

Ecological convergence in a rocky intertidal shore metacommunity despite high spatial variability in recruitment regimes

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In open ecological systems, community structure can be determined by physically modulated processes such as the arrival of individuals from a regional pool and by local biological interactions. There is debate centering on whether niche differentiation and local interactions among species are necessary to explain macroscopic community patterns or whether the patterns can be generated by the neutral interplay of dispersal and stochastic demography among ecologically identical species. Here we evaluate how much of the observed spatial variation within a rocky intertidal metacommunity along 800 km of coastline can be explained by drift in the structure of recruits across 15 local sites. Our results show that large spatial changes in recruitment do not explain the observed spatial variation in adult local structure and that, in comparison with the large drift in structure of recruits, local adult communities converged to a common, although not unique, structure across the region. Although there is no unique adult community structure in the entire region, the observed variation represents only a small subset of the possible structures that would be expected from passive recruitment drift. Thus, in this diverse system our results do not support the idea that rocky intertidal metacommunities are structured by neutral mechanisms.

community structure | ecological drift | neutral theory | interaction strength | macroecology

The extent to which the structure and diversity of natural communities is determined by interactions among species, such as predation and competition that occur at local scales, and the extent to which they are the result of regional-scale processes that can be largely independent of species interactions are central questions in ecology and are the subject of intense debate (1–4). One aspect of the debate is centered on whether niche differentiation and local interactions among species play a significant role in macroscopic community patterns (e.g., species diversity, species-abundance curves) or whether, as stated by the neutral theory of biodiversity (NTB) (2), these patterns can be generated by the neutral interplay of dispersal and stochastic demography among ecologically identical species (4–10). A related topic at the center of ecological debate since the mid-1980s is that of “supply-side” ecology (11), which proposes that the supply of individuals to local communities, a process driven largely by physical factors, can be the main determinant of population and community structure, challenging the view of control by local species interactions (12–18). If recruitment were the main determinant of adult population abundance for most species in local communities, then community structure and its spatiotemporal variation would result from environmentally driven fluctuations in the supply of individuals, largely uncorrelated with local species interactions. Similarity with the NTB argument is apparent when examining large sets of species. The fact that some static, aggregated attributes of intertidal marine communities follow predictions based on NTB (5, 8) justifies further evaluation of the neutrality of spatiotemporal variation in marine community structure to deterministic species interactions.

Instead of parameterizing a neutral model for species that share and compete for a common resource within a trophic level, as required by NTB models (1, 6, 8, 19), we start with a rocky shore metacommunity, composed of 15 local communities of coexisting species from disparate taxa at all trophic levels and exhibiting an astonishing diversity of modes of development (Table S1). These local communities are spread over 800 km of coastline and are separated by tens of kilometers (Fig. 14), surpassing the scale of movement of all adult mobile invertebrates. In this system, we ask to what extent large-scale spatial variation in species composition can be predicted solely by variation in dispersal and recruitment rates.

Rocky intertidal communities are formed by a large proportion of species with complex life cycles that include an initial pelagic larval stage that lives in the water column before settling in the adult habitat. Several studies in these communities have shown that the arrival of new individuals varies greatly from site to site, influenced largely by local and meso-scale oceanographic processes, and that different species appear to be affected by different larval transport mechanisms (20–25). Therefore, recruitment variation from site to site can be independent of local adult abundances. This open characteristic of populations over comparatively large spatial scales, together with a myriad of reproductive strategies of component species, make rocky shore invertebrate communities ideal systems for examining whether variation in recruitment of multispecific assemblages from site to site is sufficient to account for among-site variation in local community structure. Conversely, postsettlement processes could erase the signal of dispersal and buffer against spatiotemporal variation in the arrival of individuals. If such processes are deterministic across the metacommunity, they may create structures of adult assemblages that are more convergent to a common structure than would be expected by variation in the supply of individuals. Classic studies consolidating the view of local control of community structure by species interactions (e.g., predation, competitive exclusion) (26–29) have focused on relatively few sites in close proximity and on a small subset of strongly interacting species or modules (*sensu* Paine, ref. 30), making it difficult to infer the relative importance of these processes across space for the entire community. On the other hand, numerous studies have demonstrated the importance of recruitment in determining adult abundance patterns from local to regional scales (21, 31–34). However, these studies have examined the recruit–adult relationship individually for one or a few species, with widely varying results (14, 32, 35, 36). An exception is

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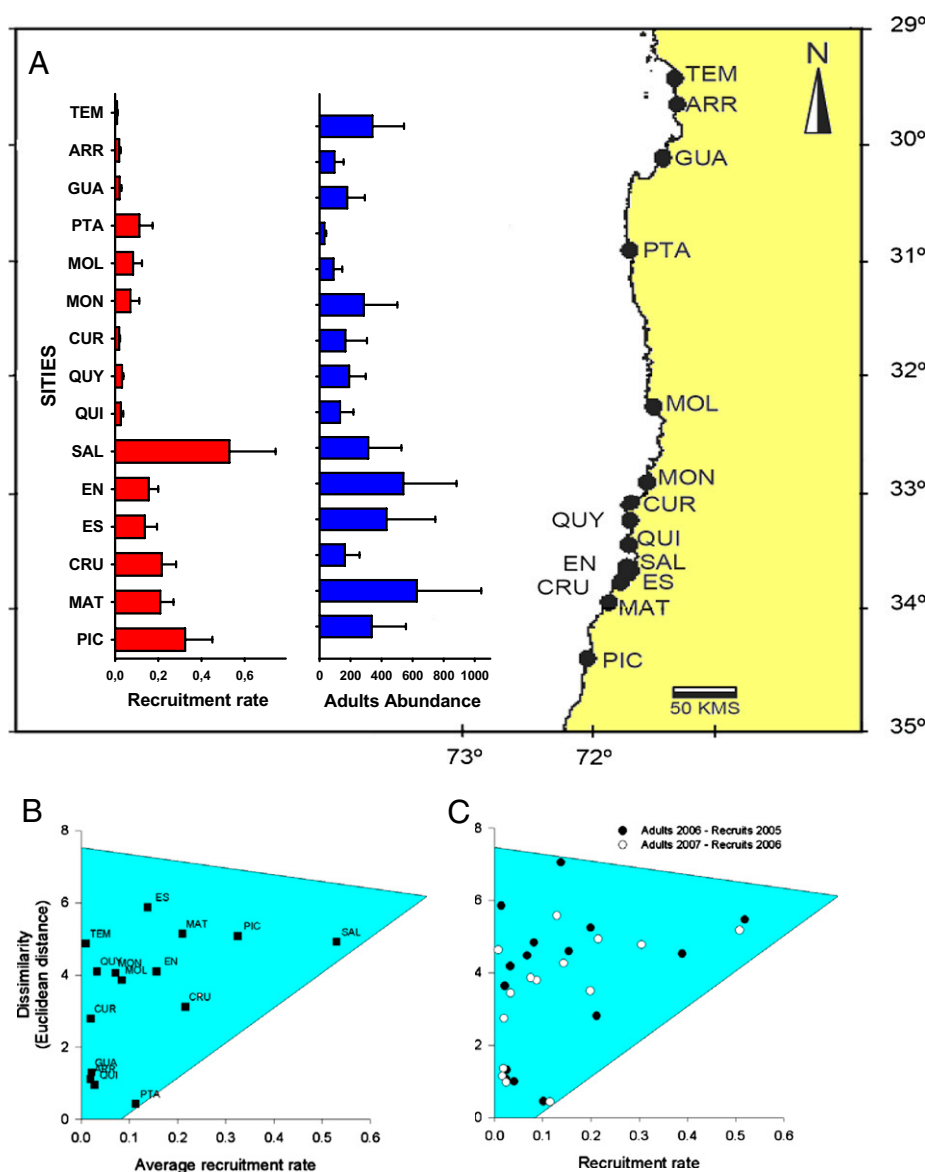


Fig. 1. Spatial variability in rates of recruitment and adult abundance in the meta-community. (A) Location of local intertidal communities along central Chile. (Left) The red graph shows the daily average recruitment for all species per site (mean \pm SE). Sites are sorted from north to south, as in the map (Right). (Center) The blue graph shows adult average abundance (individuals per square meter) at the same sites. (B) Relationship between the dissimilarity in the recruit and adult assemblages at a given site obtained through PCA ordinations and the average recruitment rates of species at that site. Relationship with entire dataset averaged per site (three sampling dates for adults, 8 y of sampling for recruits). (C) The same relationship analyzed separately for two periods. \bullet , adults measured in 2006 and recruitment rates recorded in 2005. \circ , adults measured in 2007 and recruitment rates recorded in 2005. The cyan-colored quadrangles in B and C show the dispersion of recruit-adult distances across the region. The shape and lower boundary slope are significantly different from random expectation. ARR, Arrayán; CRU, Las Cruces; CUR, Curaumilla; EN, ECIM North; ES, ECIM South; GUA, Guanaqueros; MAT, Matanzas; MOL, Los Molles; MON, Montemar; PIC, Pichilemu; PTA, Punta de Talca; QUI, El Quisco; QUY, Quintay; SAL, Salinas; TEM, Temblador.

the work by Forde and Ralmondi (37), who experimentally manipulated recruitment rates of two species of rocky intertidal barnacles to evaluate their effect on community composition, considering a total of five species. Their results show that in early stages of succession, variability in recruitment had significant impact on community structure, but in intermediate and final stages community structure was strongly influenced by postsettlement processes that produced density-dependent mortality. Although this study is valuable for understanding the regulation of species interactions by recruitment, it examined variation in recruitment rate for only two species of the diverse community investigated.

One of the main challenges in assessing the influence of recruitment on spatially varying metacommunity structure is compiling a long-term recruitment database for multiple species (38). When local communities are comprised of species with very different generation times, it often is difficult to determine the time scales on which the recruitment should be measured, and thus the signal of recruitment in adult communities must be investigated over different time scales. Here we use a multispecific, long-term (8-y) database for recruitment of 26 species of rocky intertidal invertebrates in Chile, at sites spread over 800 km of coastline, to examine the extent to which large spatial variability in local com-

munity structure of adults results simply from spatial variation in the arrival of new individuals, before niche differentiation plays a role. The rocky intertidal abundance of adults was quantified by nondestructive sampling at all study sites, including six intertidal microhabitats, on three different survey dates.

Results and Discussion

As expected, large among-site differences in recruitment rates were observed in individual species as well as in average recruitment for all species per site (ANOVA; $F_{14,120} = 3.36$, $P < 0.001$), with a trend to increased recruitment toward the southern portion of the region (Fig. 14). Similarly, average adult abundance also showed significant differences among sites (ANOVA; $F_{14,30} = 36.06$, $P < 0.001$), with overall lower abundances at most northern sites (Fig. 14). The relationship between the average recruitment rate and average local abundance of adults, evaluated individually on raw or log-transformed data for each species, did not show a consistent pattern in the community (Table S2); some species showed a significant positive linear or quadratic relationship between these variables, indicative of recruitment limitation and density dependence at some sites (14, 32), but most showed no relationship (Table S2). Consequently, after standardizing

for differences in abundance among species, the average rate of recruitment was not related to average adult abundance in this assemblage (Fig. S1). Lack of a unique recruit–adult relationship probably is common in assemblages of diverse species. However, even if the recruitment rate of a given species does not correlate with the abundance of adults across sites in a simple form, the structure of the entire recruit assemblage still might be associated with the multispecific structure of adults. The multivariate evaluation of the recruit–adult relationship was performed by calculating the Euclidean distance between ordinations of the recruit and adult assemblages at each site and then examining the association between these distances and the average or median recruitment of species at those sites. A strong positive relationship would suggest that adult communities tightly reflect the structure of recruits at low recruitment rates and depart from this structure only at high recruitment rates. Our results showed weak, non-significant association between these variables (Fig. 1 *B* and *C*). The general trend did not change when the relationship was examined using the long-term averages of recruitment and adult abundances for each site (linear fit: $F_{1,13} = 3.54$, $P = 0.082$; quadratic fit: $F_{2,12} = 2.00$, $P = 0.176$) (Fig. 1*B*) or when data from 2 separate years were used for adult abundances and recruits (Fig. 1*C*). Lack of a significant relationship was caused by the high dispersion of the distances between recruit–adult assemblages at low recruitment levels, indicating that even in communities where recruitment levels are generally low, variations in the structure of the adult assemblages can be as large as at sites where recruitment levels are high. Thus, there is no significant multispecific recruit–adult relationship in these communities. The shape of the relationship depicted in Fig. 1 *B* and *C* is significantly different from that expected from a random allocation of sites in the bivariate space (10,000 iterations, $P = 0.021$), and there is a significantly positive bottom slope in Fig. 1*C* (10,000 iterations, $P = 0.032$). This result indicates a pattern in which communities at low-recruitment sites may or may not reflect recruitment, but at high-recruitment levels the structure of the adult community always differs greatly from that at time of arrival. A generally similar result was observed in single-species analyses of intertidal barnacle species (32).

Multivariate ordination showed significant differences in the structure of recruit and adult assemblages across sites [permutational multivariate analysis of variance (PERMANOVA); $F_{1,28} = 14.3$, $P = 0.002$] (Fig. 2*A*). Importantly, there were significant differences in multivariate dispersion between the adult and recruit assemblages with significantly more drift in the structure of the recruit assemblages across local communities (PERMDISP, $F_{1,28} = 54.28$, $P = 0.001$) (Fig. 2*A*). This result also is apparent in the distributions of Bray–Curtis similarities between pairs of sites for adults and recruits (Fig. 2*B*). Pairwise similarities were significantly more dispersed and generally lower (more dissimilar) in the recruit than in the adult assemblage (Mantel test, $P = 0.0006$) (Fig. 2*B*). This pattern of relative convergence of adult communities with respect to recruits was consistent when examining the entire recruitment data period (average recruitment 1998–2006) (Fig. 2*A*), distinct seasons (Fig. S2 *A* and *B*), or different years (Fig. S2 *C–E*). Thus, the pattern is not sensible to changes in the time scale or season of the recruitment time series used in the analyses. To examine further whether the relative convergence of adult communities was caused by the temporal proximity of our surveys of adult abundances (three surveys in *ca.* 1.5 y), we assembled an independent adult dataset. This dataset contained 14 of the 15 original sites but a subset of only 10 common species for which adult data has been gathered on wave-exposed platforms in 6 different years between 2000 and 2007. Results were virtually unchanged. Adult relative convergence and dispersion in this subset of species was remarkably similar to that observed in the assemblage containing 26 species (Fig. S3). Moreover, having adult surveys over multiple years allowed us to use a second-stage

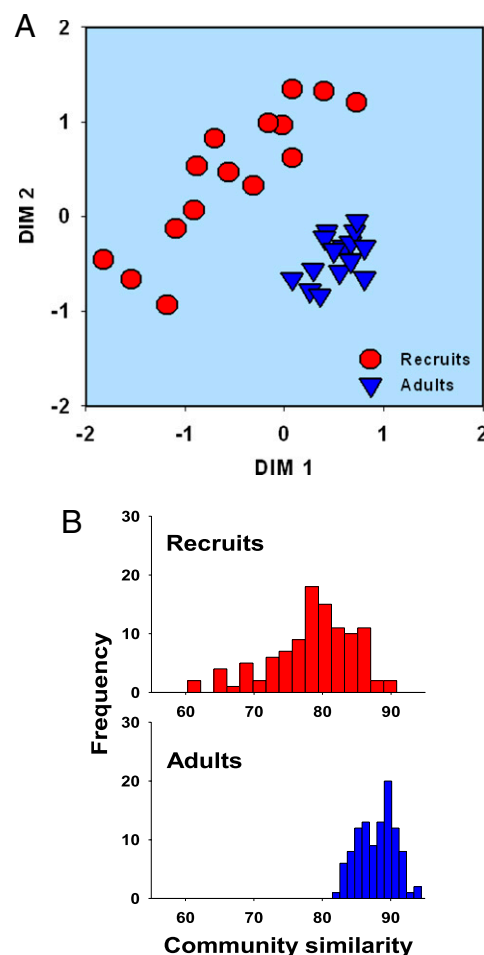


Fig. 2. (A) NMS ordination of recruit and adult assemblages across sites (stress = 0.056). (B) Frequency distributions of Bray–Curtis similarities among pairs of sites for recruit (Upper) and adult (Lower) assemblages in the metacommunity. DIM, dimension.

analysis and analysis of similarities test (39) to examine whether adult temporal trajectories over these 7 y were related to temporal trajectories of recruits in the multispecies space. Results suggest that adult and recruit trajectories (temporal drift) are not correlated (Fig. S4 *A* and *B*). However, these results should be regarded with caution because of the comparatively short time span of analysis and the inclusion of only 10 species in the community.

Our results show that, across a wide range of natural variation in recruitment rates of 26 intertidal species, along ≈ 800 km of coastline, large spatial changes in the arrival of new individuals from the plankton, which are driven largely by variation in physical factors, do not explain the spatial variation in local adult structure in this metacommunity. Thus, variability in adult community structure appears to be influenced strongly by post-settlement processes, including biological interactions and local environmental factors. These processes cause large departures in community structure from the initial composition of recruits, affecting the entire community and not only the dominant or strongly interacting species (28, 30).

Although the convergence of local adult communities across the 800-km region is striking, these adult communities still may differ in structure among sites. Convergence to a common structure is relative to the variation expected in the arrival of individuals. Indeed, if we examine separately the structure of adult communities across the region, we find clear differences, with a northern group of sites separating significantly from all other sites according

a PERMANOVA test (Fig. 3A). No such structure is observed among local assemblages of recruits (Fig. 3B), again emphasizing that among-site variation in recruit composition does not predict adult structure. Thus, as shown in previous studies, there is not a unique intertidal community structure in this region (21, 40). However, the observed variation represents only a small subset of the possible structures that would be expected from passive recruitment drift. Also, although these results demonstrate that spatial variation in adult communities is not a simple consequence of spatial variation in recruitment, they do not show that the supply of individuals is not important in these communities. First, the local dynamics of species at any given site still might be highly regulated by recruitment fluctuations, even though, across space, final abundances are not. Only detailed, species-specific temporal observations at local sites could determine the resilience of adult populations to recruitment fluctuations (34, 41). Second, and perhaps more importantly, the rate of arrival of recruits at a given site and the pattern of dispersal among local populations will be a determinant factor in the intensity and sometimes the direction of local species interactions and may or may not have a linear correspondence with equilibrium abundances (36, 38, 42, 43). In other words, variation in recruitment of some species, especially strong interactors (*sensu* ref. 30), could propagate throughout the rest of the community, as seems to be the case in Chile, where orders-of-magnitude variation in recruitment rates of the dominant competitor for space, the mussel *Perumytilus purpuratus*, explains 56% of the among-site variation observed in adult community structures (Fig. 3C). Thus, local communities do not neutrally reflect recruitment variation, but large variation in the supply of individuals of key species can affect the entire intertidal community.

Considering the degree of convergence to a common structure in intertidal communities, in comparison with the dispersion observed in recruits, we conclude that deterministic postsettlement species interactions (e.g., predation, competition, facilitation) can buffer against spatial variation produced by dispersal in multi-

species assemblages. The strength and determinism of local species interactions seems sufficient to modulate and deeply modify the signal of recruitment, which is comparatively neutral to ecological roles in the benthic habitat. Therefore, in diverse rocky shore systems and over large spatial scales, our results, which include common and rare species, negate the idea that communities are neutrally structured by ecological drift. They suggest instead that strong interactions occurring among a subset of species can produce comparatively convergent community structures that affect the entire community.

Materials and Methods

Recruitment rates of the 26 invertebrate species included in this study were quantified monthly at 15 sites between 1998 and 2006, using 10 × 10-cm Plexiglas plates for three barnacle species and a 10-cm diameter semispherical pad made of plastic mesh (Tuffly) for all other species. At each site, five plates were installed in the high and low intertidal zones, and five plastic mesh pads were installed in the mid-intertidal zone and were replaced monthly (average 29 d). This database reflects a long-term monitoring program, and details of the methods and species-specific patterns of recruitment have been reported (20, 21, 35, 44).

Abundance of adults in the rocky intertidal zone was quantified by non-destructive sampling at all study sites on three different survey dates: Winter 2006 (May–June), Spring 2006 (August–October), and Summer 2006–2007 (December–February). Thus, surveys captured potential seasonal variability. To account for differences in microhabitat distribution among species, sampling included six intertidal microhabitats: (i) exposed and semiexposed platforms (<70° inclination); (ii) cracks and crevices; (iii) vertical walls (>70° inclination); (iv) permanent tidepools; (v) rocky outcrops surrounded by sand; and (vi) shell-covered bedrock. For mobile species we used three quadrat sizes depending on species body size: 15 × 15 cm for small species (<1 cm; e.g., *Crepidula*, *Mitrella* spp.); 20 × 20 cm for mid-sized species (1–3 cm; e.g., *Nodilittorina araucana*, *Scurria* spp.); and 50 × 50 cm quadrats for larger species (>3 cm; e.g., *Concholepas concholepas*, *Fisurella* spp.). A minimum of five quadrats were surveyed in each of the six microhabitats, and the data were expressed as the number of individuals per square meter. In the case of mussels and barnacles, we estimated cover by using a 50 × 50 cm quadrat with 81 intersection points. Cover data for mussels were converted into densities using the relationship between percent cover and number of individuals per unit area for each site and species, using destructive sampling in 20 × 20 cm plots. The density of barnacles was estimated from percent cover data using counts of individuals within 5 × 5 cm quadrats in the mid- and high intertidal zones for *Notochthamalus scabrosus* and *Jehlius cirratus* and in the low intertidal zone for *Notobalanus flosculus*.

To evaluate the relationship between average recruitment rate and average adult abundance for each species separately across sites, we fitted linear and quadratic (polynomial) regression models using ordinary least squares. To determine whether a general recruit–adult relationship characterizes the entire community, we first transformed density and recruitment data per site to proportions of the maximum observed for each species across the region. In this manner, all recruitment and density data varied between 0 (absence of species in a given site) and 1 (maximum density/recruitment in the region). We then fitted linear and quadratic trends over these transformed data.

To estimate the multispecies dissimilarity (distance) between assemblages of recruits and adults and to provide a simple multispecific extension of the recruit–adult hypothesis (14), we used a multivariate statistical technique, Principal Component Analysis (PCA). The analyses were performed on relativized abundances of recruits and adults, thus preventing excessive weight by a few numerically abundant species. For recruitment data, we added all individuals collected annually per site and created an annual average per site. For adult abundance, we used an average of the three surveys per site. The similarity between the ordinations of recruits and adults at each site was estimated by calculating the linear Euclidean distance between the first two principal components obtained for each group. The distance between these assemblages at each site then was regressed against the mean and the median recruitment rate of all species at that site using ordinary least squares. This analysis was conducted considering the entire data sets as averages per site, providing 15 independent observations, as well as separately for different adult survey years. In the latter case, we used the surveys of adult abundances taken further apart (in 2006 and 2007) and examined the relationship with recruitment rates measured the year before, thus providing a total of 30 observations. These observations were not entirely independent, because each site was represented twice. To evaluate whether the shape of the relationship was significantly different from that ex-

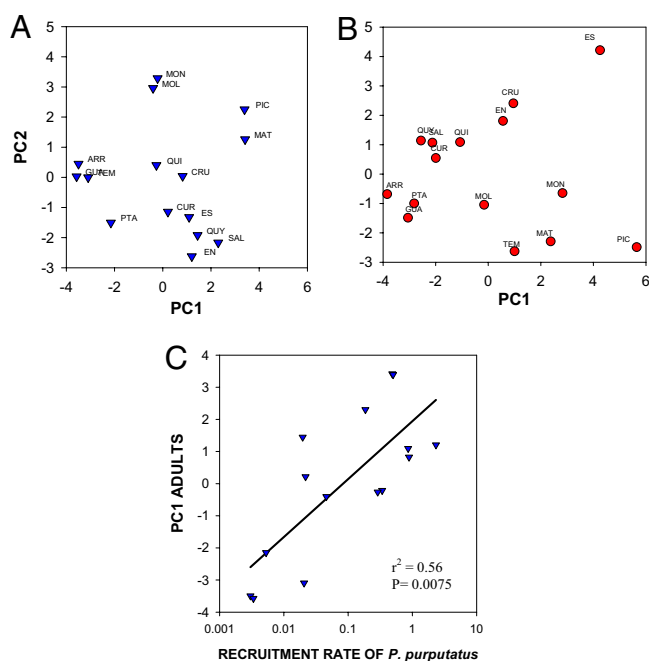


Fig. 3. Multivariate ordinations using PCA separately for (A) adult and (B) recruit assemblages. Site abbreviations are as in Fig. 1. (C) Relationship between principal component 1 (PC1) of the adult community ordination shown in A and mean of recruitment rate of the mussel *Perumytilus purpuratus* (logarithmic scale). The line shows the fit obtained from ordinary least squares linear regression.

pected by random and whether its boundaries were different from zero, we used randomization tests implemented in Ecosim V.7.7 software (45). To determine whether the structure of recruit and adult assemblages differed significantly across the region, we used PERMANOVA (46), a linear permutation test, based on 9,999 permutations of the matrix of distances calculated with the Bray–Curtis similarity index for the 26 species and using sites as replicates ($n = 15$). Densities were previously standardized by site and were square root transformed. The difference in multivariate dispersion between recruits and adults was assessed by permutation test using the multivariate dispersion PERMDISP program (47) with 9,999 permutations.

Within multispecific rocky intertidal assemblages, there is great variability in generation times and lifespan of the species; thus local populations represent the outcome of an unspecified number of recruitment events that varies among species. This variability presents a methodological complication in determining the appropriate time period to use when evaluating the effects of recruitment on local abundances of adults. Because we know the turnover rate and age structure for only a few of the species included in the study, our approach was to assess whether the results of the ordinations were robust when considering different years and seasons in recruitment.

To determine whether the relative convergence observed in adult communities was partly the result of the small number of years in which we sampled adult abundances as compared with recruitment, we assembled an independent dataset that considered six yearly surveys (summers 2000, 2003, 2004, 2005, 2007, and 2008) over a 7-y time span. Data were gathered at the

same sites [except for a site within the Estación Costera de Investigaciones Marinas (ECIM South)] but included only 10 species commonly found in wave-exposed rocky platforms. The sampling used the same quadrat method used in the original sampling conducted in platforms. Data were treated and analyzed as described above for the ordinations considering the entire dataset. Because this reduced dataset included multiple years for adult and recruit abundance, we examined the relationship between recruit and adult temporal variation using a second-stage analysis implemented in Primer v. 6 (39). The analysis evaluates the interaction between time and the recruit–adult temporal changes using first Spearman correlations between the matrices and then nonmetric multidimensional scaling (NMS) ordination to determine the association between recruit and adult temporal changes (48).

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