

Disentangling the effects of propagule supply and environmental filtering on the spatial structure of a rocky shore metacommunity

Nelson Valdivia^{1,*}, Moisés A. Aguilera², Sergio A. Navarrete^{3,4},
Bernardo R. Broitman²

¹Instituto de Ciencias Marinas y Limnológicas, Facultad de Ciencias, Universidad Austral de Chile, Campus Isla Teja, Valdivia 5110236, Chile

²Centro de Estudios Avanzados en Zonas Áridas (CEAZA), Universidad Católica del Norte, Larrondo 1281, Coquimbo 1781421, Chile

³Estación Costera de Investigaciones Marinas - Las Cruces, Pontificia Universidad Católica de Chile, Santiago 6513677, Chile

⁴Center for Marine Conservation - Las Cruces, Pontificia Universidad Católica de Chile, Santiago 6513677, Chile

ABSTRACT: Environment-driven variation in the supply of individuals to local assemblages can determine patterns of community structure. Alternatively, local environmental conditions can determine the type of species that can be successfully established in a given community. Most communities are probably found somewhere between these 2 extremes, but few studies have attempted to disentangle their effects in a community-wide context. Using multivariate approaches in rocky shore communities, we showed that environmental variables (i.e. sea surface temperature and wind stress), the benthic abundance of 108 species of invertebrates and macroalgae, and recruitment rates of invertebrates all shared significant spatial and temporal patterns of variability across a 400 km shoreline marked by the presence of a prominent upwelling centre. Variance-partition analyses for the invertebrates with pelagic development showed that spatially structured environmental filtering alone explained only 7% of the variation in community structure. In contrast, the combination of environmental conditions and recruitment variation explained 45% of the variability in community structure and an additional 18% was jointly explained by recruitment and spatial relationships among sampling sites. Unexplained variation (41%) can be attributed to factors like local species interactions that are robust to environmental variability. Therefore, environment-driven variation in recruitment rates can have, in comparison to pure environmental filtering, stronger effects on the structure of this metacommunity. Our results can serve as a foundation for predictive models of the response of biodiversity to climate change and other human-induced disturbances, which are predicted to alter local environmental conditions and dispersal pathways.

KEY WORDS: Metacommunity · Recruitment · Environmental filtering · Dispersal · Biodiversity · Chile · Marine · Mesoscale

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Understanding the processes that underpin spatial patterns of distribution and abundance of multiple species is central to the prediction of the response of natural communities to large-scale natural and

human-induced environmental changes. The metacommunity framework, in which local ecological communities are connected by dispersal of propagules, describes the role of scale-dependent processes in the organisation of local communities (Leibold et al. 2004, Logue et al. 2011). According to this view,

the interaction of environmental filtering, dispersal and eventual recruitment, and local-scale ecological processes such as species interactions, simultaneously give rise to patterns of community structure and species coexistence (Logue et al. 2011, Menge & Menge 2013). Environmental filtering occurs when environmental stress exceeds the physiological tolerances of the individuals of a given species (Pörtner & Knust 2007, Somero 2010), rendering negative population growth rates. This abiotic process generates sets of species with shared ecological tolerances at any given site; local species interactions would further modulate the type of species that can actually coexist (Cornwell et al. 2006, de Bello et al. 2012). Separating the effects of these environmental filters from those generated from other main processes, such as recruitment (Aiken & Navarrete 2011), has important theoretical and practical consequences (Gilbert & Bennett 2010, de Bello 2012).

In marine ecosystems, regional (100s to 1000s of km) and mesoscale (10s to 100s of km) environmental variability can directly affect the performance of benthic organisms and at the same time modulate the supply of planktonic larvae to coastal communities (Watson et al. 2011, Fenberg et al. 2015). Therefore, 'environmental filtering', typically synthesised in spatial and temporal patterns of sea surface temperature (SST), can affect local community structure through both abiotic environmental conditions and dispersal–recruitment variation (Bustamante et al. 1995, Wieters et al. 2009, Menge & Menge 2013). Here, we define environmental filtering as the abiotic conditions (e.g. SST) that can affect established individuals in the benthic habitat, and attempt to separate them from the effect of environment-driven variation in recruitment. Growth rates of primary producers have been shown to correlate to mesoscale structure in SST, which is closely related to nutrient concentrations (Tegner & Dayton 1987, Menge et al. 2003, McPhee-Shaw et al. 2007). In this way, patterns of community structure can result from spatial variation in abiotic environmental conditions through pure 'environmental filtering' (Pavoine et al. 2014), as well as through the modification of species interactions, e.g. change in relative competitive abilities across space leading to species sorting across local populations (Leibold et al. 2004). Much research, mostly through the analysis of species functional traits, is devoted to teasing apart the pure abiotic filtering from the role of species interactions; however, disentangling the effects of environmental filtering and environmentally mediated recruitment has received less attention (de Bello 2012, de Bello et al. 2012).

The supply of recruits from the regional pool of reproductive adults can determine population patterns and the strength of species interactions (Connolly & Roughgarden 1999, Navarrete et al. 2005), but evidence linking larval recruitment rates to community patterns is scarce and varies in consistency. On the one hand, significant links between recruitment rates and adult population size have been shown for a number of species (Connolly & Roughgarden 1999, Hughes et al. 1999, Navarrete et al. 2005, Broitman et al. 2008). Accordingly, the relative abundance of competitive pairs of species can also tightly and 'neutrally' follow the among-site variation in relative recruitment rates (Shinen & Navarrete 2014). On the other hand, recent efforts to quantify the signal of recruitment across entire communities, or at least considering a large fraction of the species in the metacommunity, have come to apparently different conclusions. For instance, work along an extensive section of the coast of central Chile suggests that post-recruitment processes lead to significantly more convergence in community structure across the region than one would expect based solely on recruitment of individuals (Caro et al. 2010). In contrast, water flow and currents, which deliver propagules to final adult habitat, have been shown to mediate the diversity and structure of benthic communities elsewhere (Watson et al. 2011, Palardy & Witman 2014). In the Southern California Bight, the predictive power of nearshore circulation can be higher than that of SST variability (Watson et al. 2011); i.e. the pure environmental filtering appeared to be much lower than the dispersal–recruitment component in the structure of those communities. Thus, there is a clear need to improve our understanding of the relative importance of environmental and recruitment factors as determinants of multi-species metacommunity structure.

In coastal ecosystems located along mid-latitude temperate west coasts, the wind-driven upwelling of cold, nutrient-rich deep waters to the surface determines mesoscale variation in environmental conditions, such as nutrient supply, phytoplankton concentration, and consumer body sizes. Upwelling activity interacts with the delivery of planktonic larvae, influencing patterns of larval arrival of marine species (Menge et al. 2004, Nielsen & Navarrete 2004, Broitman et al. 2008, Witman et al. 2010). Along the upwelling ecosystem of the Pacific coast of North America, for example, several population- and community-level properties are unimodal functions of upwelling persistence (Menge & Menge 2013). Such unimodal relationships across upwelling inten-

sities have yet to be examined along other productive coastal regions, such as the Humboldt Upwelling Ecosystem, in which coastal assemblages located around persistent upwelling centres (e.g. capes and peninsulas) show generally reduced phytoplankton biomass and reduced recruitment rates due to offshore advection of larvae and propagules (Lagos et al. 2008).

Here, we examined in a community-wide context the relative roles of environmental filtering and recruitment rates in determining the structure of a rocky intertidal metacommunity. We tested the general hypothesis that major environmental filters—imposed by SST and coastal wind patterns—and recruitment rates of benthic invertebrates jointly influence the spatial variation in community structure. As a model system, we used the intertidal rocky shores of northern-central Chile, characterised by overall moderate to low recruitment of most species and by the wind-forced upwelling of cold and nutrient-rich deep waters around a prominent headland that maintains a persistent structure of nearshore SST. By quantifying recruitment patterns of multiple species and local benthic abundance across the region, we were able to tease apart the effects of environmental variability and supply on spatial patterns of these diverse communities.

MATERIALS AND METHODS

Study region

The upwelling centre mentioned in the ‘Introduction’ is located in the Humboldt Upwelling Ecosystem and locked to Punta Lengua de Vaca (Fig. 1, 30.25° S; PLV hereafter), a prominent headland that abuts the southern end of the greater Coquimbo bay and marks a large-scale oceanographic transition along coastal Chile (Hormazabal et al. 2004, Muñoz 2008, Garreaud et al. 2011, Rahn et al. 2011). The strength of the annual cycle in nearshore *in situ*-measured SST decreases sharply south of 30.25° S, while the synoptic-scale variability (days to weeks) increases in importance to the south of this latitude (Tapia et al. 2014). Similarly, wind stress shows lower seasonal variability and a higher synoptic variability at sites located south rather than north of PLV (Tapia et al. 2014). Moreover, the strong and negative correlations between equatorward wind stress and SST variability observed south of PLV weaken at sites located north of this latitude (Tapia et al. 2014). Accordingly, sites located immediately south of PLV

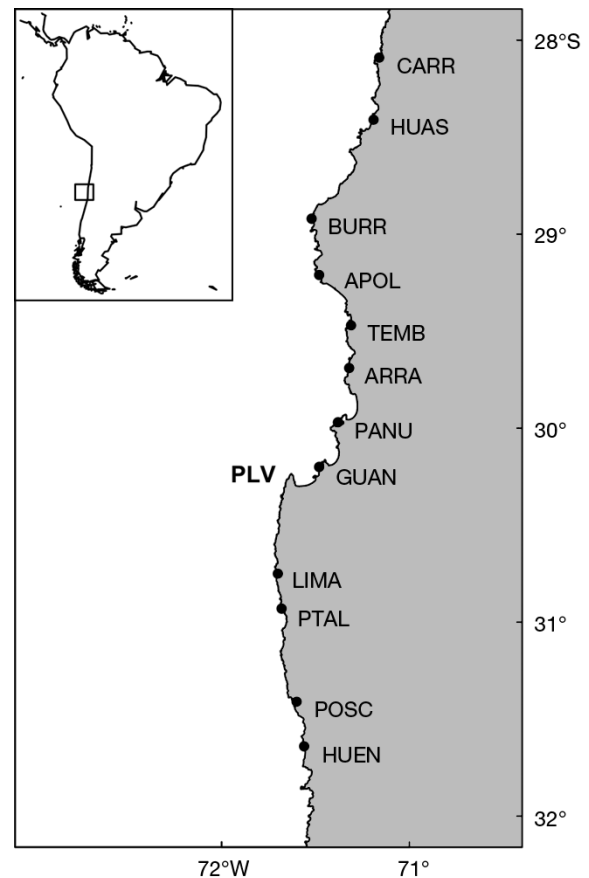


Fig. 1. The study region showing the 12 intertidal rocky shore study sites where species abundances, sea surface temperature (SST) and invertebrate larval recruitment rates were measured between 2009 and 2013. Site codes are given in Table 1. PLV: Punta Lengua de Vaca

are more strongly influenced by upwelling activity, and temperature fluctuates markedly over synoptic timescales, while sites located to the north receive waters from the upwelling centre (Moraga-Opazo et al. 2011) and temperature fluctuates over longer temporal scales (Rahn et al. 2011, Valdivia et al. 2013).

The mesoscale (i.e. 10s to 100s of km) transition in oceanographic conditions coincides with significant spatial variation in community structure, which is also associated with a biogeographic transition area (Broitman et al. 2001, Camus 2001). For example, the dominant corticated red alga *Mazzaella laminarioides* (northern lineage) and the large bull-kelp *Durvillaea antarctica* find their northern (equatorial) geographic range limit around this zone (Broitman et al. 2011, Montecinos et al. 2012). The northern and southern limits of the cryptic kelps *Lessonia spicata* and *L. berteriana*, respectively, also occur within our study region (Tellier et al. 2011); similar patterns have been observed for the scurrinid limpets *Scurria*

zebrina and *S. viridula* (Aguilera et al. 2013). In addition, beds of the purple mussel *Perumytilus purpuratus*, characteristic on the mid-intertidal zone south of 32° S, become scarce northward and are replaced by an increase in cover of ephemeral algae, empty space and patches of chthamalid barnacles (Broitman et al. 2001, Lagos et al. 2005). Similarly, overall biomass of corticated algae also changes abruptly in this region (Wieters et al. 2009, Tapia et al. 2014).

Twelve rocky intertidal sites, spanning ca. 400 km of the shore between 28° and 32° S were established during the austral winter of 2009 (Fig. 1, Table 1). In order to minimise among-site differences in terms of substratum heterogeneity, observations were conducted on gently sloping flat rocky shore benches with similar characteristics and fully facing the prevailing Southwester swell.

Environmental variability

In situ measurements of SST were used as an indicator of environmental variation and were obtained by means of digital thermographs (HOBO, Onset) deployed at ca. 1 m depth at each site. Each sensor was housed in a PVC pipe, encased in a concrete block, and deployed from the shore at ca. 1 m depth from mean low water (MLW) in the vicinity of monitoring benches. In this study, we analysed daily means of SST. More details about *in situ* measurements of SST, which are publicly available from www.ceazamet.cl/index.php?p_cod=changolab, have been published elsewhere (Tapia et al. 2009). Spatio-temporal variation in wind stress was calculated over a period of 10 yr (2003 to 2013) from daily QuikSCAT wind fields (<http://podaac.jpl.nasa.gov/datasetlist?ids=>

Platform&values=QUIKSCAT) for the study region. Previous work has shown strong and positive correlations ($r > 0.8$) between these satellite-derived wind data and *in situ* measurements of temperature for most of central-northern Chile, especially for periods of > 5 d (Tapia et al. 2014).

Species abundances

At each site, we estimated species abundances on 7 to 10 plots measuring 0.25 m² located along ca. 20 m alongshore transects. The sampling was repeated every ca. 6 mo from May 2009 to July 2012. Transects were replicated at 3 intertidal elevations, low, mid and high intertidal zones. On each bench, we used perennial marine species occurring highest on the shore as indicators of the upper intertidal boundary. Studies on wave-exposed shores conducted elsewhere have shown that their upper distribution limit on different sites represents a summary of the local wave regime (Harley & Helmuth 2003). The barnacle *Jehlius cirratus* is the sessile and perennial species occurring highest on these shores. Once the upper boundary was determined on each shore, we divided the intertidal range into 3 zones of roughly equal vertical extent (i.e. high, mid and low zones). Plots were haphazardly positioned along each elevation zone, but positions were restricted to flat and gently sloping surfaces lacking deep crevices and tide pools.

All seaweeds and invertebrates (> 5 mm) occurring on each plot were identified *in situ*. Organisms were classified to the lowest possible taxonomic level (usually species). For each plot, we used a 50 × 50 cm frame, divided in 25 equal fields with monofilament line, to estimate species abundances. Sessile and mobile species abundances were estimated as percentage covers (1% resolution) and densities (ind. m⁻²), respectively. This same protocol has been used in several studies of benthic diversity along Chile and elsewhere (Broitman et al. 2011, Bulleri et al. 2012). Part of this dataset has been published by Aguilera et al. (2013) and Valdivia et al. (2013).

Recruitment

Plastic mesh balls (Tuffy®) and 10 × 10 cm Plexiglas and PVC plates covered with SafetyWalk™ (3M) were used as standardised collectors to quantify multi-species recruitment rates (see details in Navarrete et al. 2008). Mesh balls were used to collect

Table 1. List of intertidal rocky shore sites included in this study

	Site name	Code	Lat. °S	Long. °W
1	Carrizal Bajo	CARR	28.09	71.16
2	Huasco	HUAS	28.41	71.19
3	Los Burros	BURR	28.92	71.52
4	Apolillado	APOL	29.21	71.48
5	Temblador	TEMB	29.47	71.31
6	Arrayán	ARRA	29.69	71.32
7	Panul	PANU	29.97	71.38
8	Guanaqueros	GUAN	30.20	71.48
9	Limarí	LIMA	30.75	71.70
10	Punta de Talca	PTAL	30.93	71.68
11	Puerto Oscuro	POSC	31.41	71.60
12	Huentelauquén	HUEN	31.64	71.56

mostly mussel and gastropod settlers; PVC plates were used to quantify barnacle recruitment (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m538p067_supp.pdf; Caro et al. 2010). Five replicate collectors were fastened to the rock with stainless-steel bolts in the mid (mesh balls) and the upper intertidal zones (plates) at each site. Mesh balls and plates were located in parallel alongshore transects, so that it was possible to pair the data from each mesh ball to its corresponding plate before the analyses ($n = 5$ pairs of mesh ball and plate). Replicate collectors were replaced monthly. Therefore, post-settlement mortality occurring within each month could modify the initial settlement values to a certain extent. Recruitment rates were standardised to the number of individuals per collector per day. All collectors were initially deployed in June 2009. The time series of monthly recruitment for mussels, gastropods and barnacles covered until January 2011, July 2012 and January 2014, respectively.

Statistical analyses

Principal component analyses on the temporal domain, known in the earth sciences as empirical orthogonal functions (EOF), were used to determine dominant spatiotemporal patterns of daily SST variability along the study region. The EOF analysis provides a compact representation of empirical patterns of spatial and temporal variability, and the large fraction of variance contained in the first and second orthogonal functions (i.e. principal components) is linked to dominant earth-system processes such as the annual, seasonal or synoptic cycles in temperature (Otero & Siegel 2004, Schneider & Cornuelle 2005). Given the spatial coverage and high temporal resolution of our *in situ* SST data, we used these records to construct the EOF, which was then used as a proxy of environmental filters for the coastal meta-community. Satellite wind patterns were used to complement our analyses.

Multivariate geographical patterns of adult abundances and mean daily recruitment rates were separately analysed with canonical analysis on principal coordinates (CAP, Anderson & Willis 2003). CAP is a constrained multivariate method in which an *a priori* prediction (e.g. the entire set of taxa varies among sites) is used to produce an ordination plot. In contrast to unconstrained methods (e.g. multidimensional scaling), in which each new axis is created in the direction of maximal variation of the response data, the CAP axes are drawn in the

direction of maximal difference between pairs of groups defined by the *a priori* prediction. Therefore, CAP axes are linear combinations of the response variables that maximise the between- to within-group variation, allowing the detection of patterns that could be masked by overall dispersion in unconstrained methods (Anderson & Willis 2003, their Fig. 1). We used the capscale function in the vegan package of the R environment (R Core Team 2014) to compute the CAP procedure as follows. Firstly, a matrix of axes weighted by their corresponding eigenvalues was obtained from a principal coordinates analysis of a Bray-Curtis dissimilarity matrix calculated from the abundance data (i.e. spatial time series of species abundances or daily recruitment rates). Secondly, all weighted axes were used in a canonical discriminant analysis of principal coordinates in which the X matrix contained dummy variables corresponding to the site labels. Finally, the significance of fits was determined by permutations of residuals under a reduced model (Oksanen et al. 2013). Both percentage cover and density data (i.e. sessile and mobile taxa, respectively) were included in the analyses of adult abundances by transforming taxon data to proportions of the maximum observed for each taxon across the shores. In this way, all cover and density data ranged between 0 (absence of species in a given quadrat) and 1 (maximum value across all quadrats). The adult abundance dataset included both invertebrates and macroalgae; the larval recruitment dataset included only the taxa listed in Table S1 in the Supplement. Unfortunately, we do not have recruitment rates of macroalgae for multiple sites across the region. We also analysed the subset of the adult abundance dataset that appears in the recruitment dataset (see next paragraph).

Variation-partition analyses, based on redundancy analyses (RDA; Borcard et al. 2004), were used to separate the variation of adult communities with respect to spatial distance, spatiotemporal variation in the SST signal (a proxy of environmental variation) and recruitment rates. These analyses were conducted on the subset of species that have planktonic development and for which we have recruitment data, i.e. macroalgae were not included in this analysis because we did not have estimates of recruitment for any of the sites. The spatial distances among all sampling sites were calculated from latitude-longitude data and transformed to rectangular principal coordinates of neighborhood matrices (PCNM) to use them in the variance partitioning analyses (Dray et al. 2012). PCs from each neighborhood matrix were

selected according to adjusted R^2 from RDA after stepwise model building. Then, the fractions of variation in adult community structure accounted for by the spatial relationships among sampling sites (selected PCNM), the matrix of SST and the matrix of recruitment rates were estimated as adjusted R^2 from the RDA ordinations. The significance of each individual fraction (SST, recruitment rates and spatial distance) was estimated by means of 1000 permutations. PCNM and variance partitioning analyses were conducted with the `pcnm` and `varpart` functions, respectively, in the `vegan` R package.

RESULTS

SST

SST showed a spatial structure marked by lower temperatures at sites located south of PLV in comparison to sites located to the north (Fig. 2A). The exception was BURR, a site located north of PLV where temperature was similar to sites south of PLV (compare boxplots in Fig. 2A). According to this spatial pattern, the EOF analysis showed 2 groups: one containing sites located south of PLV as well as CARR and BURR, and the second containing sites located north of PLV (Fig. 2B). The first EOF (EOF1) explained ca. 98% of the multivariate differences among sites. As expected, the temporal structure of EOF1 corresponds primarily to the seasonal cycle (Fig. 2C). The second EOF (EOF2) accounted for ca. 1% of the SST spatiotemporal variability. According to Tapia et al. (2009, 2014), who analysed the SST variation in this region, the second EOF2 in this region is mostly associated with the synoptic, days-to-weeks, variability (i.e. upwelling cycles), which is expected to be low north of about 30° S, where our study region lies. Although synoptic scale variability was low across the region, its relative importance varied among sites. In particular, sites located north of PLV, excepting BURR and CARR, were more influenced by the seasonal cycle in SST, while the remaining sites were comparatively more influenced by the synoptic-scale SST pattern (see also Tapia et al. 2014). Long-term averages of wind stress correspond well with the spatial structure observed for SST, with maximum stress values around PLV (ca. 30.25° S) and between BURR and HUAS (28.5° to 29.0° S), especially during spring (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m538p067_supp.pdf).

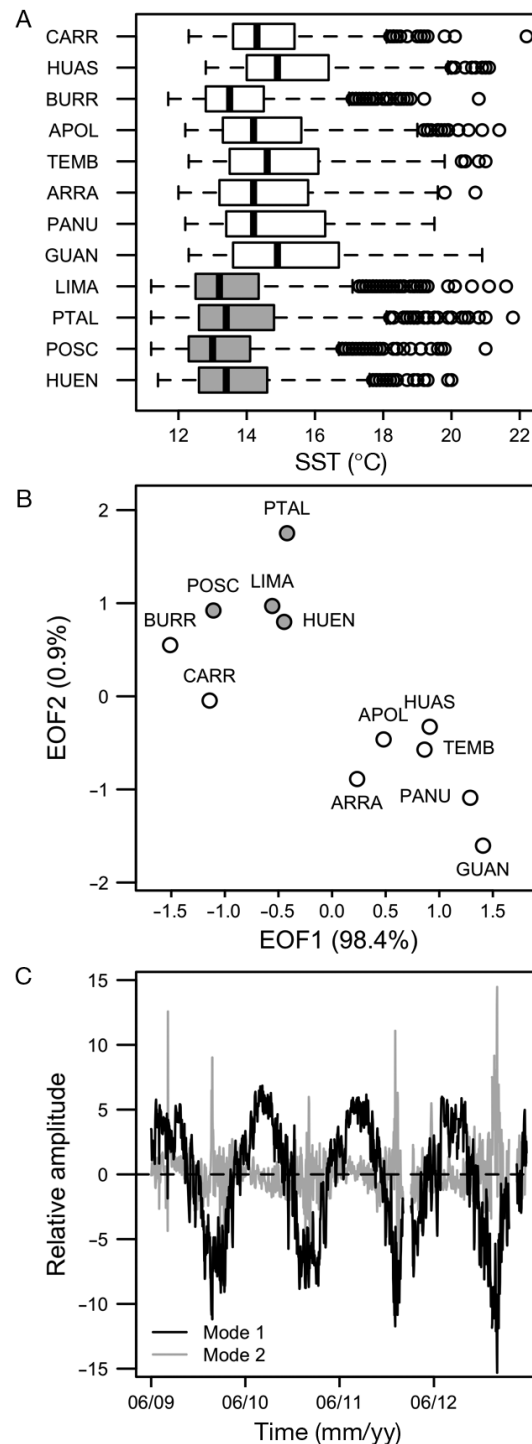


Fig. 2. Spatiotemporal variation of sea surface temperature (SST) across the study region. (A) SST at each intertidal rocky site. Line = median, boxlimits = 25 and 75% quartiles, whiskers = values within $1.5 \times$ box length, circles = outliers. (B) First 2 empirical orthogonal functions (EOF) of SST. Filled and empty symbols denote sites located south and north of Punta Lengua de Vaca, respectively. Site codes are given in Table 1. (C) Relative amplitude of the first and second modes, which accounted for most of the variance in SST

Spatial patterns of species abundances and recruitment rates

A total of 108 taxa were identified across the study region with 51 and 57 taxa representing invertebrates and macroalgae, respectively. A comprehensive taxonomic listing of these species has been published by Broitman et al. (2011). Multivariate analyses of species abundances showed a regional structure similar to SST, with sites located south of PLV—in addition to BURR and CARR—clustered at the left side of the CAP ordination (Fig. 3A, Table 2).

This spatial structure was statistically significant (pseudo- $F_{11,1568} = 7.24$, $p < 0.01$). The multivariate spatial pattern of multi-species recruitment rates (Fig. 3B, pseudo- $F_{7,32} = 14.66$, $p < 0.01$) resembled the structure observed for SST (Fig. 2B) and adult abundances (Fig. 3A), with sites located south of PLV and BURR segregated along the first axis of the CAP ordination (Fig. 3B).

The analysis of Pearson correlations with CAP axes showed that species with pelagic larval development (e.g. the barnacles *Jehlius cirratus* and *Notochthamalus scabrosus*) increased in adult abun-

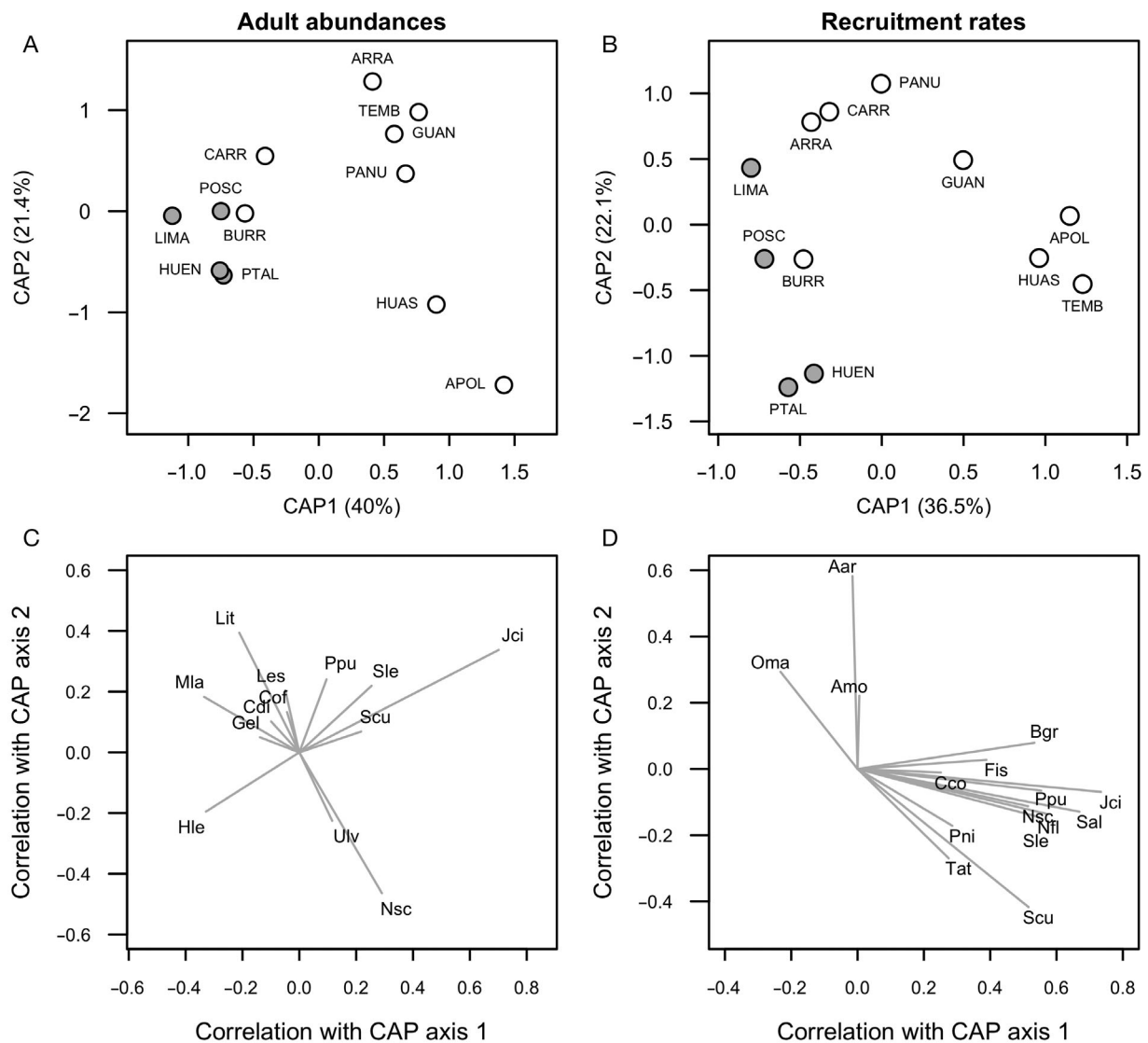


Fig. 3. Canonical analysis of principal coordinates for (A) invertebrate and algal adult abundances and (B) larval recruitment rates across the region. Correlations of (C) original proportion-transformed adult abundances and (D) recruitment rate variables with canonical axes are shown. Site and species codes are given in Tables 1 & 2, respectively. (A,B) Filled and empty symbols denote sites located south and north of Punta Lengua de Vaca, respectively

Table 2. Abbreviations of taxa shown in Fig. 3C,D. Taxa with strongest correlations with CAP axes (i.e. with arrow lengths of $\sqrt{(r_1^2 + r_2^2)} > 0.2$) are shown. DD: direct development

	Taxon	Abbreviation
Algae	<i>Codium dimorphum</i>	Cdi
	<i>Corallina officinalis</i>	Cof
	<i>Gelidium</i> sp.	Gel
	<i>Hildenbrandia lecanellieri</i>	Hle
	<i>Lessonia</i> spp.	Les
	<i>Lithothamnion</i> sp.	Lit
	<i>Mazzaella laminarioides</i>	Mla
	<i>Ulva</i> spp.	Ulv
Gastropoda	<i>Acanthina monodon</i> (DD)	Amo
	<i>Austrolittorina araucana</i>	Aar
	<i>Concholepas concholepas</i>	Cco
	<i>Fissurella</i> spp.	Fis
	<i>Onchidella marginata</i> (DD)	Oma
	<i>Prisogaster niger</i>	Pni
	<i>Scurria</i> spp.	Scu
	<i>Siphonaria lessoni</i>	Sle
	<i>Tegula atra</i>	Tat
Cirripedia	<i>Notobalanus flosculus</i>	Nfl
	<i>Notochthamalus scabrosus</i>	Nsc
	<i>Jehlius cirratus</i>	Jci
Bivalvia	<i>Brachidontes granulata</i>	Bgr
	<i>Perumytilus purpuratus</i>	Ppu
	<i>Semimitylus algosus</i>	Sal

dance toward sites located north of PLV, while macroalgae (e.g. *Mazzaella laminarioides* and the crustose alga *Hildenbrandia lecanellieri*) were more abundant in CARR, BURR and sites located south of PLV (Fig. 3C). The exceptions to this pattern were the green algae *Ulva* spp., which were relatively abundant in HUAS and APOL, both sites located north of PLV (Fig. 3C). Most invertebrate recruits and larvae showed higher abundances in HUAS, APOL, TEMB and GUAN, which are located north of PLV (Fig. 3D). The abundance of juveniles of *Onchidella marginata*, a gastropod with direct non-planktonic development, tended to increase towards sites located south of PLV (Fig. 3D). Juveniles of *Acanthina monodon*, also a direct developer, and *Austrolittorina araucana*, a species with pelagic development, were more abundant toward CARR and PANU. These results indicate that overall recruitment rates of invertebrates with planktonic development were higher at sites located north (excepting BURR) than at those south of PLV, and species with comparatively limited potential for dispersion showed an opposing pattern.

In accordance with these patterns of variation in the structure of adult communities and recruitment

rates, mean invertebrate abundance was lower south than north of PLV (see Fig. S2A in the Supplement at www.int-res.com/articles/suppl/m538p067_supp.pdf). Adult invertebrates were also scarce at BURR (Fig. S2A). Abundance of taxa with planktonic development showed a significant multivariate structure across the region with sites located south of PLV, in addition to CARR and BURR, discriminated from the other sites (Fig. S2B, pseudo- $F_{11,1488} = 15.89$, $p < 0.01$). The abundance of algal species was low at sites inside the greater Coquimbo bay system (Fig. S2C), and the multivariate ordination for algae alone was similar to that of the entire assemblage and that of planktonic dispersers (Fig. S2D, pseudo- $F_{11,1536} = 11.56$, $p < 0.01$).

Partition of variation in community structure with respect to SST, recruitment rates and spatial structure

Our variance-partition analyses showed that a relatively large amount of variation (59%) in adult community structure—considering only invertebrates with planktonic development—was accounted for by the 3 variables considered in the analyses (Space, SST and Recruitment). By far the most important explanatory variable was the joint effect of SST and recruitment rates, which accounted for 45% of the variability in the benthic assemblage (Fig. 4). After this, roughly 18% of variability in community structure could be assigned to the joint effect of recruitment and space (Fig. 4), while spatial structure alone accounted for 12% of variation (Fig. 4). Pure variation in SST and its combination with space together accounted for only 7% of the variation in adult community structure (SST: 2%, joint effect: 5%; Fig. 4). Finally, we detected non-significant proportions of variability explained directly by recruitment rates alone, and by the combination of the 3 factors investigated.

DISCUSSION

Spatially structured multi-species communities are simultaneously affected by dispersal, which drives rates of colonisation to local sites, as well as by among-site variation in environmental conditions, which act as filters to the types of species that can (co)exist at a given site (Leibold et al. 2004, Logue et al. 2011, Aiken & Navarrete 2014). Using multivariate approaches in rocky shore communities, we

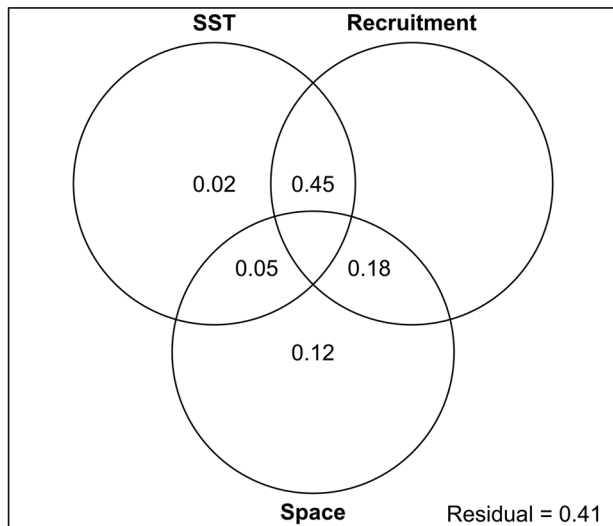


Fig. 4. Variance-partition analysis of adult community structure (planktonic developers) as a function of spatial distance and the spatiotemporal variation in sea surface temperature (SST) and recruitment rates. Only fractions of variation > 0.01 are shown

showed that environmental variables (SST), the benthic abundance of 108 species of invertebrates and macroalgae, and recruitment rates of invertebrates all shared significant spatial and temporal patterns of variability, marked by the presence of the prominent upwelling centre at Punta Lengua de Vaca (PLV, 30.25° S). Variance-partition analyses of the invertebrates with pelagic development allowed us to disentangle the effects of recruitment and environmental filtering while accounting for pure spatial variation in community structure. These results suggest that the independent and joint effects of SST with space on the established individuals in the benthic community explain only 7% of the variation in community structure in this wave-exposed metacommunity. In our analyses, this environmental filtering included effects on individual species tolerances, as well as environment-dependent species interactions. In contrast, the combination of environmental conditions and recruitment variation explained 45% of the variability in intertidal community structure, and an additional 18% was explained by the spatial structure of recruitment. Unexplained variation, which accounted for 41% of the variation in community structure, can be attributed to other factors, including local species interactions that are robust (insensitive) to observed variation in environmental conditions and recruitment rates. In this metacommunity, therefore, the combined effect of environmental filtering

and recruitment on local communities is stronger than the independent effects of these factors alone.

Spatial structure in the rocky shore metacommunity was evident when comparing multivariate patterns between sites located south and north of the persistent upwelling centre at PLV. However, 2 sites located north of PLV (i.e. Carrizal Bajo and Los Burros) showed environmental and biotic conditions similar to sites located around and south of PLV, highlighting the mosaic nature of mesoscale structures in environmental processes (e.g. Broitman & Kinlan 2006). Sites showing higher abundances of invertebrates with larval development also showed higher recruitment rates and stronger influence of the seasonal cycle in SST, in general agreement with the broad patterns and putative processes documented by Navarrete et al. (2005) in central Chile. This general result is also in agreement with studies on the effects of SST on rocky shore communities along the northwest Pacific shore (Menge & Menge 2013), where lower invertebrate abundances and recruitment rates, in addition to higher algal abundances, characterised the sites with higher synoptic (days to weeks) SST variability and stronger wind stress. Therefore, our results show that local, multi-species community structure along a broad geographic area has a fairly straightforward link to environmental fluctuations—and to limitations and temporal variation in propagule supply. But since they are both coupled, their separate and interactive effects on community structure must be teased apart (Lagos et al. 2008, Watson et al. 2011).

Few studies of marine systems have attempted to disentangle the effects of dispersal–recruitment from environmental filtering, especially in multi-species settings. We took advantage of the fact that, for 16 intertidal invertebrates, we had robust estimates (monthly samples for over 2 yr) of arrival rates and could use this information as a direct proxy for effective colonisation rates after dispersal. The results are quite striking. The geographic environmental variation imposed primarily by the upwelling centre at PLV modulates community structure of invertebrates through modulating or interacting with recruitment variability, but not through acting as an environmental filter on established individuals. Indeed, pure SST and its combination with space explained a significant, but marginal amount of variance in comparison to environment-modulated recruitment. Thus, we can conclude that interacting hydrographical processes at the PLV upwelling centre modulate the physical transport and retention of larvae in a way that affects recruitment variability (Pineda 2000,

Shanks et al. 2000, Broitman & Kinlan 2006, Pfaff et al. 2011, Navarrete et al. 2015), leaving a persistent signal in community structure.

As discussed above, in our analyses, environmental filters could act directly on community structure through affecting species tolerances, or through modifying environment-dependent species interactions. *In situ* measurements of SST were used in this study as a proxy for environmental filtering. Therefore, other variables like air temperature or food concentration could have had an uncontrolled effect on community structure. Nevertheless, SST has been shown elsewhere to significantly correlate with a suite of relevant environmental factors—including nutrient and chl *a* availability—that affect organism and population growth rates (Wieters et al. 2003) and the strength of species interactions (Wieters 2005, Menge & Menge 2013). Perhaps environmental variation across these wave-exposed rocky shores is simply too low to represent a major filter for the presence of species or to significantly alter competitive abilities, which is in accordance with the nearly nil variability in competitive interaction strengths between intertidal mussels and barnacles reported for central Chile (Caro et al. 2010, Shinen & Navarrete 2014). This is not to say that species interactions are not important. Indeed, as mentioned above, 41% of the unexplained variation in community structure may very well be related to species interactions that are insensitive to variation in environmental conditions across the study region. This interpretation of our analysis can also reconcile apparently contradicting results obtained by Caro et al. (2010), in which significant convergence in community structure ($n = 23$ species) was found across a large geographic region of central-northern Chile, despite much greater variation in recruitment. Certainly, convergence in community structure relative to recruitment variation is possible when the main post-recruitment processes (e.g. species interactions) structuring local communities are relatively insensible to environmental conditions across the region. The trivially low variance explained by pure recruitment in our analysis is also consistent with the comparatively low recruitment signal observed by Caro et al. (2010). By using differences in recruitment rates between sites, Caro et al. (2010) effectively eliminated the spatial structure of recruitment, which in our analysis is shown to explain 18% of the variability in community structure. We show here that to explain significant variation in community structure it is necessary to examine the interaction between SST and recruitment. Unfortunately, we do not have information on macroalgal

recruitment rates to perform a similar analysis for this diverse assemblage. Considering the generally much lower dispersal capabilities of macroalgae in comparison to invertebrates (Kinlan & Gaines 2003), one could expect a much higher contribution of environmental filtering over recruitment to the structure of the macroalgal assemblage. However, excessively limited dispersal capabilities could also preclude colonisation of sites, and therefore, make recruitment rates important drivers of macroalgal assemblages across the region. Further studies are therefore required. While all techniques designed for variance partitioning of spatially structured processes exhibit limitations (Gilbert & Bennett 2010), we believe the broad differences encountered will be resilient to the statistical technique used.

The variation in recruitment rates of multiple species seemed to lead to predictable patterns in community structure across a comparatively large region. Following a different approach, Watson et al. (2011) came to generally similar conclusions for the rocky shores along the California Bight. This raises an important question: How do we reconcile the fact that variability in recruitment rates of multiple species leaves a signal on the multivariate structure of benthic communities, with the many studies on this and other shores of the world illustrating the overriding and quite deterministic importance of local post-recruitment processes, such as predation and interference competition (e.g. Castilla & Durán 1985, Paine et al. 1985)? Part of the answer lies in variation in the importance of different community regulation processes across large spatial scales, which are modulated by oceanographic processes (Connolly et al. 2001, Menge et al. 2003). Navarrete et al. (2005) suggest that sharp discontinuities in upwelling regimes observed around 32° S result in a significant regional shift in recruitment rates and community structure: higher recruitment rates and adult abundances of dominant invertebrates occur at sites located south rather than north (our study region) of 32° S. Similarly, Caro et al. (2010) showed that at low to moderate mean recruitment rates, there can be a tight relationship between adult community structure and recruitment (Caro et al. 2010, their Fig. 1C). Part of the answer is also that local communities, here and anywhere, are composed of sets of species that interact strongly and usually in strongly asymmetrical ways, and sets of species that interact in nearly 'neutral' ways (Siepielski et al. 2010, Lowe & McPeck 2014). Indeed, the variability in relative recruitment rates, even when not limiting, can directly determine relative adult abundances in species that are equally

suited to compete for space (Shinen & Navarrete 2014), and environmentally driven variation in prey recruitment can lead to weak predator–prey interactions within macrobenthic assemblages (Wieters et al. 2008).

In our study, the northernmost sites, Carrizal Bajo and Los Burros, clustered with the southern sites around PLV in terms of SST and adult abundances, but not in terms of recruitment rates (at least not for Carrizal Bajo). This indicates that coastal environmental conditions could still be influencing the spatial patterns in community composition in this region. Our variance-partition analysis suggests that, in the case of invertebrates with pelagic development, such filtering effects are trivial across the study region—a different situation is probably experienced by the macroalgal assemblage. Cold and nutrient-rich upwelled waters can boost algal growth rates at sites exposed to persistent upwelling activity and inhibit growth of others at areas with more frequent nutrient-depleted waters (Blanchette et al. 2002, Gallon et al. 2014). This can explain why in our study the increasing influence of synoptic SST variability and wind stress was related to higher abundances of corticated and crustose red algae (observed at the southern sites and Los Burros), a pattern also shown by Tapia et al. (2014) using an independent dataset. The trend of green algae to be abundant at sites further from the upwelling centre has also been reported by Nielsen & Navarrete (2004) and explained as a response to competitive release with corticated algae or changes in the intensity of herbivory. Further research on macroalgal recruitment variation is necessary to determine to what extent environmental filtering (e.g. nutrient limitations) or environment-induced recruitment variability modulates the assemblage.

In summary, our results indicate that environmental filtering in the traditional sense, as affecting individuals' ecological tolerances, has a minor modulation effect on the structure of benthic invertebrate communities. The spatial structure of recruitment variability and, especially, the modulation of recruitment by environmental conditions are the most significant processes explaining community structure of the metacommunity. It is still necessary to untangle the relationships between recruitment rates and dispersal, which are central to the prediction of population dynamics and patterns of coexistence in spatially structured environments (Watson et al. 2011, Aiken & Navarrete 2014, Burgess et al. 2014), as well as the mechanisms of interaction between recruitment and environmental variability. Similar studies need to be

done on macroalgal recruitment over larger spatial scales. Since climate change and other human-induced disturbances will affect environmental conditions and dispersal pathways in different ways (e.g. Aiken & Navarrete 2011), our results could be extremely useful for building predictive models about variability of biodiversity in this and in other benthic marine systems.

Acknowledgements. Tatiana Manzur, Jhon Gajardo, Andrés González and Osvaldo Cerda provided invaluable support during fieldwork. Carlos Moffat provided long-term fields of wind stress data. We thank Dr. Lisandro Benedetti-Cecchi and 4 anonymous reviewers for constructive criticism. The Consejo Nacional de Ciencia y Tecnología (CONICYT) financially supported this study through FONDECYT grants #1120988 to B.R.B., #11121360 to M.A.A., and #3100014 and #1141037 to N.V., B.R.B. and S.A.N. were supported by the Millennium Nucleus Center for the Study of Multiple-drivers on Marine Socio-Ecological Systems (MUSELS, MINECON NC120086) and the Center for Marine Conservation (P10-033F), respectively. While writing, N.V. was supported by the MECESUP grant AUS0805 and the UACH-DID grant S-2013-2.

LITERATURE CITED

- Aguilera MA, Valdivia N, Broitman BR (2013) Spatial niche differentiation and coexistence at the edge: co-occurrence distribution patterns in *Scurria* limpets. *Mar Ecol Prog Ser* 483:185–198
- Aiken CM, Navarrete SA (2011) Environmental fluctuations and asymmetrical dispersal: generalized stability theory for studying metapopulation persistence and marine protected areas. *Mar Ecol Prog Ser* 428:77–88
- Aiken CM, Navarrete SA (2014) Coexistence of competitors in marine metacommunities: environmental variability, edge effects, and the dispersal niche. *Ecology* 95: 2289–2302
- Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. *Ecology* 84:511–525
- Blanchette CA, Miner BG, Gaines SD (2002) Geographic variability in form, size and survival of *Egretta menziesii* around Point Conception, California. *Mar Ecol Prog Ser* 239:69–82
- Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85:1826–1832
- Broitman BR, Kinlan BP (2006) Spatial scales of benthic and pelagic producer biomass in a coastal upwelling ecosystem. *Mar Ecol Prog Ser* 327:15–25
- Broitman BR, Navarrete SA, Smith F, Gaines SD (2001) Geographic variation of southeastern Pacific intertidal communities. *Mar Ecol Prog Ser* 224:21–34
- Broitman BR, Blanchette CA, Menge BA, Lubchenco J and others (2008) Spatial and temporal patterns of invertebrate recruitment along the West Coast of the United States. *Ecol Monogr* 78:403–421
- Broitman BR, Véliz F, Manzur T, Wieters EA and others (2011) Geographic variation in diversity of wave exposed rocky intertidal communities along central Chile. *Rev*

- Chil Hist Nat 84:143–154
- Bulleri F, Benedetti-Cecchi L, Cusson M, Maggi E and others (2012) Temporal stability of European rocky shore assemblages: variation across a latitudinal gradient and the role of habitat-formers. *Oikos* 121:1801–1809
- Burgess SC, Nickols KJ, Griesemer CD, Barnett LAK and others (2014) Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design. *Ecol Appl* 24:257–270
- Bustamante RH, Branch GM, Eekhout S, Robertson B and others (1995) Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102:189–201
- Camus PA (2001) Marine biogeography of continental Chile. *Rev Chil Hist Nat* 74:587–617
- Caro AU, Navarrete SA, Castilla JC (2010) Ecological convergence in a rocky intertidal shore metacommunity despite high spatial variability in recruitment regimes. *Proc Natl Acad Sci USA* 107:18528–18532
- Castilla JC, Durán LR (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* 45:391–399
- Connolly SR, Roughgarden J (1999) Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. *Ecol Monogr* 69:277–296
- Connolly SR, Menge BA, Roughgarden J (2001) A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* 82:1799–1813
- Cornwell WK, Schilck DW, Ackerly DD (2006) A trait-based test for habitat filtering: convex hull volume. *Ecology* 87:1465–1471
- de Bello F (2012) The quest for trait convergence and divergence in community assembly: Are null-models the magic wand? *Glob Ecol Biogeogr* 21:312–317
- de Bello F, Price JN, Munkemüller T, Liira J and others (2012) Functional species pool framework to test for biotic effects on community assembly. *Ecology* 93:2263–2273
- Dray S, Pelissier R, Couteron P, Fortin MJ and others (2012) Community ecology in the age of multivariate multiscale spatial analysis. *Ecol Monogr* 82:257–275
- Fenberg PB, Menge BA, Raimondi PT, Rivadeneira MM (2015) Biogeographic structure of the northeastern Pacific rocky intertidal: the role of upwelling and dispersal to drive patterns. *Ecography* 38:83–95
- Gallon RK, Robuchon M, Leroy B, Le Gall L, Valero M, Feunteun E (2014) Twenty years of observed and predicted changes in subtidal red seaweed assemblages along a biogeographical transition zone: inferring potential causes from environmental data. *J Biogeogr* 41:2293–2306
- Garreaud RD, Rutllant JA, Muñoz RC, Rahn DA, Ramos M, Figueroa D (2011) VOCALS-CUPEx: the Chilean Upwelling Experiment. *Atmos Chem Phys* 11:2015–2029
- Gilbert B, Bennett J (2010) Partitioning variation in ecological communities: do the numbers add up? *J Appl Ecol* 47:1071–1082
- Harley CDG, Helmuth BST (2003) Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. *Limnol Oceanogr* 48:1498–1508
- Hormazabal S, Shaffer G, Leth O (2004) Coastal transition zone off Chile. *J Geophys Res C* 109:C01021
- Hughes TP, Baird AH, Dinsdale EA, Moltschanowskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59–63
- Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020
- Lagos NA, Navarrete SA, Véliz F, Masuero A, Castilla JC (2005) Meso-scale spatial variation in settlement and recruitment of intertidal barnacles along the coast of central Chile. *Mar Ecol Prog Ser* 290:165–178
- Lagos NA, Castilla JC, Broitman BR (2008) Spatial environmental correlates of benthic recruitment: a test using intertidal barnacles along the coast of northern Chile. *Ecol Monogr* 78:245–261
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P and others (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Logue JB, Mouquet N, Peter H, Hillebrand H, Metacommunity Working Group (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends Ecol Evol* 26:482–491
- Lowe WH, McPeck MA (2014) Is dispersal neutral? *Trends Ecol Evol* 29:444–450
- McPhee-Shaw EE, Siegel DA, Washburn L, Brzezinski MA, Jones JL, Leydecker A, Melack J (2007) Mechanisms for nutrient delivery to the inner shelf: observations from the Santa Barbara Channel. *Limnol Oceanogr* 52:1748–1766
- Menge BA, Menge DNL (2013) Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. *Ecol Monogr* 83:283–310
- Menge BA, Lubchenco J, Bracken MES, Chan F and others (2003) Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proc Natl Acad Sci USA* 100:12229–12234
- Menge BA, Blanchette CA, Raimondi P, Freidenburg TL and others (2004) Species interaction strength: testing model predictions along an upwelling gradient. *Ecol Monogr* 74:663–684
- Montecinos A, Broitman BR, Faugeron S, Haye PA, Tellier F, Guillemin ML (2012) Species replacement along a linear coastal habitat: phylogeography and speciation in the red alga *Mazzaella laminarioides* along the south east pacific. *BMC Evol Biol* 12:97
- Moraga-Opazo J, Valle-Levinson A, Ramos M, Pizarro-Koch M (2011) Upwelling-triggered near-geostrophic recirculation in an equatorward facing embayment. *Cont Shelf Res* 31:1991–1999
- Muñoz RC (2008) Diurnal cycle of surface winds over the subtropical southeast Pacific. *J Geophys Res Atmos* 113:D13107, doi:10.1029/2008JD009957
- Navarrete SA, Wieters EA, Broitman BR, Castilla JC (2005) Scales of benthic-pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. *Proc Natl Acad Sci USA* 102:18046–18051
- Navarrete SA, Broitman BR, Menge BA (2008) Interhemispheric comparison of recruitment to rocky intertidal communities: pattern persistence and scales of variation. *Ecology* 89:1302–1322
- Navarrete SA, Largier JL, Vera G, Tapia FJ and others (2015) Tumbling under the surf: wave-modulated settlement of intertidal mussels and the continuous settlement-relocation model. *Mar Ecol Prog Ser* 520:101–121
- Nielsen KJ, Navarrete SA (2004) Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. *Ecol Lett* 7:31–41
- Oksanen J, Blanchet FG, Kindt R, Legendre P and others

- (2013) vegan: community ecology package. R package version 2.0-10, <https://cran.r-project.org/web/packages/vegan/index.html>
- Otero MP, Siegel DA (2004) Spatial and temporal characteristics of sediment plumes and phytoplankton blooms in the Santa Barbara Channel. *Deep-Sea Res II* 51:1129–1149
- Paine RT, Castillo JC, Cancino J (1985) Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zealand, and Washington State. *Am Nat* 125:679–691
- Palardy JE, Witman JD (2014) Flow, recruitment limitation, and the maintenance of diversity in marine benthic communities. *Ecology* 95:286–297
- Pavoine S, Baguette M, Stevens VM, Leibold MA, Turlure C, Bonsall MB (2014) Life-history traits, but not phylogeny, drive compositional patterns in a butterfly metacommunity. *Ecology* 95:3304–3313
- Pfaff MC, Branch GM, Wieters EA, Branch RA, Broitman BR (2011) Upwelling intensity and wave exposure determine recruitment of intertidal mussels and barnacles in the southern Benguela upwelling region. *Mar Ecol Prog Ser* 425:141–152
- Pineda J (2000) Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. *Oceanogr East Pacific* 1:84–105
- Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315:95–97
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rahn DA, Garreaud RD, Rutllant JA (2011) The low-level atmospheric circulation near Tongoy Bay—Point Lengua de Vaca (Chilean coast, 30°S). *Mon Weather Rev* 139:3628–3647
- Schneider N, Cornuelle BD (2005) The forcing of the Pacific decadal oscillation. *J Clim* 18:4355–4373
- Shanks AL, Largier J, Brink L, Brubaker J, Hooff R (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnol Oceanogr* 45:230–236
- Shinen JL, Navarrete SA (2014) Lottery coexistence on rocky shores: weak niche differentiation or equal competitors engaged in neutral dynamics? *Am Nat* 183:342–362
- Siepielski AM, Hung KL, Bein EE, McPeck MA (2010) Experimental evidence for neutral community dynamics governing an insect assemblage. *Ecology* 91:847–857
- Somero GN (2010) The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers’. *J Exp Biol* 213:912–920
- Tapia FJ, Navarrete SA, Castillo M, Menge BA and others (2009) Thermal indices of upwelling effects on inner-shelf habitats. *Prog Oceanogr* 83:278–287
- Tapia FJ, Largier JL, Castillo M, Wieters EA, Navarrete SA (2014) Latitudinal discontinuity in thermal conditions along the nearshore of central-northern Chile. *PLoS ONE* 9:e110841
- Tegner MJ, Dayton PK (1987) El Niño effects on southern California kelp forest communities. *Adv Ecol Res* 17:243–279
- Tellier F, Tapia J, Faugeton S, Destombe C, Valero M (2011) The *Lessonia nigrescens* species complex (Laminariales, Phaeophyceae) shows strict parapatry and complete reproductive isolation in a secondary contact zone. *J Phycol* 47:894–903
- Valdivia N, Gonzalez AE, Manzur T, Broitman BR (2013) Mesoscale variation of mechanisms contributing to stability in rocky shore communities. *PLoS ONE* 8:e54159
- Watson JR, Hays CG, Raimondi PT, Mitarai S and others (2011) Currents connecting communities: nearshore community similarity and ocean circulation. *Ecology* 92:1193–1200
- Wieters EA (2005) Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. *Mar Ecol Prog Ser* 301:43–54
- Wieters EA, Kaplan DM, Navarrete SA, Sotomayor A, Largier J, Nielsen KJ, Véliz F (2003) Alongshore and temporal variability in chlorophyll *a* concentration in Chilean nearshore waters. *Mar Ecol Prog Ser* 249:93–105
- Wieters EA, Gaines SD, Navarrete SA, Blanchette CA, Menge BA (2008) Scales of dispersal and the biogeography of marine predator-prey interactions. *Am Nat* 171:405–417
- Wieters EA, Broitman BR, Branch GM (2009) Benthic community structure and spatiotemporal thermal regimes in two upwelling ecosystems: comparisons between South Africa and Chile. *Limnol Oceanogr* 54:1060–1072
- Witman JD, Brandt M, Smith F (2010) Coupling between subtidal prey and consumers along a mesoscale upwelling gradient in the Galapagos Islands. *Ecol Monogr* 80:153–177

Editorial responsibility: Lisandro Benedetti-Cecchi,
Pisa, Italy

Submitted: February 16, 2015; Accepted: September 18, 2015
Proofs received from author(s): October 14, 2015