic conditions are modulated by mesoscale topographic features, recruitment patterns should be more persistent at these than at smaller spatial scales. Whether recruitment fluctuates stochastically or exhibits persistent order is not only critical for population and community dynamics, but also for the effectiveness of marine protected areas. Indeed, models of marine protected areas assume that the spatial structure of sources and sinks remains invariant over several generations (Lockwood et al. 2002, Kaplan 2006, Aiken et al. 2007). An interesting question is whether predictability of recruitment patterns and their characteristic spatial and temporal scales of variation (Legendre and Legendre 1998) can be anticipated from knowledge of natural history of the adults or their larval stages. Regions where dominant oceanographic conditions are similar could impose similar spatial scales of variation in recruitment of species with comparable planktonic larval durations, regardless of taxonomic affinities. For example, a recent study showed that recurrent physical–biological coherence can emerge in complex coastal systems, which exhibit coincident spatial scales of variation in topography, sea surface temperature, chlorophyll *a*, and kelp forest abundance along the coast of North America (Broitman and Kinlan 2006).

Coastal upwelling ecosystems represent excellent systems for comparative studies of recruitment variation and for testing general hypotheses about the influence of supply on marine communities. These ecosystems are often tightly coupled to oceanographic processes that are modified by topography and can influence rates of larval supply over the mesoscale (e.g., Wing et al. 1995, Lagos et al. 2005, 2007). Here we take advantage of unique “long-term” (eight years) data sets of monthly recruitment of dominant sessile intertidal species at a large number of sites along the eastern Pacific coasts of

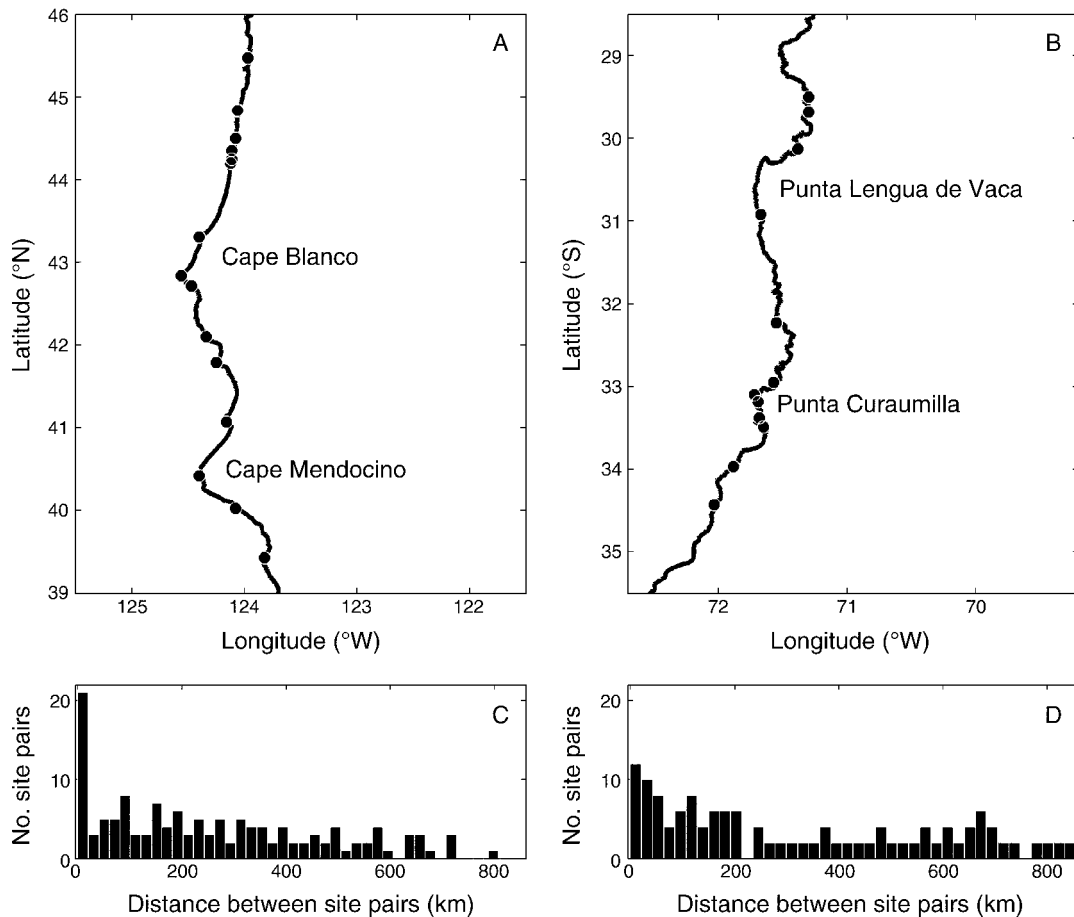


FIG. 1. Map of (A) Oregon–northern California (OR–NCA) and (B) the central Chile (CC) regions showing the major topographic features along the region and the location of the study sites (solid circles). The distribution of distances between any two sites is shown in histograms for all pairs of sites in (C) Oregon–northern California and (D) central Chile.

North and South America to evaluate several broad “null” hypotheses: (1) Despite different latitudinal ranges on their respective coasts, recruitment seasonality will be similar. (2) Despite taxonomic differences and presumably different evolutionary histories, temporal variation on monthly scales will be similar. (3) Likewise, spatial variation at meso- to macroscales will be similar, and (4) spatial pattern is equally persistent at meso- and small scales.

We note that rigorous testing of these broad hypotheses through experimentation, for example, is impossible, and thus view them as guides for the exploration of recruitment patterns. Our expectations were that (1) because seasonality of hydrographic and environmental conditions is stronger along the Oregon–northern California coast than central Chile (Strub et al. 1998, Mendelssohn and Schwing 2002), hypothesis 1 would be rejected; (2) because large-scale climate, oceanography, and life histories were similar among species, hypotheses 2 and 3 would be supported; and (3) because key processes such as hydrography and larval

behavior are likely to have differing influences at smaller and larger scales, hypothesis 4 would be rejected.

MATERIAL AND METHODS

Study sites and organisms

We quantified monthly recruitment rates of intertidal mussels and barnacles from 1997 to 2005, using exactly the same field methods along the coasts of Oregon–Northern California (OR–NCA) in North America and central Chile (CC) in South America (Fig. 1; also see Plate 1). The multispecies data sets include the most conspicuous and ecologically dominant sessile invertebrates of these rocky shores (Appendix: Species Ecology). Recruitment of these species was quantified at 16 sites distributed between 45.47° and 39.43° N along OR–NCA and 16 sites between 29.5° and 34.65° S along CC, separated from few to tens of kilometers (Fig. 1). Due to the proximity of some sites in central Chile, only 12 sites were used for spatial analyses. The spatial distribution of sites provided an adequate and similar sample of between-site distance classes up to 400 km, the distance we use as the limit for the

interpretation of spatial patterns (Fig. 1C, D). Because trends observed over hundreds of kilometers have been the focus of previous studies (Connolly et al. 2001, Navarrete et al. 2002, 2005), we concentrate here on patterns at the small- (meters) and mesoscales (kilometers). Small-scale variation in barnacle and mussel recruitment was captured by five to eight plate and Tuffy pad collectors, respectively, separated by no less than 3 m and no more than 20 m in the mid- and high intertidal zones (Appendix: Field Methods).

Data analyses

To assess whether the strength of seasonal trends was similar across regions and species, and whether temporal scales of variation in monthly recruitment were similar, regardless of the taxa examined, we: (1) calculated means and coefficients of variation in recruitment for each calendar month of the year at each site as well as for each month across the region, and (2) calculated the spatially averaged rank-based temporal autocorrelation of each time series at each site and then examined the across-sites average at each lag (Appendix: Statistical Methods).

To determine the proportion of variance in recruitment explained by variation at the scale of sites (kilometers) and collectors (meters), we used maximum likelihood estimates of variance components, fitting a nested analysis of variance model to nonzero recruitment data in each month, considering sites as a random factor and collector as a random factor nested within sites (Appendix: Statistical Methods). To assess whether the spatial pattern was temporally persistent, we examined the spatial rank correlation of all sites within each hemisphere and species, at increasing time lags. Similar analyses were performed to examine pattern persistence at the scale of collectors located meters apart, but these analyses could only be performed for OR–NCA because in Chile there was no tracking of the position of collectors (Appendix: Statistical Methods).

To determine whether synchrony in monthly recruitment rates was observed over comparable spatial scales between upwelling ecosystems and among species, we calculated a spatial coherence using a spline correlogram function (Bjørnstad et al. 1999) for each species, from which we estimated the spatial length scale of recruitment synchrony (Appendix: Statistical Methods).

RESULTS

Seasonality of recruitment patterns

Mussel and barnacle recruitment rates were between two to three orders of magnitude higher along the OR–NCA coast than CC (Fig. 2). Recruitment of *Mytilus* in the OR–NCA region was strongly seasonal, with a well-defined peak in the late boreal summer–fall. The average interannual variability (coefficients of variation) was moderate and remarkably similar for all months of the year, suggesting that there were no shifts in seasonality of recruitment over the eight-year window

considered in this study. Variation in seasonality across sites was comparable to interannual variation within sites, except for a sharp increase in June–July, suggesting that the onset of the *Mytilus* recruitment season does not occur simultaneously through the region (Fig. 2A). However, by the time of peak recruitment, variation across sites was comparable to within-site variation.

The three mussel species along CC exhibited different patterns. The competitively dominant *Perumytilus* recruited throughout the year, with a shallow peak in austral summer (January–February). While interannual variation within sites was moderate and similar for all months of the year, there was large variation among sites (Fig. 2D). These results indicate that seasonality in this species did not shift over time within sites, but that among-site variation in terms of when peak recruitment occurs was high. The mussel *Semimytilus* also recruited year round with peaks in austral winter (June–July) and in summer (December; Fig. 2E). Again, interannual variation in seasonality within sites was comparatively low, but high (CV, ~200%) among sites. The mussel *Brachidontes* recruited at low rates throughout the year, with no clear seasonal trend (Fig. 2F). Interannual variation in seasonality within sites and variation among sites were similar for this species. Thus, in the northern hemisphere mussel recruitment presented a stronger seasonal pattern, with lower interannual variation within sites and higher coherence across sites in the region than all mussels in the southern hemisphere.

Recruitment of *Balanus* in the OR–NCA region exhibited two peaks, one in early spring (March) and a broader one in summer–late fall (July–October; Fig. 2B). Interannual variability and variation across sites were slightly higher in winter and early spring months, when recruitment was lower. Recruitment of *Chthamalus* peaked in summer and fall months (July–September) and, like *Balanus*, both interannual and among-site variability was higher in winter, at times of low recruitment (Fig. 2C). Recruitment of the two barnacles in the CC region exhibited sharp peaks, with one peak in spring (November) for *Notochthamalus* (Fig. 2G) and two peaks, one in fall (March) and one in spring (November) for *Jehlius* (Fig. 2H). Large interannual and among-site variability in these seasonal patterns was observed in CC barnacles (notice the different right-side y-axes in Fig. 2G, H). Thus, all southern and northern hemisphere barnacles exhibited seasonal recruitment, but the seasons of CC were shorter and more variable within and among sites.

Temporal scales of variation

The nonparametric temporal autocorrelations for each species provide further support for the existence of contrasting temporal patterns among hemispheres on seasonal timescales (Fig. 3). Autocorrelations of mussels and barnacles in OR–NCA showed clear seasonal signals (Fig. 3A, B), while no species in CC exhibited a seasonal trend likely due to high spatial and temporal

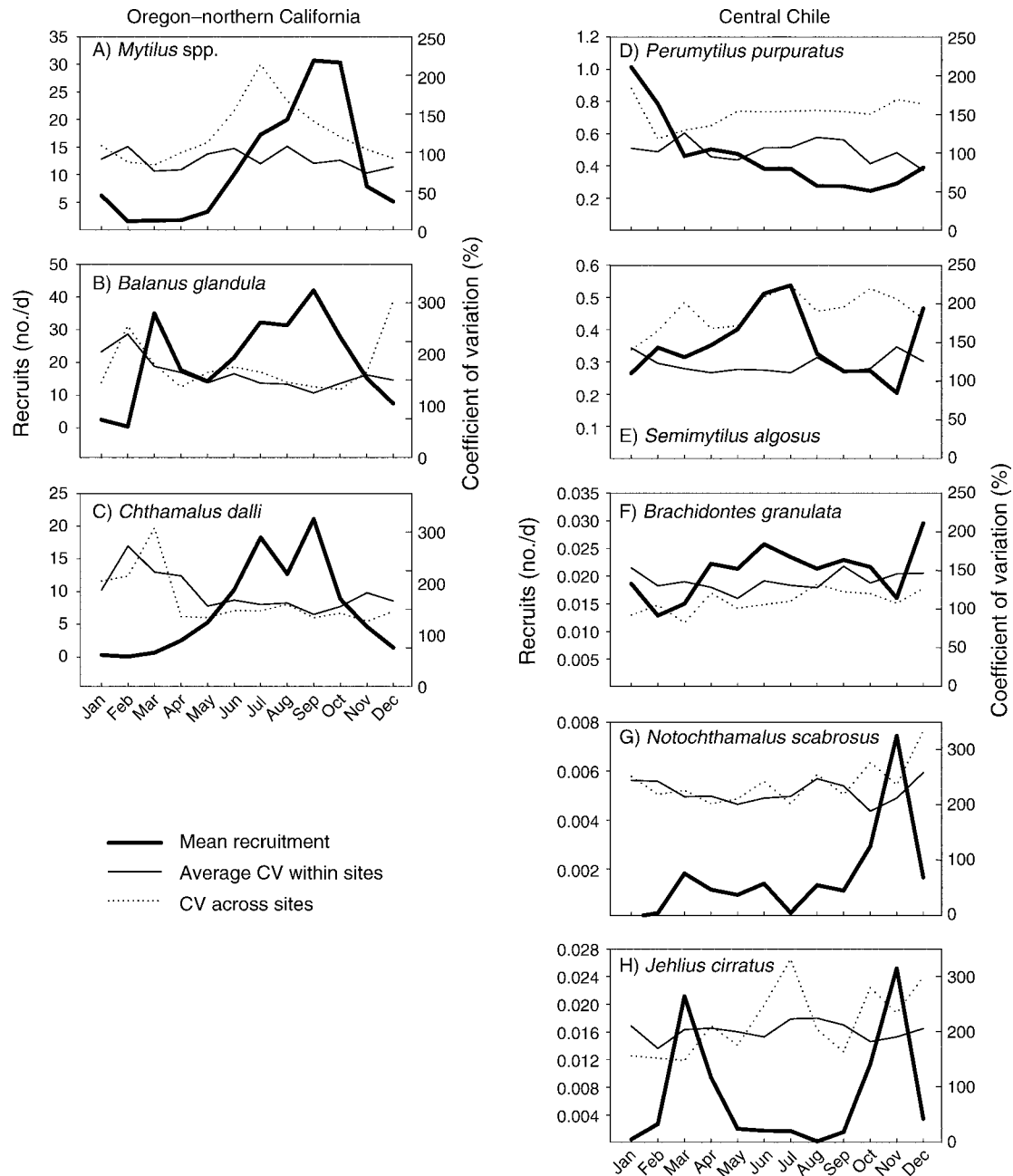


FIG. 2. Temporal partitioning of patterns of spatial variation among all the species considered in this study for Oregon–northern California (left-hand panels) and central Chile (right-hand panels). Thick solid lines show the mean monthly recruitment rates; the coefficient of variation (CV) for monthly recruitment rates is shown by thin solid lines for interannual within-site variability and by dotted lines for among-site variability.

variation (Fig. 3C, D). Consequently, the average maximum autocorrelations observed at lags of 6–12 months, indicative of seasonality, were higher for the three species in the OR–NCA than the five species in CC (Fig. 3E). A nested analysis of variance showed that these coefficients were significantly larger in the OR–NCA than CC and that the intensity of seasonality also changed significantly across sites within species (see

Appendix: Table A2). Despite these large differences in seasonality, at higher frequencies temporal decorrelation scales were of comparable magnitude (1–3 months) among species and between hemispheres (Fig. 3; Appendix: Table A1).

Regional vs. local recruitment variation

Spatial components of variance showed that for all mussel species except *Brachidontes*, more of the total

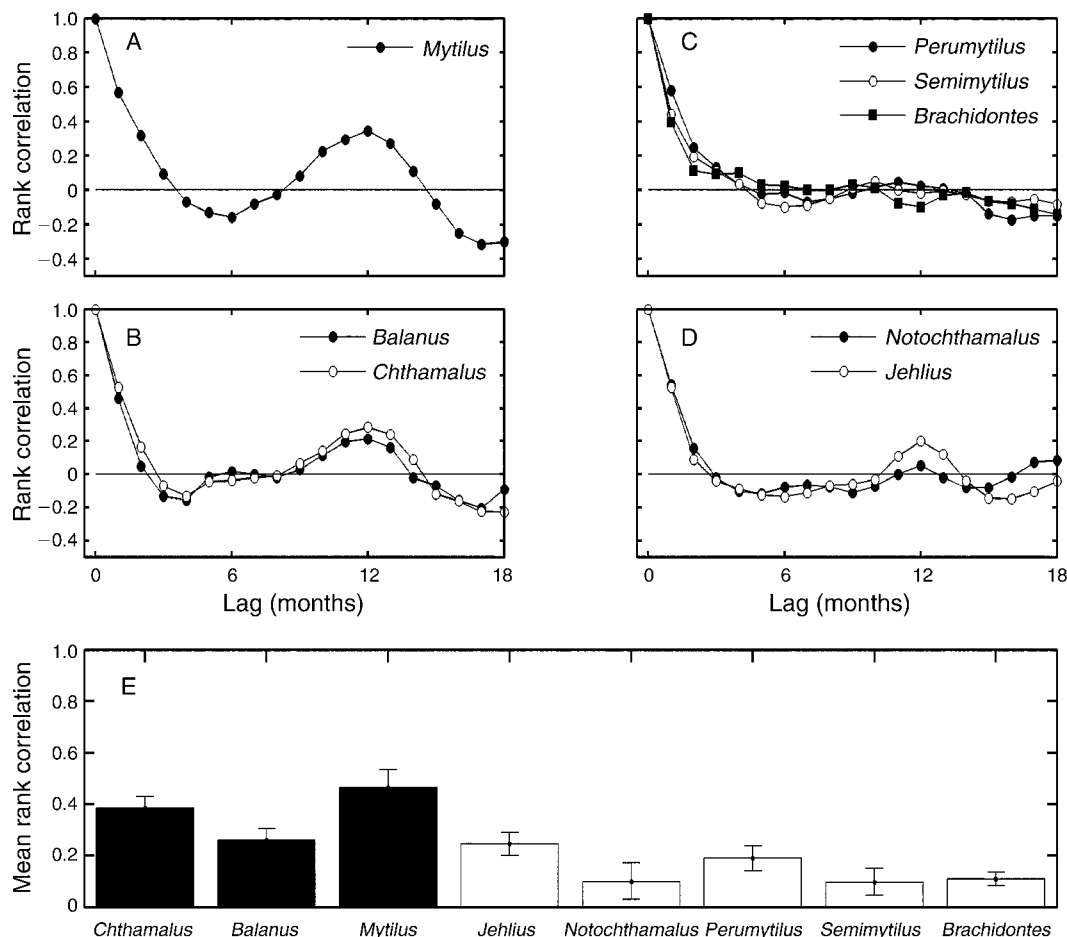


FIG. 3. Patterns of temporal rank-based average autocorrelation in the recruitment rates of all species considered in this study averaged across all sites within (A, B) the Oregon–northern California and (C, D) central Chile regions. Full species names are as in Fig. 2. The average maximum autocorrelation for lags 6–12 months is shown for each species in panel (E). Error bars (\pm SE) correspond to variation across sites.

variance in recruitment occurred at larger, mesoscales (among sites a few to tens of kilometers apart) than at smaller, more local scales (among collectors a few meters apart; Fig. 4A). The mussel *Brachidontes* exhibited the opposite pattern. Barnacles showed contrasting patterns between hemispheres. In the CC region, local-scale variation was greater, while in the OR–NCA region, larger-scale variation was greater (Fig. 4B). The proportion of the total variance due to large-scale differences (variation among sites) increased with increasing overall mean recruitment rate of the species across all species in both regions (Fig. 4C).

Characteristic spatial scales of recruitment

In OR–NCA within a range of 220–235 km, the average spatial synchrony in recruitment rates was remarkably similar for all species, thereby defining this as the “characteristic spatial scale” of recruitment (Fig. 5A–C). In the CC region patterns of recruitment were more variable among mussel species. The characteristic spatial scale for the mussels *Perumytilus* and

Semimytilus was \sim 260–295 km, and spatial synchrony was weaker than for mussels and barnacles in the northern hemisphere (note the broad confidence intervals and shallower slope of the correlogram in Fig. 5D, E). The mussel *Brachidontes* exhibited no spatial synchrony in recruitment rates (Fig. 5F). For barnacle species in the CC region, synchrony in recruitment was intermediate between those for mussels in CC and OR–NCA with characteristic scales of \sim 230–260 km (Fig. 5G, H).

Persistence of recruitment spatial patterns

For all mussels but *Brachidontes*, ranking the magnitude of recruitment by site over time suggests that spatial patterns of recruitment were remarkably persistent (Fig. 6A, C). Rank correlations among sites were between 0.7 and 0.85 for these species, with a clear seasonal cycle in the case of *Mytilus* (Fig. 6A). When calculating the persistence of the spatial pattern on a yearly basis, i.e., using the average annual recruitment of a species in a given site, average (\pm SE) interannual rank

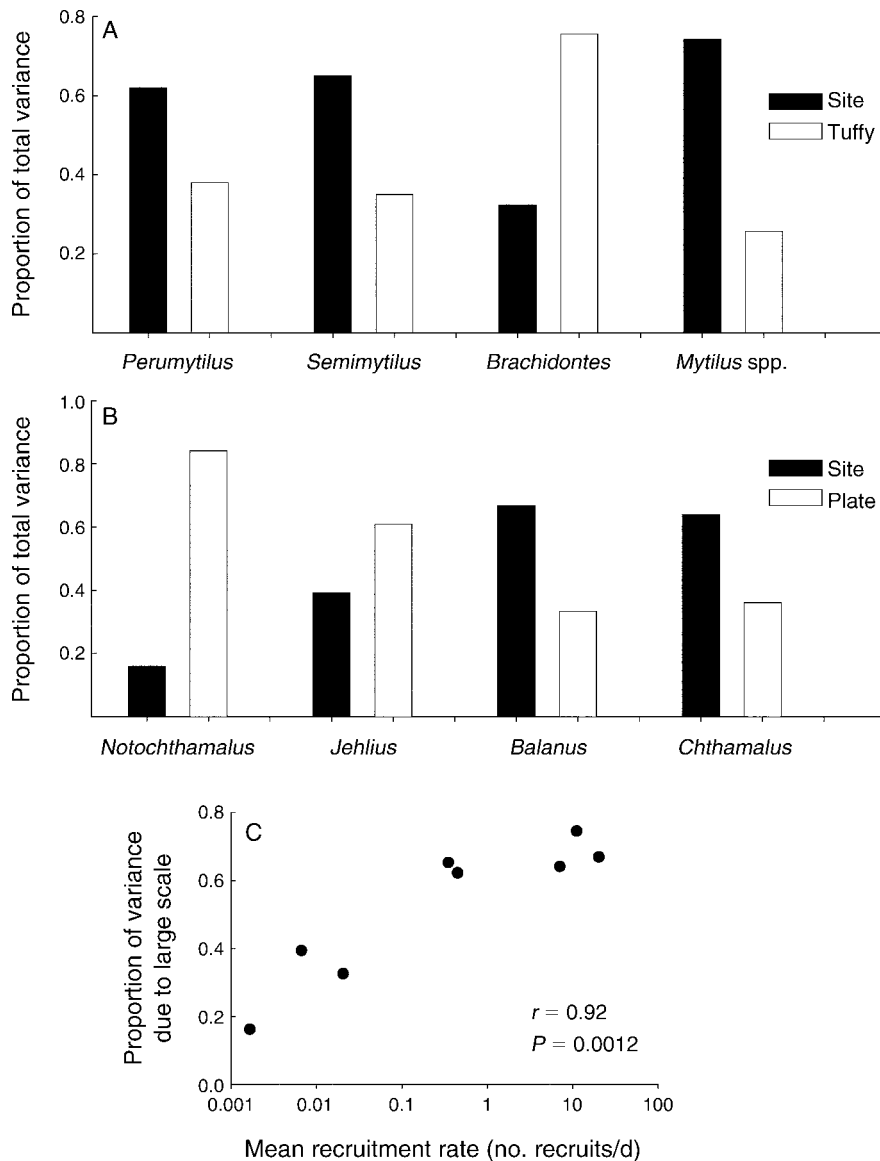


FIG. 4. Long-term variance components of monthly recruitment data expressed as a proportion of the total variance for all species of (A) mussels and (B) barnacles in the Oregon–northern California and central Chile regions. Solid bars represent variance among sites at a mesoscale, kilometers apart. Open bars represent variance within sites at a fine scale, among collectors (Tuffy pads for mussels, plates for barnacles). Full species names are as in Fig. 2. (C) Relationship between the proportion of recruitment variance due to large spatial scales (among sites kilometers apart) and mean recruitment rate (log scale) across both regions and across all species in both regions.

correlations were 0.90 (0.01), 0.80 (0.02), 0.78 (0.01), and 0.59 (0.02) for *Perumytilus*, *Mytilus*, *Semimytilus*, and *Brachidontes*, respectively.

For barnacles in the OR–NCA region, persistence of recruitment patterns among sites was lower than for *Mytilus*, but was also markedly seasonal (Fig. 6B). However, using the average annual recruitment per site, the pattern was again highly persistent from year to year for *Balanus* (average rank correlations among sites of 0.87 ± 0.02) and moderately persistent for *Chthamalus* (0.62 ± 0.02). The least persistent among-site patterns

were observed in the chthamaloid barnacles along the CC coast, where rank correlations fluctuated around 0.3 (Fig. 6D). However, year-to-year variation in the ranking of annual recruitment was also comparatively high, leading to moderately positive correlations of 0.45 (0.03) and 0.46 (0.06), for *Jehlius* and *Notochthamalus*, respectively. The average rank correlation among sites (a measure of spatial persistence) was positively correlated with the proportion of variance explained by among-site variation (Fig. 6E), suggesting that processes topographically anchored (persistent) were

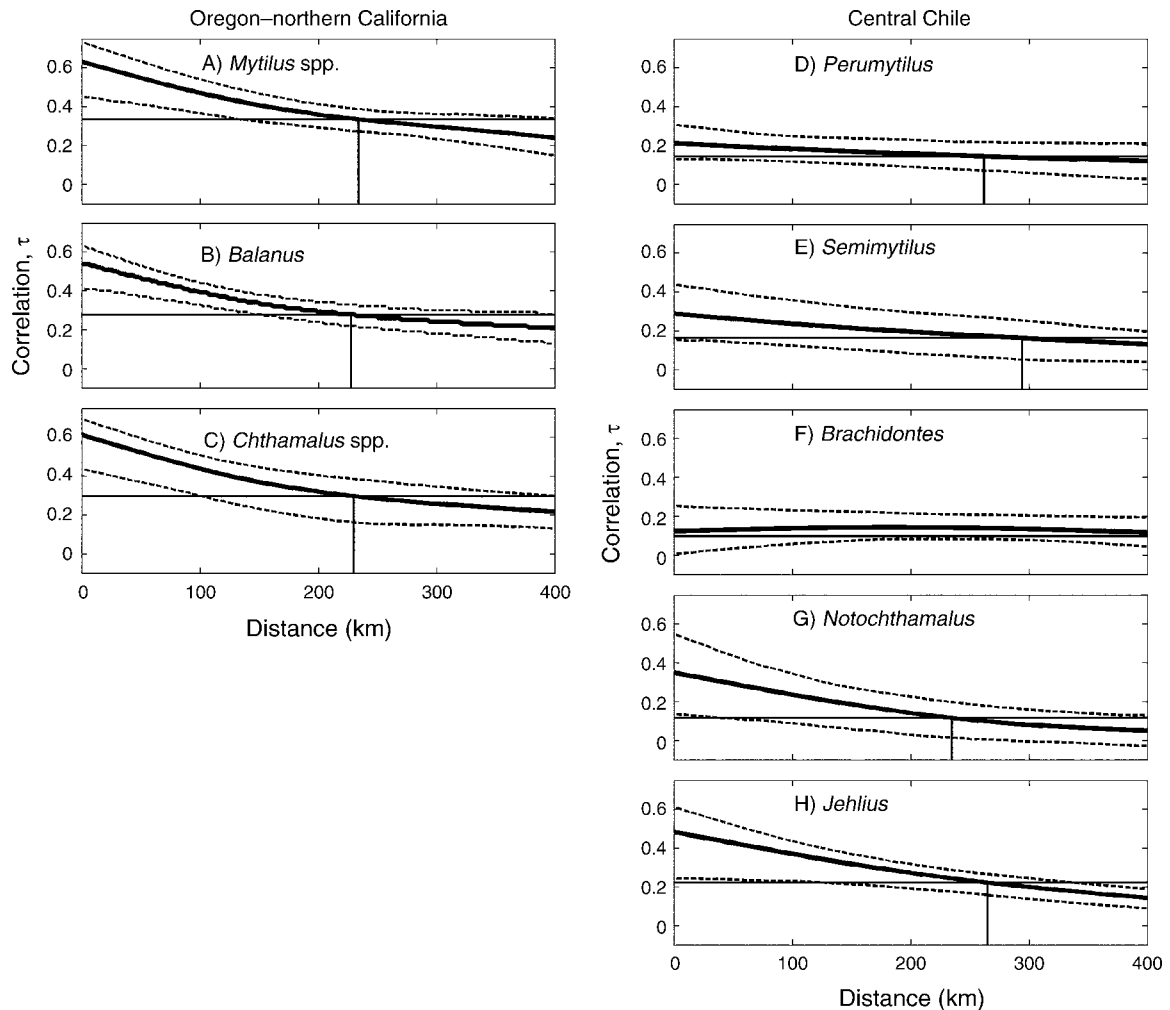


FIG. 5. Spline correlograms for all species. The three parallel lines indicate decaying nonparametric spatial coherence between time series with the spline correlogram (heavy line) bounded by 95% confidence intervals. The intersection of the correlogram with the horizontal line (the regional correlation) indicates the spatial scale of regional coherence (vertical line). Full species names are as in Fig. 2. Distance is measured between members of a site pair.

also responsible for a large fraction of spatial variation in recruitment.

A very different result was observed when estimating pattern persistence over small spatial scales, among collectors, for species in the OR–NCA region (Fig. 7A–C). Although rank correlations among collectors separated meters apart were generally positive across all lags, they were low and nonsignificant for all sites and all species (*Mytilus*, *Balanus*, and *Chthamalus*) examined (Fig. 7). These results suggest that regardless of the larger-scale pattern found across sites, small-scale processes responsible for larval delivery fluctuate considerably in position from time to time. No data were available for the CC region to perform this analysis.

DISCUSSION

Rates of recruitment of ecologically dominant sessile species, mussels and barnacles, were between two to

three orders of magnitude higher, and patterns of seasonality were stronger and more coherent within the region along the Oregon–Northern California (OR–NCA) coast than along the coast of central Chile (CC). Thus, as expected, hypothesis 1 is rejected: large-scale seasonal patterns differed between hemispheres. Despite these differences in seasonality, however, temporal patterns of recruitment at shorter timescales, quantified using temporal decorrelation scales in monthly recruitment data, were similar (<3 months) for all species and hemispheres. Further, characteristic spatial scales of recruitment were only slightly smaller (~220 km) for mussels and barnacles in OR–NCA than for comparable species along CC (~260 km). Thus, hypotheses 2 and 3, that shorter-term temporal and larger-scale spatial scales of variation did not differ between hemispheres, were supported. Finally, contrary to hypothesis 4, over the eight years of this study, we observed remarkably

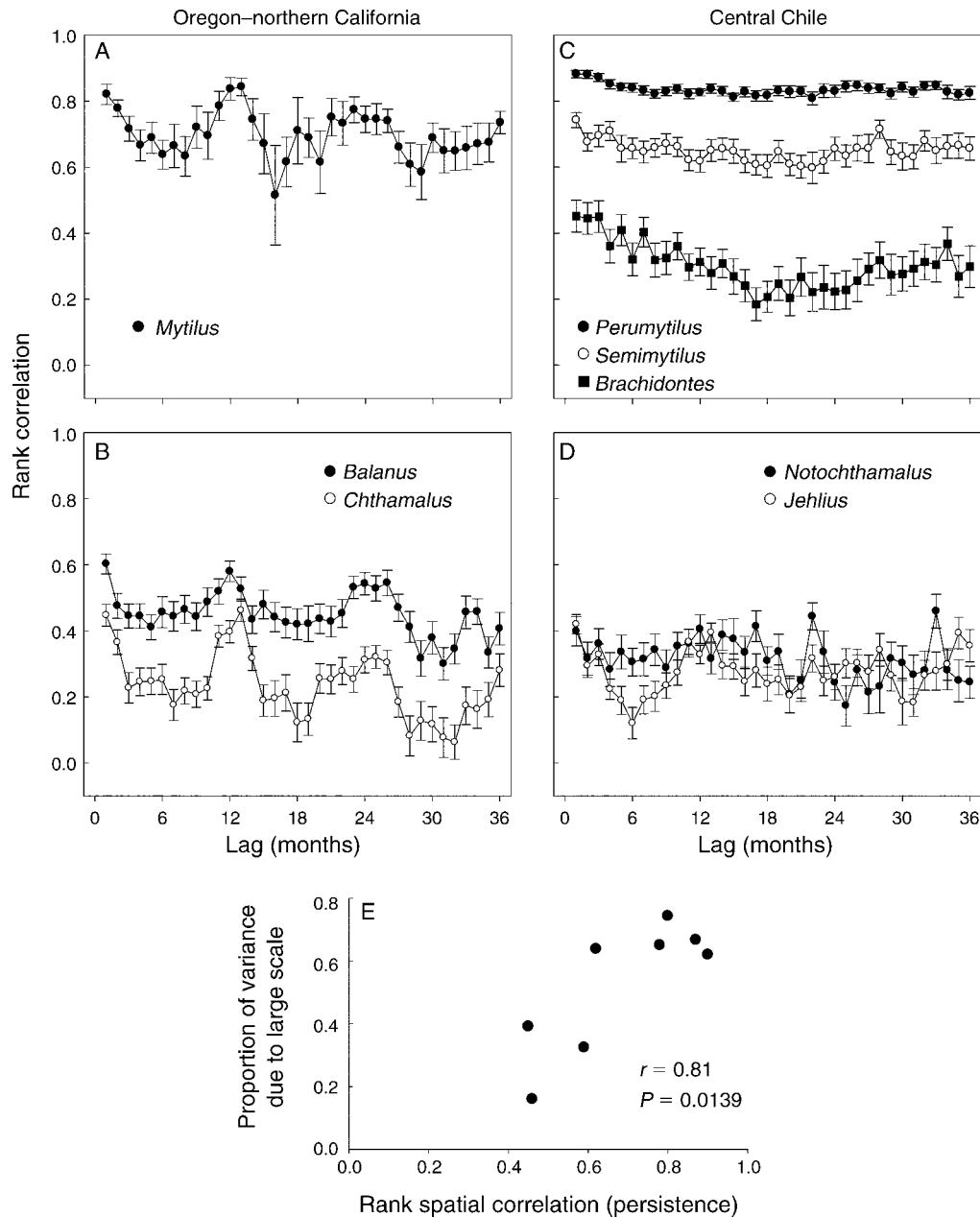


FIG. 6. Temporal persistence of the spatial pattern (ranks) of recruitment rates across mesospatial scales (few to tens of kilometers) in (A, B) the Oregon–northern California region and (C, D) central Chile. Full species names are as in Fig. 2. (E) Relationship between the proportion of recruitment variance due to large spatial scales and the average ranking of sites over time (spatial pattern persistence).

persistent patterns of recruitment at mesoscales (kilometers) for the ecologically dominant species in both hemispheres, while the same species showed highly stochastic recruitment over spatial scales of a few meters. Across species, increased recruitment variation at large scales was positively associated with increased persistence. Here we suggest the potential driving processes behind these patterns and discuss their

consequences for our understanding of spatial dynamics of rocky intertidal communities.

Spatiotemporal recruitment patterns and environmental forcing

Strong, temporally and spatially coherent seasonality characterized recruitment of mussels and barnacles along the OR–NCA coast. This was reflected in significant seasonal signals in autocorrelation analyses.

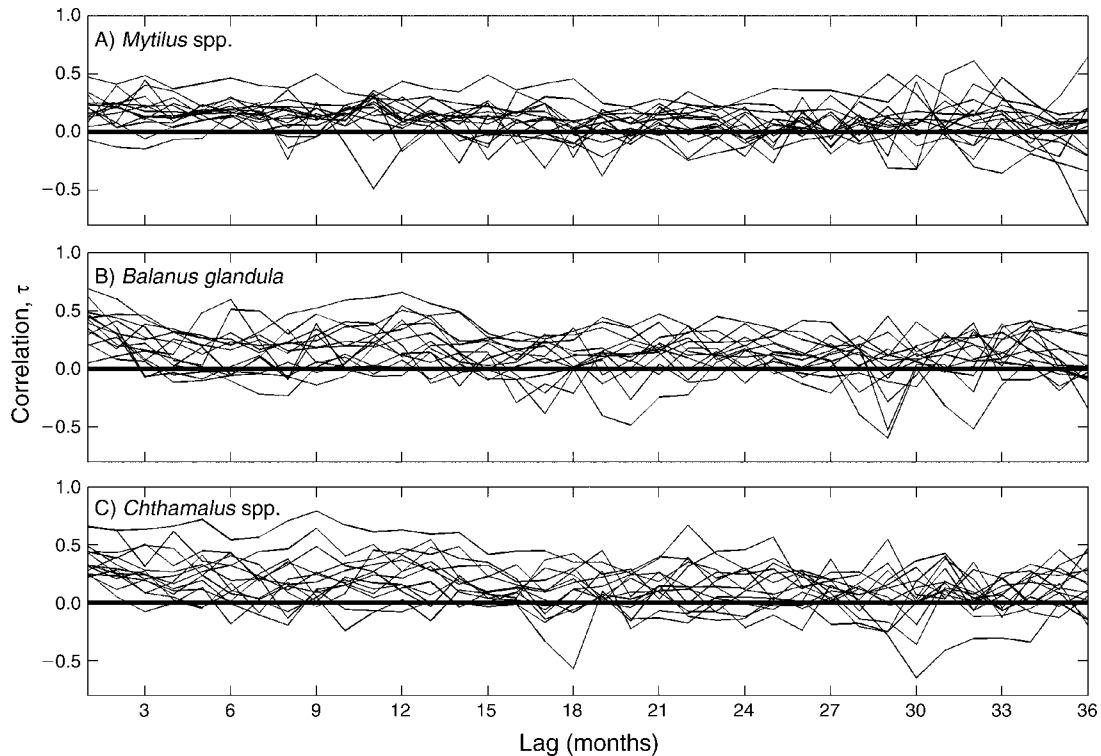


FIG. 7. Temporal persistence of the spatial patterns at small spatial scales (few meters) for species in the Oregon–northern California region. Each line represents the temporal persistence among recruitment collectors based on ranks within a single site.

The onset of the seasonal peak in *Mytilus* spp. recruitment changed slightly to earlier months of the year toward higher latitudes (among sites), but peak recruitment was fairly synchronous through the region. In contrast, along the CC coast recruitment was less seasonal (mussels) and/or presented marked interannual and among-site variability. Because larval duration for all of these species likely ranges between 10 and 30 days (Strathmann 1987, Venegas et al. 2000, O'Connor et al. 2007), seasonal recruitment patterns should mostly reflect temporal fluctuation in larval production, modulated by environmental factors. The species studied produce larvae most of the year (Leslie et al. 2005, Fernández et al. 2007) and the higher latitude conditions of the OR–NCA region could impose stronger limitations on investment in gonads during colder months than the lower latitude conditions along CC, leading to more pulsed larval release when spring conditions set in, consequently producing stronger pulses of recruitment onshore. However, colder waters lead to substantially longer development times (O'Connor et al. 2007), increasing the overlap in recruitment of larvae released at different times. These possibilities could be evaluated by more intensive studies on reproduction of these species. Another explanation for stronger seasonality is that conditions favorable to onshore larval transport are more seasonal along OR–NCA. A recent study suggested that the occurrence of the spring transition in

oceanographic conditions could be the major determinant of delivery of crab larvae to shore (Shanks and Roegner 2007), which seems to force tighter synchrony of recruitment across sites on seasonal timescales, reducing among-site variability. While at any given site barnacle recruitment along CC occurs over a narrow time window (Lagos et al. 2005, 2007), the peak seasons varied greatly among years and among sites a few kilometers apart, particularly for chthamaloid barnacles, but also for the mussels *Perumytilus* and *Semi-mytilus*. This suggests that in central Chile larval production is less seasonal, and recruitment can be strongly modulated by within-site conditions, even over seasonal timescales. Indeed, a numerical model of coastal flows and larval dispersal for the coast of central Chile suggested that wind-driven circulation alone could produce varying alongshore seasonal patterns for species that reproduce year round (Aiken et al. 2007). Unfortunately, we do not have recruitment data at higher latitudes in the southern hemisphere and comparisons with lower latitudes in the northern hemisphere are complicated by the presence of the Southern California Bight, which imposes distinctly different oceanographic regimes from those occurring to the north (Winant et al. 2003). In any case, the regionally coherent seasonality in recruitment suggests that the OR–NCA would be an ideal system to observe long-term shifts in seasons produced by climate change or other global-scale



PLATE 1. Mytilid mussels are dominant components of many rocky intertidal communities around the world. This is the case for the mussel *Mytilus californianus* along the Pacific coast of North America (left) and the mussel *Perumytilus purpuratus* along the Pacific coast of South America (right). Photo credits: left, B. A. Menge; right, Evie A. Wieters.

phenomena. As has been suggested recently, seasonal shifts in recruitment can have long-term effects on monospecific fisheries and could produce dramatic coupled changes in benthic and pelagic ecosystems (Barth et al. 2007, Shanks and Roegner 2007).

In contrast to differences in seasonal patterns between hemispheres, decorrelation timescales in monthly recruitment data were similar across all species and continents, around 1–3 months. Many factors preclude the use of monthly recruitment data to infer larval transport processes (Pineda 2000). However, this result suggests that, despite differences in larval biology among species (e.g., between mussels and barnacles), the interaction of physical processes and larval duration produces time windows of about 1–3 months with favorable conditions for recruitment in both of these upwelling ecosystems. The extent to which this reflects the decorrelation scale of time-integrated physical transport processes, reproductive and larval biology, or post-settlement mortality can only be elucidated through more specific larval transport studies.

Analyses of variance at two spatial scales showed that for all mussel species but *Brachidontes* in CC sites, tens of kilometers apart, explained a larger fraction of recruitment variance than did collectors just meters apart. Lack of taxonomic influence on patterns of variance components was also observed in barnacles.

The two species in the northern hemisphere, a chthamaliid and a balanid, showed greater variance among sites, while both chthamaliids in Chile exhibited a larger fraction of total variance at the smallest spatial scale. Comparison of these results with published studies is difficult due to differences in spatial scales among studies, as well as differences in the frequency of sampling and length of time spanned by recruitment observations. Some studies have found large variability at the smallest sampling scale (usually a few meters) (e.g., Ladah et al. 2005) while others found significant and/or large variation (not always reported) at “large” spatial scales, which are usually hundreds of meters, but sometimes a few to hundreds of kilometers (Jenkins et al. 1997, Hughes et al. 1999, Palma et al. 1999, Jenkins et al. 2000, Flores et al. 2002, O’Riordan et al. 2004, Broitman et al. 2005, Hamilton et al. 2006). Moreover, large spatial scales may represent distant but otherwise similar areas (e.g., Flores et al. 2002), or topographically (oceanographically) different areas identified a priori (e.g., Broitman et al. 2005, Hamilton et al. 2006, Palma et al. 2006). The interpretation of such patterns of variance will vary under the different scenarios. Moreover, whether processes producing larger variation at a given scale are also more persistent is not resolved by these analyses.

In our study, large-scale variation is probably produced by differences in mesoscale oceanographic processes that influence the spatial distribution of the larval pool or transport larvae to nearshore waters, as suggested by previous studies (Connolly et al. 2001, Menge et al. 2004, Lagos et al. 2005, Narváez et al. 2006). Small-scale variation is probably produced by localized hydrodynamic factors that interact with larval selectivity for settlement substratum. Contrasting patterns of variance among taxonomically related species within the same oceanographic region such as those documented in CC might suggest changes in the relative importance of small- and large-scale transport processes among species. Moreover, the relative contribution of small- and large-scale processes, as determined by variance components, could be influenced by the overall level of recruitment. That is, a higher supply of larvae could swamp any potential for larval behavior to generate small-scale variability. If so, then species with overall low recruitment rates should tend to be more variable at small than large spatial scales. The strong positive correlation between the proportion of the total variance explained by among-site variation and the long-term average recruitment rate of the species (Fig. 4C) suggests that this possibility should be explored in other species and coasts.

The scales of spatial synchrony in recruitment rates reflect the degree to which recruitment rates covary temporally in space. The broad agreement in the scales of spatial synchrony between hemispheres and among species with comparable planktonic larval developmental periods, but different adult ecologies, suggests that mesoscale shoreline topography, through its influence on hydrographic conditions, may be generating this structure. Recently Broitman and Kinlan (2006) suggested that topographically driven alongshore hydrographic features generate patchiness in the pelagic environment adjacent to the coast at scales of ~180 km, which in turn influence the abundance of kelp forests along the coast of North America from Oregon to Baja California Sur. The scale found by their continuous analysis of the topographic and thermal structure along the coast is in rough agreement with the ~230 km that we detected for recruitment of northern hemisphere species in examining fewer locations over a smaller region. While no similar analyses have been carried out in Chile, recent studies of patterns of recruitment along small sections of the coast (Lagos et al. 2005, Palma et al. 2006) also found large spatial variation in recruitment and a similar association with temperature and topography. Our results and the remarkably persistent nature of the spatial patterns at mesoscales that we discuss, indicate that the spatial and temporal scales of recruitment (shorter than seasonal) are strongly associated with topographic forcing of nearshore oceanography. Better understanding of the regulation of open populations will therefore be fostered

by the study of transport processes at a given locale (Pineda 1991, Vargas et al. 2004), but particularly by those processes determining persistent variation over the mesoscale.

Recruitment and community dynamics

There are many implications of the reported patterns of temporal and spatial variation in recruitment of these species. Here we highlight some aspects of these results that have deep implications for community dynamics and conservation. First, recruitment rates of the dominant competitor species in the northern hemisphere were orders of magnitude higher than along central Chile. The differences might be due to: (1) differences in overall larval production, which could be constrained by the more restricted tidal range and steeper shores in CC than OR–NCA (Finke et al. 2007), limiting the adult population size, (2) lower per capita larval production of all species along CC, (3) higher larval mortality of all CC species in the plankton for yet undetermined reasons, or (4) fewer opportunities of larval transport back to shore along the narrow continental shelf of the CC region. Whatever the mechanism behind these differences, they should certainly impose contrasting community dynamics, such as rates of replenishment after disturbance and rates of competitive displacement by dominant species.

Probably the most remarkable finding of this study was that patterns of spatial variation in recruitment of most species were highly persistent among sites, at least over the eight years of this study. This suggests that physical processes acting over these scales likely are spatially locked to coastal topography and produce highly predictable patterns over time, which in this case, are also the scales over which most recruitment variation is observed. Similar results were recently documented for fish species in St. Thomas Island by Hamilton et al. (2006) in an 11-year-long study (but see Sale et al. 2005, for a contrasting pattern in tropical fish recruitment), for barnacles by Jenkins et al. 2000 in a large scale (hundreds of kilometers) but only two-year-long study, and by Hughes et al. (1999) for corals across the Great Barrier Reef. In contrast and regardless of the patterns of variance components, discussed previously, recruitment fluctuations among collectors were highly stochastic over time.

Our results are encouraging from the point of view of conservation and models of metacommunity dynamics. First, models of marine protected areas, which are usually thought to apply over a few to tens of kilometers, assume that dispersal kernels and onshore recruitment patterns remain fairly invariant over relevant timescales (e.g., Lockwood et al. 2002, but see Kaplan 2006). Our results generally support the applicability of these models. It must be noted, however, that our results also show that even within the same oceanographic region, some species with broadly similar larval durations do not exhibit spatially persistent recruitment patterns (the mussel *Brachidontes*). In this

case, the species is rather cryptic and rare in the intertidal zone. Fixed protected areas might not be very efficient for such species and, at present, we do not know how to anticipate which species will show spatially fluctuating recruitment and which ones will show coherent recruitment patterns.

Second, many models of species coexistence and maintenance of species diversity in meta-communities depend on differences in effective dispersal of dominant and subordinate species to local communities (Amarasekare 2003, Holyoak et al. 2005). If oceanographically driven patterns of connectivity are persistent over population timescales, as they appear to be in this case, at least judging from recruitment patterns, then these metacommunity models might offer new insights into the spatial dynamics of marine communities and help explain coexistence between competitors, or between predators and prey (e.g., White 2007, Wieters et al. 2008). A possible case in point is the coexistence between *Perumytilus* and *Semimytilus*. These species strongly compete for space in the intertidal zone. If the persistent differences in recruitment patterns at mesoscales reflect dispersal among sites, then mass effects (source-sink dynamics) could facilitate their regional coexistence. That is, sites where the competitively dominant species recruits poorly (due to physical processes), could allow larger local populations of the subordinate species, which would self-recruit to those sites, but also disperse and “rescue” populations of conspecifics at sites where they are competitively displaced by the dominant. While existing “paradigms” of meta-communities have not considered physically driven, obligate dispersal (Leibold et al. 2004), these models could be easily adapted to account for life history attributes of marine organisms (White 2007, Navarrete and Manzur 2008) and deserve explicit consideration by empirical ecologists.

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APPENDIX

A description of species ecology and field and statistical methods, a table showing temporal decorrelation scales and spatial scales of synchrony in recruitment rates, a table showing results of nested ANOVA on the maximum autocorrelation coefficient between lags 6 and 12 for each species and site, and a list of references (*Ecological Archives* E089-079-A1).