Scales of benthic–pelagic coupling and the intensity of species interactions: From recruitment limitation to top-down control

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Large and usually unpredictable variation in species interaction strength has been a major roadblock to applying local experimental results to large-scale management and conservation issues. Recent studies explicitly considering benthic-pelagic coupling are starting to shed light on, and find regularities in, the causes of such large-scale variation in coastal ecosystems. Here, we evaluate the effects of variation in wind-driven upwelling on community regulation along 900 km of coastline of the southeastern Pacific, between 29°S and 35°S during 72 months. Variability in the intensity of upwelling occurring over tens of km produced predictable variation in recruitment of intertidal mussels, but not barnacles, and did not affect patterns of community structure. In contrast, sharp discontinuities in upwelling regimes produced abrupt and persistent breaks in the dynamics of benthic and pelagic communities over hundreds of km (regional) scales. Rates of mussel and barnacle recruitment changed sharply at ≈32°-33°S, determining a geographic break in adult abundance of these competitively dominant species. Analysis of satellite images demonstrates that regional-scale discontinuities in oceanographic regimes can couple benthic and pelagic systems, as evidenced by coincident breaks in dynamics and concentration of offshore surface chlorophyll-*a*. Field experiments showed that the paradigm of top-down control of intertidal benthic communities holds only south of the discontinuity. To the north, populations seem recruitment-limited, and predators have negligible effects, despite attaining similarly high abundances and potential predation effects across the region. Thus, geographically discontinuous oceanographic regimes set bounds to the strength of species interactions and define distinct regions for the design and implementation of sustainable management and conservation policies.

coastal ecosystems | upwelling | community regulation | Chile

Variation in the supply of new individuals to local populations has long been recognized as a major factor controlling species interactions and community regulation in marine ecosystems (1–3). Recruitment variation has generally been thought to add stochasticity to population and community dynamics; however, recent studies using long-term and spatially extensive databases are starting to find persistent regularities in the effect of oceanographic processes on benthic communities. One of these oceanographic processes is upwelling, which can influence larval delivery to coastal habitats (4–7). During upwelling, equatorward winds produce offshore Ekman transport (OET) of surface waters along eastern oceanic boundaries, exporting larvae of coastal organisms that are entrained in the moving waters. Reversals or breakdown of winds bring offshore waters and larvae back to the coastal zone (6–8). Regional gradients in the intensity of wind-driven upwelling that determine the rate of larval recruitment of dominant intertidal invertebrates have been discovered along the south island of New Zealand and the coasts of western North America and South Africa (9–12). Because the rate of recruitment is a major factor controlling the strength of species interactions (13, 14), atmospheric circulation seems to determine the latitudinal variation in the strength of species interactions over thousands of kilometers (9, 11, 12). Upwelling can be modulated by meso-scale changes in coastal topography (15, 16), and these land features have been associated with spatial patterns of population structure (17–19). However, few experimental studies have directly examined which scales of oceanographic changes are linked to variations in the strength of species interactions (but see ref. 11).

Here, we examine the effects of meso- and regional-scale variation in upwelling along the southeastern Pacific. The evidence supports the hypothesis that abrupt regional-scale discontinuities in oceanographic regimes, but not meso-scale variation, can couple the dynamics of benthic and pelagic systems and regulate the strength and outcome of species interactions in intertidal communities. These discontinuities set spatial limits to ecological generalizations derived from field experiments.

Methods

Mussels, *Perumytilus purpuratus*, and chthamaloid barnacles are dominant competitors for space in the mid and high intertidal zones of southeastern Pacific shores, respectively, capable of excluding other species from the primary substratum and thereby affecting the entire intertidal community (20–22). These sessile invertebrates have broadly dispersing pelagic larvae, whose return to the adult habitat depends on cross-shelf transport processes and is often highly variable over space and time (17, 23). We characterized the patterns of recruitment of these species at 14 sites spread >900 km of coastline in central Chile between 29°S and 35°S during 72 months (January 1998 to December 2004). In addition, to evaluate in more detail the effects of variation in upwelling intensity, between 2002 and 2003, we sampled four additional sites toward the center of the study region (Fig. 1*a*). Thus, we had similar information for a total of 18 sites across the region. Recruitment of mussels and barnacles was quantified on larval collectors deployed over 20- to 50-m transects on wave-exposed benches at each study site at the mid and high intertidal zones, respectively (23, 24). Barnacle recruitment plates and mussel recruitment pads were replaced every 25 to 70 days. Two common species of chthamaloid barnacles are found in the upper intertidal zone at roughly similar abundances, *Jehlius cirratus* and *Notochthamalus scabrosus*. They both recruit and survive on the recruitment collectors, but they cannot accurately be identified to species at small postmetamorphic size. Thus, we pooled both species of barnacles

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Abbreviations: OET, offshore Ekman transport; SST, sea-surface temperature; AVHRR, advanced very high resolution radiometer; LOWESS, locally weighted scatterplot smoothing; ECIM, Marine Reserve; chl-*a*, chlorophyll-*a*; SeaWiFS, Sea-Viewing Wide Field-of-View Sensor.

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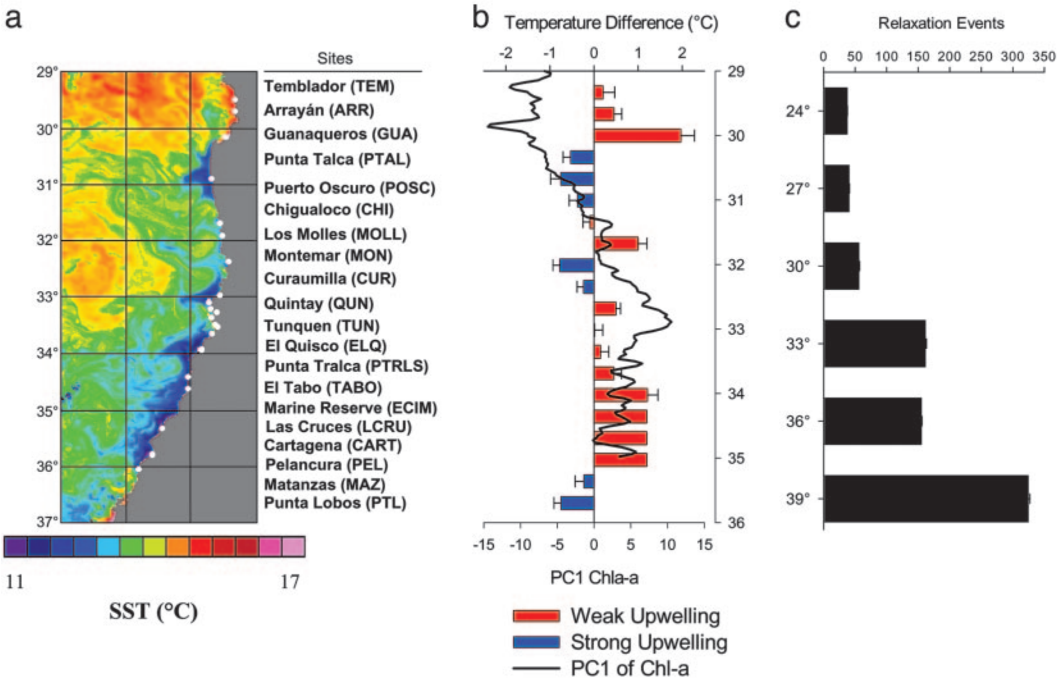

Fig. 1. Spatio-temporal oceanographic and biological patterns across the region. (*a*) Selected AVHRR satellite image for the study region showing spatial structure in SST during November 1999 and the locations of study sites. Abbreviations of sites listed on the right as used in other figures. (*b*) Mean ± SE difference in SST between pixels 2 km and 25 km offshore in front of each study site. Negative values indicate strong upwelling with water nearshore colder than offshore. The line superimposed on the figure is the first empirical orthogonal function (principal component) of chl-*a* concentration (mg/m^3) for the study region. Data were 8-day averages of SeaWiFS satellite images every 4 km alongshore between September 1997 and August 2001. (*c*) Frequency of relaxation events (OET ≤ 0) across the region based on 6-hourly observations for austral spring–summer 2000–2001 and 2001–2002.

in analyses. To characterize patterns of intertidal abundance (cover) of mussels and barnacles, between spring and summer of 2001 and again in 2003, we sampled the low, mid, and high intertidal zones at each of the 18 study sites for which we had recruitment data and five additional sites interspersed among the former (Fig. 1*a*), which provided better spatial coverage. Between 7 and 12 50 × 50-cm quadrats with 81 intersection points were sampled along 20- to 50-m-long transects at each of three benches separated by 50–400 m.

We identified the main spatial scales of variation in hydrographic conditions across the region by using different types of information. The spatial structure of sea-surface temperature (SST) was obtained from 62 advanced very high resolution radiometer (AVHRR, 1-km resolution) images. For each of the 23 sites, we calculated the mean difference in SST between a station *ca*. 2 km offshore and that observed 25 and 50 km offshore. Colder temperatures inshore are indicative of strong coastal upwelling whereas warmer temperatures reflect weak upwelling conditions, and the latitudinal gradient in SST does not affect the classification of sites (25). This classification of sites as having strong or weak upwelling was contrasted with the pattern of *in situ* measured temperature recorded by loggers (StowAway Tidbit, Onset Computer Corporation, Bourne, MA; ±0.01°C precision) deployed at a 1- to 2-m depth ($n = 13$ sites). These loggers registered SST between 5- and 20-min intervals from 1997 through 2004 and are well correlated with nearshore AVHRR temperature (17). Monthly upwelling indices (OET) spanning our study region from 1997 to 2000 are publicly available from the National Marine Fisheries Service Pacific Fisheries Environmental Laboratories of the National Oceanic and Atmospheric Administration (NOAA, www.pfeg.noaa.gov). In addition, we obtained 6-hourly OET indices during the spring and summer months, when upwelling-favorable conditions are maximal. The OET is calculated over quadrats of 3° × 3° (30°S, 33°S, and 36°S) and is based on the average wind field and the Coriolis parameter for that latitude. Time series of coastal chlorophyll-*a* (chl-*a*) concentration (mg/m^3) for the study region, from 1997 to 2001, were obtained from 8-day composites of the Sea-Viewing Wide Field-of-View Sensor (SeaWiFS, 4-km resolution) satellite (26).

To distinguish spatial correlation resulting from spatial trends in recruitment and adult abundance (cover) across the entire region, from those resulting from site-to-site variation, we decomposed spatial variability into its trend (i.e., variation common to several sites adjusted throughout the study region) and the residual variation (site variation not accounted for by the trend). A locally weighted scatterplot smoothing (LOWESS) (27) was fit separately to the spatial patterns in recruitment and cover of each species as a function of the distance (km) to the southernmost site (Fig. 1*a*) for the smoothing factor that produced normal and symmetric LOWESS residuals and was independent from geographic distance (Kolmogorov–Smirnov Tests, $P > 0.05$) (28). We then calculated the correlations between recruitment and cover based on the regional-scale trend (predicted LOWESS), site-variation (residuals from LOWESS), and the raw data. A sequential Bonferroni correction (29) was applied to adjust significance levels for multiple comparisons. Because LOWESS smoothing will produce spatially autocorrelated data (regional trends), the effective degrees of freedom for significance tests of cross-correlations can be lower than the standard tests (30, 31). Therefore, significance values close to 0.05 should be taken with caution. The effect of meso-scale variation in upwelling intensity (strong versus weak) was evaluated by using one-way ANOVA on the raw data and on the residuals of LOWESS regression, using sites as replicates.

Two field experiments were conducted between 1999 and 2000 to quantify spatial variation in the strength of predator–prey interactions. We concentrated in the predator–mussel interaction because its outcome is critical for the entire intertidal community (21, 22, 32). First, to evaluate whether regional changes in adult mussel abundance were the result of variation in predation intensity caused by changes in predator abundances and/or per capita predation rates, or by higher mussel mortality due to abiotic conditions, we transplanted mussels from a common source to different sites. Ten clumps of 100 juvenile *Perumytilus* mussels each were transplanted to the mid-low intertidal zone at each of four sites [Matanzas (MAZ), Marine Reserve (ECIM), Las Cruces (LCRU), and El Quisco (ELQ); Fig. 1] located south of 32°S, where mussel recruitment rates are relatively high, and three sites [Temblador (TEM), Punta Talca (PTAL), and Guanaqueros (GUA); Fig. 1] north of 32°S, where mussel recruitment rates are relatively low. Plastic mesh was used to hold mussels against the rock surface to allow them to reattach and to prevent predation. After two months, the mesh on five randomly chosen clumps per site was removed, exposing half of the mussel clumps to predators while the other half were protected by dome-shaped mesh predator exclusion cages. Mussel survival was monitored every 2 days for the first week and every 15 days thereafter. We present mussel survival in the two treatments after 50 days from the beginning of the experiment. In such experiments, in which a fixed number of prey are followed over time, mussel survival can be described by $N_t = N_0 e^{(-\alpha P + m)t}$, where N_t is the number of live mussels at time = t, N_0 is the initial number of mussels transplanted, αP is the total or population predator–prey interaction strength, and m is the natural mussel mortality rate (33, 34). Calculating the slopes of the regressions between $\mathrm{Log}_e(N_t/N_0)$ and time for each replicate under different treatments and using average predator density as an estimate of P allow estimation of all mussel mortality terms (35, 36).

The mussel transplant experiment evaluated whether there was geographic variation in natural mussel mortality (m) or predation intensity (αP). To determine the role of these factors in the regulation of mussel populations, a predator exclusion experiment that allows mussels to settle at natural rates must be conducted. Therefore, we set up a series of replicated predator-exclusion experiments at five sites with similar physical characteristics. Stainless-steel cages, control plots, and roofs (procedure controls) were used to exclude predators, allow all predators to access experimental plots undisturbed, and control for cage artifacts, respectively. Five replicates of each treatment were deployed over short turfs of the alga *Gelidium chilense*, which mediates mussel recruitment to the intertidal zone. Experiments were conducted in 1999 and again in 2000 at three sites south of 32°S (ECIM, Las Cruces, and El Quisco) and two to the north (Punta Talca and Guanaqueros). In all cases, no differences were observed between roofs and control plots ($P > 0.05$). Thus, for simplicity, we present results for controls and treatments.

Results and Discussion

Our analyses revealed two scales of variation in hydrographic conditions associated directly or indirectly with variation in upwelling activity across the region. First, coastal topography and coastline orientation are associated with meso-scale spatial structure in SST, which is apparent in AVHRR satellite images (Fig. 1*a*). Several studies in central Chile have shown that colder inshore waters in the images correspond to areas of intensification of wind-driven upwelling, whereas warmer waters correspond to areas of weak upwelling or upwelling shadows, which often occur <15 km away from upwelling centers (17, 37, 38). Superimposed on this meso-scale variation in upwelling intensity, which occurs irregularly across the entire region (Fig. 1*b*), there is a clear regional-scale discontinuity in oceanographic regimes. Due to the seasonal migration of the Pacific anticyclone and continental topography, upwelling-favorable winds are generally weaker, but more persistent throughout the year north of ≈32°S (39–41). Indeed, OET is upwelling-favorable year-round north of ≈30°S–32°S, whereas they are downwelling-favorable (OET $\leq$ 0) during austral winter south of this latitude (39). Analysis of high-frequency, 6-hourly upwelling indices during spring and summer months, when upwelling and therefore offshore transport are more intense, shows that there are fewer episodes of upwelling relaxation to the north of 32°S (Fig. 1*c*). Changes in upwelling intensity and oceanographic regimes can have important effects on larval transport to the shore (15, 42).

Results from the long-term recruitment monitoring study showed high among-site variation, but also a sharp, coincident geographic discontinuity in average recruitment rates of mussels and barnacles at about latitudes 32°S–33°S, with generally lower recruitment to the north (Fig. 2 *a* and *b*). Regional trends in barnacle and mussel recruitment were highly correlated, whereas site residuals were not (Table 1), suggesting that barnacle and mussel recruitment are similarly affected by regional-scale processes, but not by local, site-specific factors. Field surveys of adult cover of these same sessile species showed that the abrupt changes in recruitment rates were mirrored by persistent breaks in intertidal community structure. Mussel cover in the mid zone and, to a lesser extent, barnacle cover in the high intertidal zone changed abruptly at ≈32°S–33°S (Fig. 2 *c* and *d*), with larger abundances to the south than to the north of this latitude. Low mussel cover at the marine reserve of ECIM, where mussel recruitment is high (Fig. 2), is attributable to locally intensified predation by the commercially collected gastropod *Concholepas concholepas*, which is protected in the reserve (21). Barnacle and mussel cover were highly correlated in terms of both their regional trends and site residuals (Table 1), suggesting that regional-scale processes as well as site-scale postrecruitment factors affect adult cover of these species in similar ways. Recruitment was highly correlated with adult cover when we examined regional trends for mussels and barnacles, presumably as a result of these groups sharing similar spatial structure across the study region (Table 1). These strong correlations indicate that, over scales of hundreds of kilometers, recruitment limitation dominates the patterns of adult abundance. In contrast, site residuals of recruitment and cover showed no correlation (Table 1), suggesting again that postrecruitment processes that vary over scales of sites are the main determinants of local adult abundance. Strong correlations between recruitment and intertidal abundance are observed in the region of low recruitment to the north of 32°S ($r = 0.91$ and 0.80, for mussels and barnacles, respectively), suggesting that, within this region, intertidal populations are recruitment–limited (3, 43). To the south of this latitude, correlations are weak and nonsignificant (r = 0.37 and 0.03, for mussels and barnacles, respectively.

Although regional-scale discontinuities in upwelling regimes had profound effects on mussel and barnacle recruitment, apparently leading to similar patterns of regional variation in intertidal abundances, meso-scale variation in upwelling intensity had only weak effects on these groups. Evaluating the effect of upwelling intensity by using site residuals from LOWESS regressions reduced the large variability observed across sites within upwelling condition produced by the strong regional trends (Fig. 2 *Inserts*). Analysis of these site anomalies showed that recruitment and cover of mussels and barnacles were slightly higher (lower) than expected at weak (strong) upwelling sites, as predicted by the upwelling-relaxation model (13). However, these differences were small and significant only for mussel recruitment (Fig. 2).

If discontinuous oceanographic regimes cause major breaks in benthic community dynamics, one would expect to detect this signal in the pelagic environment as well. A sharp change in chl-*a* concentration at ≈32°S has been reported in nearshore waters (39, 44). Similarly, empirical orthogonal function analysis of SeaWiFS

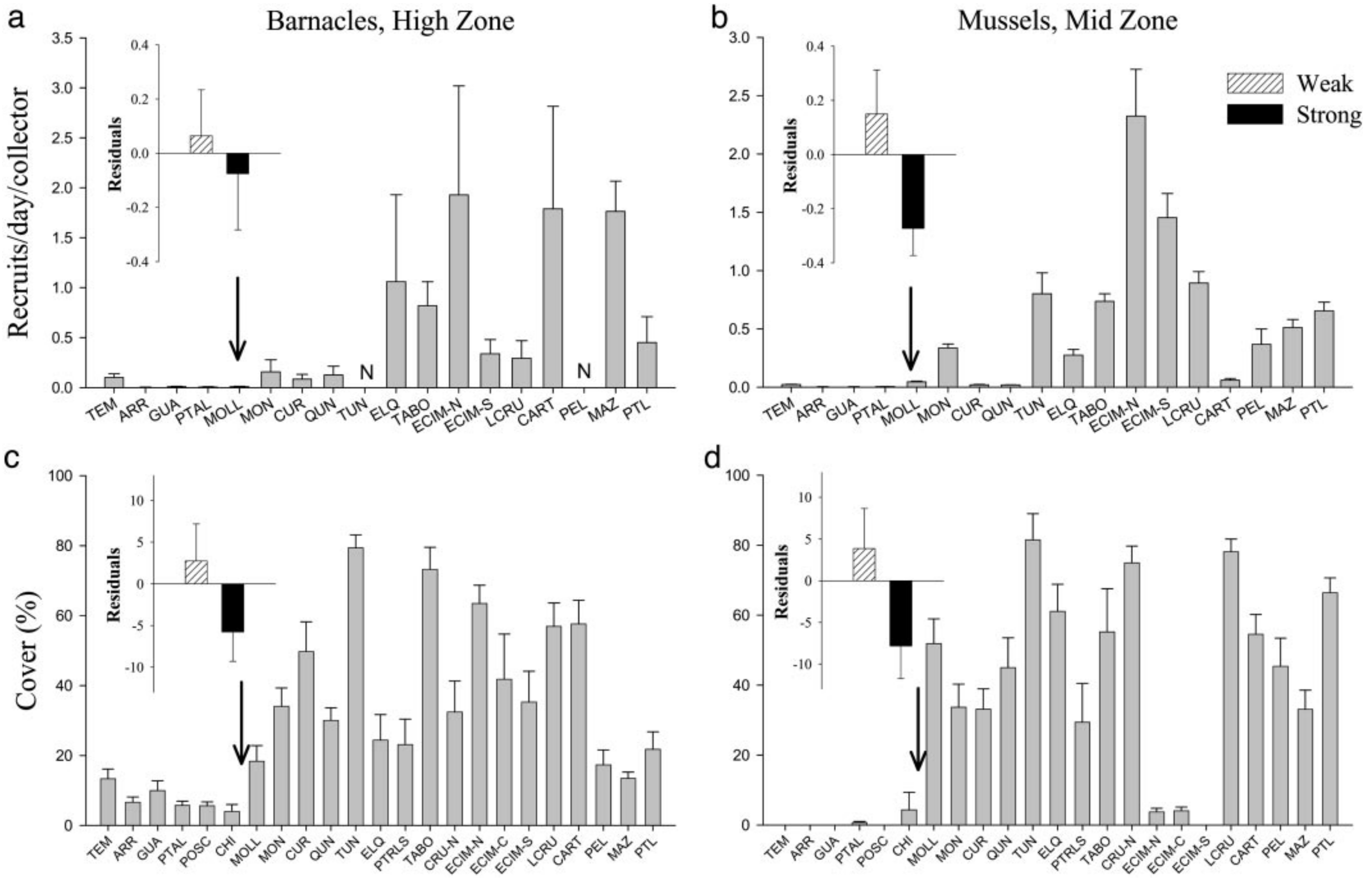

Fig. 2. Patterns of recruitment and adult abundance across the region. (*a* and *b*) Monthly recruitment to collectors, standardized by days of exposure and averaged from January 1998 through December 2004 at each study site for chthamaloid barnacles *J. cirratus* and *N. scabrosus* in the high intertidal zone settling on 10 × 10-cm Plexiglass plates coated with safety walk (*a*) and *P. purpuratus* mussels in the mid zone settling on plastic Tuffy pads (*b*) (23). (*c* and *d*) The intertidal adult abundance estimated from replicated transects and 50 × 50-cm quadrats at the same sites and tidal heights for barnacles (*c*) and mussels (*d*). The segmented lines show location of the geographic discontinuity. The arrows indicate the position of Los Molles, the site located at 32°S. (*Inserts*) The average cover (*a* and *b*) or recruitment (*c* and *d*) of barnacles and mussels at sites of strong (black bars) and weak (hatched bars) upwelling, after removing the regional trend in the data by using LOWESS regression (residuals). Error bars in these panels represent variation across sites within upwelling-intensity condition.

chl-*a* time series showed a marked shift in the intensity of the annual cycle of surface chl-*a* concentration around 32°S (Fig. 1*b*). These striking coincidences in spatial structure between the benthic and pelagic communities are indicative of strong coupling over regional scales. The sharp spatial transition in phytoplankton biomass and dynamics has not yet been explored in detail, but changes in phytoplankton biomass associated with upwelling dynamics involve changes in phytoplankton species composition and cell size spectrum, which in turn can have important effects on invertebrate larval condition (45). Although our results suggest that adult mussels grow and survive well at sites north of 32°S–33°S (see below), it is possible that the lower phytoplankton availability to the north could lead to a decrease in adult reproductive output. Lower reproductive output over such an extensive geographic region would reduce total larval production, which in turn could be responsible for low adult abundances.

Results from the mussel transplant experiment showed that transplanted mussels protected from predators survive well at all sites across the entire region (Fig. 3*a*, cross-hatched bars). Natural mortality of mussels in the absence of predators (m) was low and similar across sites ($P > 0.05$), suggesting that abiotic factors do not play a major role in the observed pattern of mussel abundance. High mortality of transplanted mussels was observed in the presence of predators at all sites (Fig. 3*a*, filled bars), with the largest interaction strengths (αP) inside the marine reserve of ECIM and the management and exploitation area of El Quisco (ELQ), where

Table 1. Pearson correlation coefficients between recruitment and cover of barnacles and mussels based on raw data

Variables	Raw data	Regional trend	Site residuals
Mussel recruitment vs. cover	0.53 (0.0220)	0.81 (**0.0001**)	0.24 (0.3453)
Barnacle recruitment vs. cover	0.31 (0.2736)	0.67 (**0.0081**)	−0.21 (0.4786)
Recruitment of mussels vs. barnacles	0.26 (0.3710)	0.97 (**0.0001**)	−0.42 (0.1310)
Cover of mussels vs. barnacles	0.67 (0.0025)	0.79 (**0.0001**)	0.53 (**0.0240**)

Regional trends fitted by LOWESS regression. Significance of correlations in parentheses. Bold face indicates significant correlations after Bonferroni adjustment.

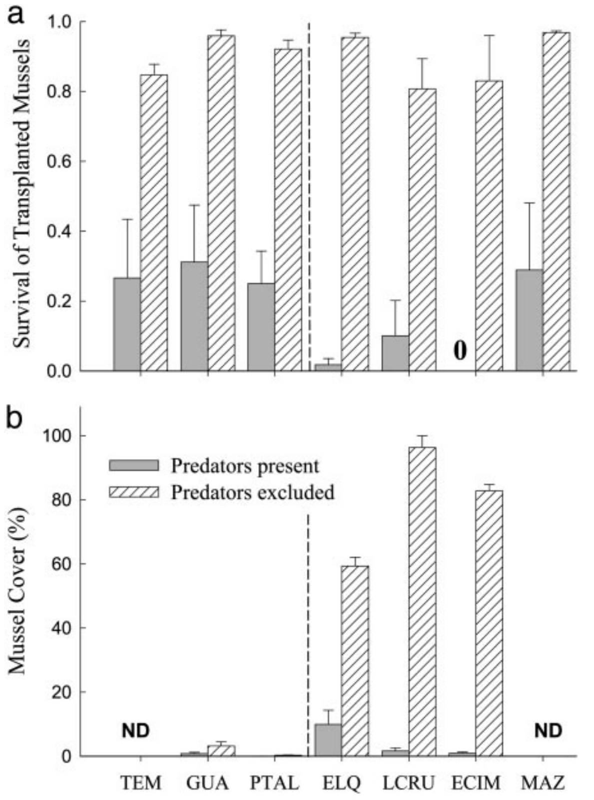

Fig. 3. Results of two independent field experiments. (*a*) Survival of transplanted mussels at sites north (TEM, GUA, PTAL) and south (ELQ, LCRU, ECIM, MAZ) of the recruitment discontinuity observed ≈32°S–33°S (segmented line). Bars are average (± SE) survival of mussels in replicated clumps in the presence (filled bars) and absence of predators (hatched bars) after 50 days in the field. (*b*) Effects of predator exclusions on resultant community structure at a subset of the sites north and south of the discontinuity. Bars are the average abundance of mussels (% cover ± SE) in replicated plots in the presence of predators (filled bars) and in predator exclusions (hatched bars). For simplicity, procedural controls (roofs) are not presented.

harvesting of the carnivorous gastropod *C. concholepas* and other invertebrates is excluded or regulated, respectively (46, 47). No differences were observed between sites located north and south of 32°S. This result suggests that predation intensity can vary among sites but is similar across the geographic discontinuity. Indeed, predator abundance does not vary systematically across the region (25). Probable causes for the lack of a geographic response in abundance of the major mussel and barnacle predators are that their larvae are not affected by the same oceanographic processes influencing barnacle and mussel larvae and that they are generalists that can switch to feeding on other prey and that their own recruitment is not directly dependent on local prey consumption. In addition, seastars and gastropod predators are long-lived and could withstand several years of low prey recruitment (48).

Do discontinuous oceanographic regimes ultimately modify the outcome of species interactions and the regulation of benthic communities? In the predator-exclusion experiments, mussels covered between 60% and 95% of the primary space within the first 3 months of initiating the experiments at sites south of 32°S (Fig. 3*b*) out-competing other invertebrate and algae species from the rock. In contrast, at the two northern sites, neither mussel nor barnacle cover increased in predator exclusion plots. At the three sites south of 32°S, prey abundances in exclusions differed from those in controls ($P < 0.001$), whereas no differences were found at northern sites ($P > 0.05$). Thus, predators play a major role in the regulation of intertidal communities south of ≈32°S–33°S, but their role is negligible to the north, at least up to around 28°S.

The paradigm of top-down control of intertidal communities along the coast of Chile (20, 22, 32) was built on field experiments conducted in a limited geographic range in central Chile, at around 33°-34° and a few places in the south (49). Similar conclusions in other parts of the world are similarly based on geographically restricted studies where logistic limitations have constrained the geographic extent of ecological studies. The use of the comparative experimental approach (24) and the recently developed availability of long-term, spatially extensive data sets of recruitment and oceanographic conditions are starting to reveal more persistent and regular patterns than many envisioned a decade ago. With similar studies elsewhere (11, 12), our results suggest that patterns of species interactions in benthic communities can be bound by regional discontinuities in oceanographic conditions. Discontinuous upwelling regimes also cause major changes in the temporal dynamics of phytoplankton biomass, which in turn can have far-reaching effects in the pelagic food web. It is therefore not surprising that the anchovy fisheries along the coast of Chile and Peru shows a sharp decrease in total captures in an extensive region of the coast north of ≈32°S (50). Considerations of the scale and geographic location where oceanographic conditions produce major changes in the pattern of species interactions, like those found here north and south of 32°S, must be incorporated in designing policies for the sustainable management of benthic and pelagic resources, as well as in establishing marine coastal reserves worldwide.

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